Diversity and Distributions, (Diversity Distrib.) (2010) **16**, 267–276

A Journal of Conservation Biogeography
Diversity and Distributions

BIODIVERSITY RESEARCH

Half a century of succession in a temperate oakwood: from species-rich community to mesic forest

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ABSTRACT

Aim Lowland woodlands in Europe went through dramatic changes in management in the past century. This article investigates the influence of two key factors, abandonment of coppicing and increased pressure of ungulates, in thermophilous oakwoods. We focused on three interconnected topics: (1) Has the assumed successional trend lead to impoverishment of the vegetation assemblages? (2) Has it resulted in vegetation homogenization? (3) Are the thermophilous oakwoods loosing their original character?

Location Czech Republic, Central Europe.

Methods The vegetation in 46 semi-permanent plots was recorded three times: firstly, shortly after the abandonment of coppicing (1953) and then, after four to six decades of secondary succession and strong game impact (1992 and 2006). Overall trends and changes in species spectra were analysed.

Results There is a marked successional shift towards species-poorer communities growing in cooler, moister and nutrient-richer conditions. The change was significantly different in parts affected and unaffected by high numbers of ungulates yet only for herbs, not the woody species. However, observed change in species composition was not accompanied by significant homogenization process that is the general process reported from elsewhere. A sharp decline in plant species typical for thermophilous woodland communities and in endangered species indicates that the original character of the woodland has been gradually lost.

Main conclusions Thermophilous oakwoods have been largely replaced by mesic forests. Lowland oakwoods in continental parts of Europe historically depended on active management, which kept the understorey conditions light and warm. Successional processes in the 20th century caused a critical loss of species diversity at various spatial levels. However, artificially high numbers of ungulates, which otherwise have a negative impact, probably held up succession, so that the changes may still be reversible.

Keywords
Endangered species, homogenization, long-term changes, loss of diversity, natural woodland, semi-permanent plots.

INTRODUCTION

In densely inhabited European lowland areas, many forests have been intensively managed for millennia. Coppicing, litter raking, hay-making and wood pasture were routine practices all over Europe (Szabó, 2005; Rackham, 2006; Bergmeier, 2008; Gimmi *et al.*, 2008). After many centuries of varying historical management (e.g. Verheyen *et al.*, 1999; Szabó, 2010), European lowland woodlands have faced new threats in the past few decades (Rackham, 2008). Intensive biomass and nutrient output connected with a fine-scale regime of disturbances were replaced by a massive input of nitrogen (Thimonier *et al.*, 1994) and other pollutants, while the management regime has changed in favour of timber production. This has gradually lead to taxonomic impoverishment and homogenization of the woodland vegetation (Keith *et al.*, 2009), which

DOI: 10.1111/j.1472-4642.2010.00637.x
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may be part of biotic homogenization in general (McKinney & Lockwood, 1999).

The abandonment of former management and the subsequent conversion to high forest, including re-planting by non-native species, have been especially prevalent in Central and Northwestern Europe. However, conservation-motivated neglect helped to preserve the ancient character of some forests, now often declared nature reserves because of their biological values. The history of the management regime has been increasingly used as a causal factor in studies of long-term changes in herb layer composition (Baeten *et al.*, 2009; Corney *et al.*, 2008; Van Calster *et al.*, 2008a), soil seed bank (Van Calster *et al.*, 2008b) and even in soil properties (Strandberg *et al.*, 2005).

Geographically, most studies focusing on vegetation changes in lowland woodlands come from historically little-forested Northwestern Europe (Belgium, England). Information on more continental parts of Europe is largely missing. In terms of historical management practices, parallels between the Atlantic, continental and southern parts of Europe are apparent (Grove & Rackham, 2003; Loidi, 2005; Szabó, 2005). Nevertheless, the biological and ecological properties of these large biogeographical regions differ in various aspects; therefore, transferring knowledge directly from west to east may be misleading. Only a few studies deal with long-term changes in the lowland woodlands of continental Europe (Chytrý & Danihelka, 1993; Kwiatkowska, 1994; Jakubowska-Gabara, 1996). The latter author attributed the decline of thermophilous oakwood communities to declining human activities, namely pasturing.

The decline and abandonment of coppicing, one of the formerly common forms of woodland management in Europe (Rackham, 2006), has until relatively recently not been regarded as a plausible explanation for vegetation changes in the woods of the continental parts of Europe. Recent studies by entomologists have clearly shown a causality between a frustrating decline in the diversity of butterflies (Beneš *et al.*, 2006; Freese *et al.*, 2006; Konvička *et al.*, 2008), xylophagous beetles (Vodka *et al.*, 2009) or ground invertebrates (Spitzer *et al.*, 2008) and forest succession after the abandonment of coppicing. Unfortunately, we have scarce evidence for other groups of organisms and communities.

In this article, we deal with a thermophilous wood intensively managed for at least six centuries as coppice-with-standards (the first management survey dates back to 1386, Bretholz, 1930; Szabó, 2010), which has undergone a major change since the mid-20th century, including establishment of a large game preserve. Milovice Wood constitutes a core locality of the subcontinental loess thermophilous oakwoods at the north-western fringe of the Pannonian Basin. It is one of the largest remaining oakwoods in this part of Europe. We used a set of re-surveyed semi-permanent vegetation plots first recorded in the early 1950s (Horák, 1972) reflecting the composition of coppice-with-standards oakwood, now converted to oak high forests.

Our aims are (1) to test for the effects of abandonment of the traditional management on compositional changes in vegetation, (2) to test for the effects of the game preserve on the assumed successional trend, (3) to detect changes in vegetation heterogeneity, assuming a trend towards vegetation homogenization because of succession and (4) to assess the current conservation status of thermophilous woodland communities based on the occurrence of endangered species and of plant species typical for these communities. Finally, we will discuss the naturalness of Central European thermophilous oakwoods in the light of their dependency on management.

METHODS

Study site

With its 25-km^2 area, Milovice Wood is one of the largest continuous complexes of subcontinental oak and Pannonian hornbeam woodland communities in Central Europe and is protected as a Site of Community Interest CZ0624100. The Wood is located in SE Czech Republic, 16°41′38″ E, 48°49′26″ N, in the north-western edge of the Pannonian biogeographic province according to the Natura 2000 division. The site is a gently undulating loess plateau with altitudes ranging between 180 and 324 m a.s.l. Climate is relatively warm and dry with 9.0°C of average annual temperature and 550 mm of precipitation (Tolasz *et al.*, 2007). The most frequent soils are luvisols. Three woodland communities prevail in the forest vegetation (cf. Chytrý *et al.*, 2001; Commission of the European Communities, 2003): Pannonian oak-hornbeam forests, *Primulo veris-Carpinetum* (part of habitat type 91G0); Pannonian thermophilous oak woods on loess *Quercetum pubescenti-roboris* (part of habitat type 91I0); and Peri-Alpidic basiphilous thermophilous oak forests, *Corno-Quercetum* (part of habitat type 91H0).

Milovice Wood has most probably not changed in extent for at least the past seven centuries. Management consisted of short-rotation coppice-with-standards (cf. Szabó, 2010). The ownership of nearly the entire Milovice Wood was remarkably stable with only two major landlords from *c.* 1300 to the 1940s. The cutting period of the coppice was only 7 years in the Middle Ages (data from 14th to 15th centuries, Bretholz, 1930) and gradually increased to 12 years in the 17th century. Coppice compartments were several tens of hectares. The demand for underwood (coppice shoots) was high even in the pre-WW II period (Szabó, 2010). The post-WW II confiscation of private estates by the State could have been the principal reason leading to the abandonment of coppicing around the mid 20th century.

In 1965 and 1966, two game preserves were established, taking up most of the Wood's area. In 1991, the larger Bulhary preserve (1250 ha) was populated mainly by red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). The smaller Klentnice preserve (500 ha) has been burdened by two to three times higher densities of mainly fallow deer and mouflon (*Ovis musimon*). Densities of animals per hectare were 0.34 in Bulhary and 1.13 in Klentnice in 1991, and 0.39 in Bulhary and 0.55 in Klentnice in 2006. (Komárek, 2008).

Vegetation datasets

Complete lists of plant species with visual estimates of cover-abundances using the Braun-Blanquet scale (Van der Maarel, 2004) were recorded in square plots sized 500 m^2. Vertical layers of trees, shrubs and herbs were distinguished. Woody saplings were considered as part of the shrub layer (Chytrý & Danihelka, 1992).

The first sampling was performed in 1953–1954 by Horák (1972) before establishing the game preserves, reflecting 'the relatively homogeneous structure of a coppice' (pers. comm. cited by Chytrý & Danihelka, 1993). Horák's original dataset consisted of about 80 vegetation plots marked in topographical map scaled 1:25,000. In 1992, after three decades of the existence of game preserves, 46 of Horák's original plots were re-sampled using the same approach by Chytrý & Danihelka (1992). Horák's map and the information on the slope and aspect of the sites were used for defining the positions of the original plots. Only sites still covered with continuous forest vegetation were included, so that the results reflect mainly the succession process and not effects of cutting or re-planting (Chytrý & Danihelka, 1992). A total of 22 plots were in the Bulhary preserve, 15 in the Klentnice preserve, and nine plots remained outside both preserves. In summer 2006, Komárek (2008) sampled the 46 plots again. In total, 138 vegetation records were used in the analyses.

Data analysis

All analyses were carried out separately for herb and woody species (tree, shrub and woody saplings layers merged together), numbering 251 and 35, respectively. In all multivariate analyses, we used square-root transformation of percentage mid-points of respective cover-abundance values as species data. As a measure of compositional dissimilarity between plots, we used abundance-based Morisita–Horn index (Horn, 1966), which is insensible to differences in species richness (Wolda, 1981; Chao *et al.*, 2006). In our case, to use a dissimilarity index independent from species richness is necessary, because subsequent vegetation records largely differ in species richness. Using some of other widely used dissimilarity indexes (e.g. Bray–Curtis) would lead to misleading conclusions because of their dependence on species richness (Chao *et al.*, 2006; Jost, 2007).

1. To reveal the overall pattern in the vegetation, we performed non-metric multidimensional scaling (NMDS) in two dimensions and with a maximum of 400 random starts to achieve convergence. To facilitate visualization, the final configuration was rotated by principal components analysis and ordination axis scaled in half-change units.

Moreover, we calculated arithmetic means of Ellenberg indicator values (Ellenberg *et al.*, 1992) of herb species present within the plot. We also counted the number of species present in each plot (herb and woody species taken together). To help the interpretation of the pattern visualized by NMDS, we projected the vectors of these variables into an NMDS diagram, but only if they significantly correlated with some of the ordination axes ($P < 0.05$, based on a permutation test with 1000 permutations).

2. We tested the significance of the vegetation change by permutation-based MANOVA (Anderson, 2001). Time was coded as a continuous variable, i.e. 1953, 1992 and 2006. Because plots were semi-permanent (exact position not known), we used their IDs as covariables to remove the effect of spatial variability at the plot level. We assessed the significance of the vegetation change by a permutation test with 1000 permutations restricted by plot IDs.

3. We used permutation-based MANOVA also for testing the impact of game. The difference of vegetation change between plots inside and outside the game preserves was analysed. As explanatory variable, we used the interaction between time (year of recording) and the position of plots inside or outside the game preserves (binary coding). Time and plot IDs were used as covariables. Significance was tested by nonparametric test with 1000 permutations. We used a permutation scheme for split-plot design – unrestricted permutation of the whole plot (i.e. all three replicates from the same plot) and time series permutation within the whole plot (i.e. among replicates from the same plot).

4. We compared vegetation heterogeneity in three sampling periods through the analysis of multivariate homogeneity of group dispersions (Anderson *et al.*, 2006). To asses whether the dispersions of groups are different, we performed a nonparametric permutation test with 1000 permutations (Anderson, 2006). We performed all multivariate analyses with *vegan* package (Oksanen *et al.*, 2009) for R software (R Development Core Team, 2009).

5. To assess the status of the thermophilous oakwoods and the degree of assumed 'mesophication' (cf. Nowacki & Abrams, 2008), we analysed plant species typical for thermophilous oakwood and mesic forest communities in the three subsequent datasets. Typical species were statistically defined diagnostic species for higher vegetation units of the Czech vegetation (Chytrý & Tichý, 2003). Vegetation units were alliances *Aceri tatarici-Quercion* (with six diagnostic species), *Quercion pubescenti-petraeae* ($N = 18$) and *Quercion petraeae* ($N = 19$) representing thermophilous oakwoods, and alliance *Carpinion betuli* ($N = 55$) and order *Fagetalia sylvaticae* excluding *C. betuli* ($N = 47$) representing mesic forests of the Czech Republic. In each of the three datasets (1953, 1992 and 2006), we calculated the sum of presences of typical species for each vegetation unit and divided it by the sum of the presences within a unit in all three datasets.

6. Changes in conservation values were assessed using the occurrence of endangered species. We used the three highest-ranked categories of endangerment from the red list of vascular plant species of the Czech Republic (Holub & Procházka, 2000), i.e. C1 (critically endangered), C2 (strongly endangered) and C3 (endangered). The presence of endangered species in plots was summed within years and plotted. The analysed endangered species hardly overlap with the sets of typical species (see Appendix S1 in Supporting Information).

RESULTS

Species richness, vegetation composition and heterogeneity

Total species richness in 46 plots decreased between 1953 and 2006 from 181 to 159 herb species and from 33 to 24 woody species (for individual species see Appendix S1). In 1953, about one-third (58 herb species) were rare, present in 1–3 plots, and were subsequently not re-encountered in 1992 and 2006. The same was observed for six woody species. Only 15 rare herb species (occurring in 1–3 plots) were unique for the 1992 dataset and 25 for the 2006 dataset. No woody species were unique for either recent datasets.

The vegetation composition of Milovice Wood has markedly changed during the last 53 years. Regarding herb species (NMDS diagram, Fig. 1a), the 1953 plots are clearly separated from more recent plots (1992, 2006). They were also more species rich and contained more species demanding higher temperature. By contrast, species with a higher demand for soil nutrients and moisture are more common in recent plots. Regarding woody species, the change in species composition is much less pronounced (Fig. 1b). The composition of woody species changed much less than the composition of herb species, reflecting rather the changing proportions of present species than species turnover.

Overall temporal change tested by permutation-based MANOVA explained 9.5% of the variation in herb species composition, and its effect was highly significant ($F = 14.6$, $P < 0.001$). For woody species, the change was also apparent; time explained 2.0% of the variance in species data, and its effect was statistically significant ($F = 3.0$, $P < 0.001$). Concerning the vegetation development inside and outside the game preserves, our results showed a significant difference, but only for herb species. The interaction between time and game preserve explained 1.2% of the variation in herb species composition and was statistically significant ($F = 2.0$, $P < 0.001$). However, the effect was not significant for woody species ($F = 0.44$, $P = 0.27$).

Vegetation heterogeneity has not significantly changed over time. This holds true for herb species (global test of homogeneity of multivariate dispersion: $F = 0.6$, $P = 0.26$) as well as woody species ($F = 0.5$, $P = 0.19$). The assumed vegetation homogenization was not confirmed in this respect.

Occurrence of typical and endangered species

A marked decline was detected in species typical for the three units of thermophilous oakwoods. The most severe was the decline in the alliance *Aceri tatarici-Quercion*, that is, subcontinental thermophilous oakwoods (Fig. 2). In the other two alliances of thermophilous oakwoods, *Quercion pubescenti-petraeae* and *Quercion petraeae* and in the mesic oak-hornbeam woods (alliance *C. betuli*), there is a nearly identical trend of moderate decline from 1953 to 1992 followed by a milder decrease onwards to 2006 (Fig. 2). Species typical for mesic woods of the Czech Republic *Fagetalia sylvaticae* (excl. *C. betuli*) showed almost no change at all. For individual species, see Appendix S1.

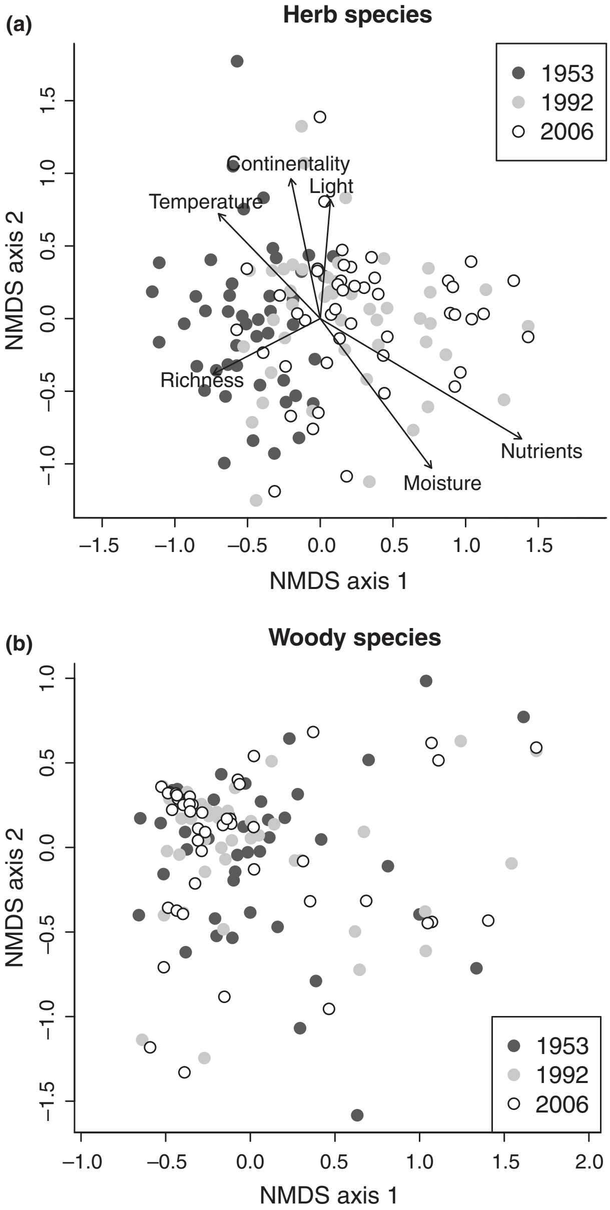

Figure 1 Shift in species composition during last 50 years in Milovice Wood shown in diagrams from non-metric multidimensional scaling (NMDS) for herb (a) and woody (b) species. Symbols represent 46 triplets of plots in three subsequent periods. Vectors of mean Ellenberg indicator values and species richness significantly ($P < 0.05$) correlated with ordination axes are projected into NMDS diagram for herb species. The change in species composition is accompanied by the decline in species richness. Moreover, environmental conditions in plots got cooler, moister and richer in nutrients.

The presence of the endangered species markedly declined during the study period (Fig. 3). From seven species occurring in more than 10% of the plots in 1953 (*Iris variegata*, *Carex*

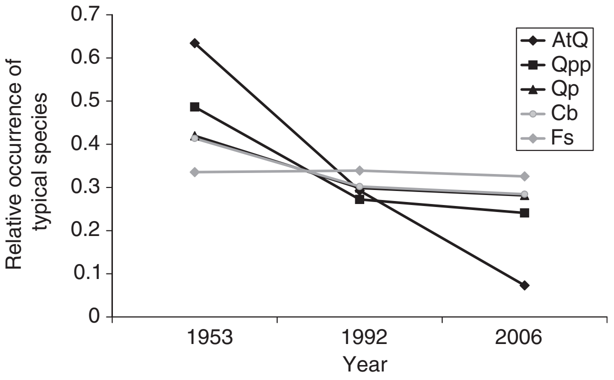

Figure 2 Temporal trends in the relative occurrence of species typical for three thermophilous (black) and two mesic (grey) woodland communities; for full version of the abbreviations in legend, see text. A marked decline in the former indicates the loss of the original thermophilous character of the woodland. Species of mesic woods have slightly decreased; however, they gained relative importance at the cost of thermophilous woodland.

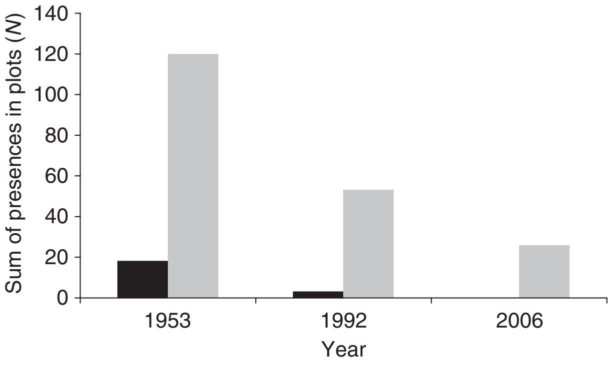

Figure 3 Trends in the occurrence of endangered plant species, sums of the presences in three subsequent records. Occurrences from 1953 were reduced to about one-fifth by 2006 in the group of endangered species (C3, grey bars). Critically (C1) and strongly (C2) endangered species (black bars) have completely vanished.

michelii, *Dictamnus albus*, *Lithospermum purpurocaeruleum*, *Melica picta*, *Melittis melissophyllum* and *Vicia pisiformis*; all scientific plant names follow Kubát *et al.*, 2002), only four persisted above the 10% threshold in 1992, and only one did so in the last survey (*M. melissophyllum*) – see Appendix S1. The marked impoverishment of species typical for thermophilous oakwoods and of endangered species clearly indicates the declining conservation value of Milovice Wood. This decline concerns not only rare and endangered species but also the vanishing plant communities constituted by them.

DISCUSSION

Species and vegetation change

Loss of taxonomic diversity in deciduous woodlands, or simply the decrease in species richness, was observed in a number of studies based either on repeated plots (Taverna *et al.*, 2005; von Oheimb & Brunet, 2007; Rogers *et al.*, 2008; Keith *et al.*, 2009) or on chronosequences (Bartha *et al.*, 2008). Most of the vanished rare herbs are thermophilous and, perhaps more importantly, light-demanding species (e.g. *Lathyrus pannonicus*, *Centaurea stoebe*, *Stachys recta*), some of which are also endangered (e.g. *Iris pumila*, *Stachys germanica*, *Campanula bononiensis*). Furthermore, a steep decline in the once-abundant species of Central European thermophilous woodlands can be observed (e.g. *Serratula tinctoria*, *C. michelii*, *D. albus*). As for woody species, same holds true for *Quercus pubescens*, *Ligustrum vulgare*, *Viburnum lantana* and *Sorbus torminalis*.

About the same number of herbs as vanished since 1953 has arrived since the 1990s, even though many of them temporarily (present in only one of the recent datasets). Few became frequent (*Impatiens parviflora*, *Urtica dioica*, *Mycelis muralis* and *Artemisia absinthium*) while most were rare, present in 1–3 plots (e.g. *Viola arvensis*, *Chaerophyllum temulum*, *Capsella bursa-pastoris*). In general, they are species of disturbed habitats, not forest specialists. Three woody species increased their abundance (but not frequency of occurrence in plots) to the extent that this change can be called expansion: *Acer campestre*, *Carpinus betulus* and *Fraxinus excelsior*.

The Wood is losing its thermophilous character. This was clearly proven by a steep decline in the once-abundant species typical for thermophilous woodland communities, including rapidly vanishing endangered species. By contrast, virtually all markedly increased species prefer productive sites rich in nitrogen. Among them, *I. parviflora* is a neophyte that has recently become one of the dominants in a great number of habitats in the Czech Republic (Sádlo *et al.*, 2007). As shown in the analysis by Chytrý *et al.* (2009), lowland habitats are more invaded by alien plant species than those in the higher altitudes. However, thermophilous oakwoods including the Milovický Wood (cf. maps in Chytrý *et al.*, 2009) are still relatively unaffected when compared with the invaders-flooded riparian woods.

As to woody species, a shift from xerothermic to mesic and/or nutrient-demanding species supports the presented pattern. The expansion of nutrient-demanding species is consistent with the observed increase in mean Ellenberg indicator value for nutrients. This trend is obviously the direct reason for the expansion of *F. excelsior*, as reported from several other places (Hofmeister *et al.*, 2004; Střeštík & Šamonil, 2006; von Oheimb & Brunet, 2007). Shading by the expanding mesophilous woody species may soon become a serious threat to woodland biodiversity at the landscape scale.

Interestingly, the assumed homogenization trend was not detected, which contradicts the general predictions (McKinney & Lockwood, 1999) and case-study observations in forests (Rooney *et al.*, 2004; Keith *et al.*, 2009). Our study demonstrates that homogenization and the loss of taxonomic diversity can be independent processes within one site.

Causes of change

The principal cause of the observed vegetation change is the shift from coppice-with-standards to high forest. Impoverishment because of secondary succession was detected both in managed woodlands and in natural forests after canopy disturbances (e.g. Woods, 2000). Younger successional phases of woods are apparently more diverse in vascular plants than older phases. The very same process has affected the Milovice Wood in the past half-century. Recent studies by entomologists from this site (Beneš *et al.*, 2006; Spitzer *et al.*, 2008) arrived at similar conclusions.

Regarding our dataset, this means only secondary succession uninterrupted by felling, because all sampled plots were intentionally placed in compartments uncut since the initial survey in the 1950s (Chytrý & Danihelka, 1993). The greater part of Milovice Wood went through this half-natural process; the other part was either clear-cut or turned into small crop-fields to feed the deer or planted by *Aesculus hippocastanum* in lines along the motorways. We do not know the exact proportions of the development trajectories yet, however, the scenario of decreasing diversity is likely typical for the whole wood. If the process continues in the future, we will lose not only individual species but also whole communities of thermophilous woodlands – the very reason why Milovice Wood is protected under Natura 2000.

The decline in species diversity has been interpreted as a consequence of secondary succession (cf. Vera, 2000). Following the abandonment of traditional management, this process was documented in chestnut coppices in southern France (Gondard *et al.*, 2001), in Danish oak and beechwoods (Strandberg *et al.*, 2005) or in the oakwoods of the Netherlands (Haveman & Schaminée, 2005). In Milovice Wood, the increasingly eutrophic conditions give way to mesic forests dominated by *F. excelsior*, *Acer* spp., *Tilia* spp., *C. betulus* and possibly also *Fagus sylvatica* (now absent). As in other regions, this process was most probably supported by nitrogen depositions (Thimonier *et al.*, 1994; Lameire *et al.*, 2000). However, having no data on past deposition in the area of Milovice Wood, we could not separate the influence of this factor on the overall change.

We could, however, assess the relative influence of another important factor – deer. Chytrý & Danihelka (1993) emphasized the impact of deer with regard to impoverishment, loss of 'xeric' character and ruderalization of the woodland vegetation in Milovice Wood. Some 15 years later, we support this view. The reason for the significant difference of vegetation change inside and outside the preserves is probably the deer-proof fence (that is, ultimately men who like shooting deer), which maintains abundant populations of ungulates inside the Wood. Increasing deer density was denoted the cause for decreasing plant diversity also in upland forests in Wisconsin Rooney *et al.* (2004) as well as in British woodlands, yet not of all groups of organisms (Fuller & Gill, 2001). Nevertheless, intensive grazing affected the rejuvenation of woody species; browsing impact was pointed out already by Chytrý & Danihelka (1993). Thus, the succession of woody species is likely to have been slowed down or even blocked by deer (compare Strandberg *et al.*, 2005; Rooney, 2009).

The results of various studies can, however, be specific for regions or particular sites. It seems that in densely inhabited Central European lowlands, coppicing, and not wood pasture, was the most common type of woodland management. Milovice Wood was not an exception. From historical documents, it may be concluded that in the Middle Ages (until the 16th century), the Wood was almost entirely used as an intensive, short-rotation coppice with a cutting period of only 7 years. In the Early Modern and Modern Periods, the management became more heterogeneous; it included litter raking, hay-making, and the coppices had standards as well. Management was also less intensive – the cutting period increased to 12 years by around 1700 and to 30 years by the end of the 19th century (cf. Szabó, 2010). Typical consequence of the 20th-century conversion of the coppice-with-standards to high forest was a marked decline in the abundance of *Tilia cordata* and *Tilia platyphyllos* in the tree layer. In the neighbouring Děvín Hill (where the original woodland structure has survived thanks to protection), *Tilia* still constitutes the vast majority of coppice stools and trees in general.

In brief, the story of Milovice Wood in the past half a century would be as schematized in Fig. 4. First, succession because of conversion from open coppice wood to closed-canopy high forest has resulted in a massive loss of light- and warmth-demanding species and to a decline in thermophilous oakwood vegetation. Next, deer and mouflon enhanced the expansion of several nitrophilous herbs. However, game animals might have retarded the expansion of woody species by browsing, slowing down the succession, possibly halting

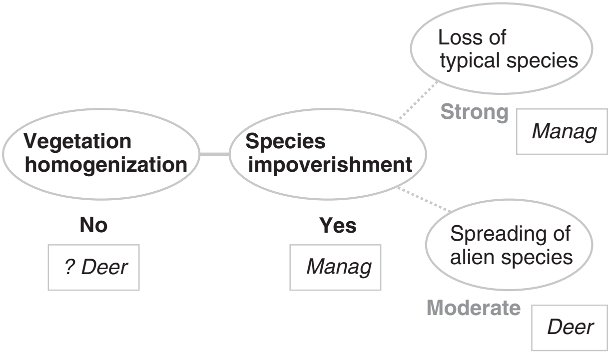

Figure 4 Summary interpretation of the main processes in Milovice Wood in the past half a century. Overall, there has been species impoverishment mainly because of the management shift from coppicing to high forest. This change has strongly affected the light-demanding species of thermophilous oakwoods. The second main factor, the high density of ungulates, has had a moderately negative effect because of the facilitation of the spreading of aliens. However, the same factor might have halted vegetation homogenization.

homogenization and keeping some of the conservation value of the forest. The effect of animals on homogenization is nevertheless not very clear and deserves further examination.

How natural are thermophilous oakwoods in Central Europe?

Thermophilous oakwood is an ecosystem dependent on traditional management practices that keep the canopy open and understorey disturbed. This finding invokes some older views considering the origins and pre-history of European lowland woods. There are two basic hypotheses (Bradshaw *et al.*, 2003; Birks, 2005). According to both of these, a great part of primary lowland woods in Europe are deciduous mixed woods at least partly dominated by oak species. The older 'high forest' hypothesis has its source in the concept of climax. It assumes that closed-canopy oakwoods are the natural vegetation of the warmest and driest areas of Central Europe (Bohn & Neuhäusl, 2000) reflecting macroclimatic and substrate conditions. Management may rather distort the natural dominance of oak.

The much newer 'wood pasture' hypothesis by Vera (2000) has put the discussion on the origins of and pre-cultural processes in European lowland woods on a new basis. It also relies upon natural agents, namely large herbivores. In the early Holocene, these would have been abundant enough to naturally maintain a mosaic of successional phases from open grassland through prickly bushy to mature forest with oak and other trees. The 'wood pasture' hypothesis has been, however, disputed by ecologists (e.g. Mitchell, 2005; Rackham, 2006). Vera's claim for the remnants of the Mesolithic aurochs-grazed woods surviving to the Middle Ages is unfounded (Szabó, 2009).

Our results clearly refuted the 'high forest' hypothesis for continental oakwoods, and the 'wood pasture' hypothesis seems unrealistic in the light of recent criticism. Where would then the light- and warm-demanding species have found suitable habitats in the dark, closed-canopy mesic woods of the Holocene? We argue that human impact enabled the existence of open woodlands in the early Holocene and their continuation in the following period of beech expansion. However, the 'human impact' scenario refers only to the present interglacial and not to the previous ones (Lang, 1994; Bradshaw *et al.*, 2003). Human-created canopy openness could maintain suitable conditions for species diversity in lowland woods throughout the Holocene, for human impact can be traced back to the Mesolithic (Bos *et al.*, 2006; Tinner *et al.*, 2007; Kuneš *et al.*, 2008). Possibly human-induced fires may well have been important in the pre-history of the European oakwoods (Kalis *et al.*, 2003; Tinner *et al.*, 2005), and even, coppicing is archaeologically proved to have been present several thousand years before the present (Billamboz, 2001; Haneca *et al.*, 2005). Based on this evidence, we suggest that prehistoric human impact was essential to keep populations of open-woodland herbs and insects alive.

ACKNOWLEDGEMENTS

This article was written with the support of GAAV ČR grants AV0 IAA600050812 'Lowland woodland in the perspective of historical development' and AV0 Z60050516 (long-term institutional research support) and GAČR grant 206/08/H049. We thank Péter Szabó for his unpublished information and inspiring discussions about historical management; Péter also revised our English. Milan Chytrý and Jiří Danihelka kindly allowed us to use their by now historical vegetation relevés from the early 1990s. We are grateful to Tomáš Herben and Zoltán Botta-Dukát for their advice as to the correct design of multivariate analyses. Petr Kuneš kindly reviewed the part on prehistoric human impact. We also thank to the Editor and three reviewers for their comments.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

Appendix S1 Species presence and status.

BIOSKETCHES

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Editor: Marcel Rejmanek