

Charles University in Prague

Faculty of Science

Doktorský studijní program: Botanika

Ph.D. Study Program: Botany



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Vegetační změny českých nížinných lesů během posledních desetiletí

Vegetation changes in Czech lowland forests over the past decades

Disertační práce

Ph.D. Thesis

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Praha, 2015

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Kabátech, 30.06.2015

Acknowledgements

I thank all people who helped me to see things from different sides.

First of all, my supervisor Radim Hédli - he helped me many times and he (usually) stayed patient even when I strongly disagreed with him.

Other people who influenced my thinking – Jan Wild, Tomáš Herben, Péter Szabó, František Máliš, Jiří Doležal and Jarda Vojta.

The ultimate goal for each teacher is to have at least one student better than himself. I was so lucky that my first student was it. Martin, thanks for good thoughts, a lot of help and fun in the field and lab.

The biggest thanks go to my family.

My parents supported me all the time and without their support, this thesis would not happen.

My wife Petra deserves canonization because she must be saint (otherwise it is not possible that she survived it).

THANKS!

Grant support

I received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no 278065.

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ABSTRACT

To explore decadal changes in plant species diversity and composition of typical lowland forests in the Czech Republic, I compared vegetation on plots sampled decades ago with vegetation on the same plots sampled recently.

First I evaluated the robustness of the approach used in my thesis. In Chapter 1, we provided the first direct test of the effect of uncertainty in original plot location on results from vegetation resurvey. We found that temporal trends in vegetation diversity and composition were comparable between exactly relocated permanent and only approximately relocated semi-permanent plots. Therefore, we conclude that the resurvey of semi-permanent plots is robust to the uncertainty in original plot location.

Then, we showed that vegetation in lowland oak forest shifted from species-rich communities of thermophilous forest toward species poorer communities of mesic forest (Chapter 2). The species typical for thermophilous oak forests and nationally endangered species suffered the most significant decline. We identified as the main driver behind these changes shift from traditional coppicing toward high forest management after WWII.

Further, we explored the processes behind temporal shifts in species diversity and composition after the abandonment of coppicing (Chapter 3). To disentangle simultaneous changes in species richness and composition, we developed a novel Temporal Nestedness Analysis. We found that the main process was the ecologically non-random extinction of originally present light-demanding species. Therefore, the current vegetation is impoverished, compositionally nested subset of previously species rich assemblages historically maintained by regular coppicing.

We also assessed the long-term effects of highly invasive herb *Impatiens parviflora* on forest plant community in lowland forest (Chapter 4). Specifically, we tested if the invasion of *Impatiens parviflora* contributed to the vegetation changes described in Chapter 3. We found that, despite common believe, the massive invasion of this species did not affect plant communities even after decades from its invasion. *Impatiens parviflora* was therefore passenger, not driver of the observed vegetation change.

In summary, my thesis showed that 1) vegetation of studies lowland forests substantially changed during last decades, 2) important driver of these changes has been abandonment of traditional coppicing, 3) the main process after abandonment of coppicing was the non-random extinction of light-demanding species and 4) at least some highly invasive species are passengers rather than drivers of these changes.

INTRODUCTION

Decadal vegetation change

Vegetation change in time and space is central concept in ecology (Davis et al., 2005). From the ideas of climax and temporally stable communities, science moved toward more dynamical understanding of plant communities (Vellend, 2010). However, this paradigm shift came to forest ecology only recently, presumably because forest have been traditionally considered as the climax – i.e. the final stage of succession under temperate climate. During last decades, increasing evidence suggests that this static view is wrong and that temperate forest plant communities are much more dynamic than we used to think (Foster et al., 2003; Taverna et al., 2005; Woods, 2007).

Many individual - even herbaceous - plants can live for decades, if not centuries (Inghe & Tamm, 1985; Ehrlén & Lehtilä, 2002; Nobis & Schweingruber, 2013). Some plant species are therefore able to persist at the site even under conditions which no longer support its reproduction (Kuussaari et al., 2009). This phenomenon is called extinction debt (Tilman et al., 1994). To study temporal vegetation dynamics, we thus need to explore vegetation changes over decades, centuries and millennia. Obviously, this needs different approaches than are used in most ecological studies spanning only few years (Magnuson, 1990; Rees et al., 2001).

The long-term insights into vegetation dynamics spanning centuries and millennia can be provided by paleoecology (Mitchell, 2011; Jackson & Blois, 2015). However, the spatial and temporal resolution of paleoecological data is limited and restricted to the taxa which are paleoecologists able to sample and recognize (Vera, 2002; Goring et al., 2013). Moreover, most plant diversity in temperate forest represents herbaceous species (Gilliam, 2007), which are paleoecologically almost invisible.

To study temporal dynamics of plant communities at the plot and species level, we therefore need another approach. During last decades, such approach has been developed through resurvey of historical vegetation plots (Brewer, 1980; Persson, 1980).

Resurvey of historical vegetation plots

Thanks to century old tradition of vegetation ecology, millions of vegetation plots have been collected across the World (Ewald, 2003; Waller et al., 2012; Chytrý et al., 2014). These historical data capturing plant species growing at the particular spot are increasingly digitised and subsequently stored in electronic vegetation databases (Dengler et al., 2011).

Fortunately, the legacy data associated with these vegetation plots sometimes allow plot re-localization and repeated sampling of plant species composition. Such vegetation resurvey allows researchers to explore detailed vegetation dynamics over several decades (von Oheimb & Brunet, 2007; Rogers et al., 2008; Newton et al., 2012). With the exception of few really long-term experiments (Silvertown et al., 2006; Chytrý et al., 2009), vegetation resurvey is the only way how to explore the decadal plant community dynamics at the plot level (Vellend et al., 2013b; Chytrý et al., 2014).

The data from vegetation resurvey have been most often used to describe patterns of vegetation change through time (Brewer, 1980; Kirby & Thomas, 2000; Hédli, 2004; Bennie et al., 2006). Recently, these data are increasingly used also to explore species traits affecting species persistence (Naaf & Wulf, 2011a; Amatangelo et al., 2014; Mccune & Vellend, 2015) or to explore the drivers of large-scale changes in plant communities (Smart et al., 2005; Verheyen et al., 2012; De Frenne et al., 2013).

The vegetation resurvey can concern either exactly or only approximately localized plots. When exactly localized permanent plots are available, the resampling is straightforward (Wiser et al., 1998; Nygaard & Ødegaard, 1999; Taverna et al., 2005; Bunn et al., 2009). However, for most historical plots exact locations are not known and these plots can be relocated only approximately (Bakker et al., 1996; Chytrý et al., 2014).

These approximately localized plots are increasingly called semi-permanent. For the first time, this term have been used by Persson in his seminal paper about forest vegetation changes in Dalby Söderskog, forest in southern Sweden (Persson, 1980). Since that time, resurvey of semi-permanent plots has been used to document vegetation changes in various parts of the world (Sang & Bai, 2008; Harrison et al., 2010; Amatangelo et al., 2011; Daniëls et al., 2011; Kapfer et al., 2012) Recently, individual studies have been combined in several meta-analyses exploring large-scale changes in species richness and composition (Verheyen et al., 2012; De Frenne et al., 2013; Vellend et al., 2013a)

Changes in lowland forest vegetation

In my thesis, I used resurvey of semi-permanent plots to explore decadal vegetation changes in Czech lowland forests. These forests are dominated by broadleaved tree species mainly from genus *Quercus*, *Carpinus*, *Tilia*, *Acer* and *Fraxinus* and belong to vegetation classes *Carpino-Fagetea* and *Quercetea pubescentis* (Chytrý et al. 2013). These forest plant communities are assumed to be dominant natural vegetation of lowland regions (ca below 500 m a.s.l.) of temperate Europe (Bohn & Neuhäusl 2000). They occupy wide range of environmental conditions except extra-zonal sites, like floodplains, steep screes and deep sandy soils (Ellenberg 1998; Bohn & Neuhäusl 2000).

Since the mid-20th century, vegetation of European lowland forests have gone through dramatic changes (Rackham 2008) and shifts in plant diversity and composition were recently documented in a number of lowland forests (Van Calster et al., 2007; Corney et al., 2008; Baeten et al., 2009; Keith et al., 2009; Naaf & Wulf, 2011b; Verheyen et al., 2012). While there is no common temporal trend in species richness, species composition shifted towards more shade-adapted and nutrient-demanding plant species in most forests (Verheyen *et al.* 2012).

It has been suggested that these changes has been caused by nitrogen deposition (Thimonier et al., 1994; Diekmann et al., 1999; Dirnböck et al., 2014), ongoing climate change (Lenoir et al., 2008; Bertrand et al., 2011) or changing number of ungulates (Chytrý & Danihelka, 1993; Kwiatkowska, 1994; Boulanger et al., 2014). Recently, these suggestions have been challenged by the hypothesis that the ultimate driver behind the observed changes is the demise of traditional forest management, in particular its most widespread form – coppicing (Decocq et al., 2005; Van Calster et al., 2007; Baeten et al., 2009).

Introduction

Temporal changes in vegetation of lowland forests have been however documented mostly in western Europe (Debussche et al., 2001; Corney et al., 2008; Baeten et al., 2009; Verheyen et al., 2012). At the beginning of my PhD study, there were only few studies from eastern-central Europe (Chytrý & Danihelka, 1993; Kwiatkowska, 1994). Nevertheless, these studies and anecdotal evidence suggest that forest vegetation of lowland forest is rapidly changing also in this region. However, we did not know if the changes are similar to the changes described from other parts of Europe and how they relate to the changes in forest management, particularly to the abandonment of coppicing. Therefore, my study aimed to fill this knowledge gap.

Aims of my thesis

To explore decadal changes in plant species diversity and composition of several typical lowland forests in the Czech Republic, I used resurvey of semi-permanent vegetation plots.

Specifically, I aimed:

- To evaluate the effects of uncertainty in original plot location on results from resurvey of semi-permanent vegetation plots (*Chapter 1*)
- To explore temporal changes in species diversity and composition of lowland broadleaved forests after the abandonment of centuries-long coppice management (*Chapters 2, 3*).
- To analyse taxonomic homogenization of the plant species composition in the forest understory (*Chapters 2, 3*).
- To test the potential long-term contribution of highly invasive herb *Impatiens parviflora* to the observed vegetation changes (*Chapter 4*).

Uncertainty in original plot location

Most historical plots is not permanently marked in the field and these semi-permanent plots are relocated only approximately. Therefore, resurvey may in fact concern a spatial location with different species composition (Fischer & Stocklin, 1997; Ross et al., 2010).

Surprisingly few studies have explored this specific limitation of semi-permanent plots. Persson (1980) compared temporal vegetation changes on plots resurveyed at the most probable locations of the historical plots with changes on plots shifted five meters apart. Fisher & Stocklin (1997) showed that pseudo-turnover increases with increasing distance between the most probable location of the historical plot and the new relocated plot. Hédli (2004) sampled several new plots for each historical plot and compared vegetation changes observed on the most topographically similar pair of plots with temporal changes of the whole dataset. Finally, Ross et al. (2010) found lower spatial turnover among several new plots established within the probable location of the historical plot than the temporal turnover between all possible pairs of historical and new plots. Collectively these studies indicate that resurvey of semi-permanent plots is relatively robust to location uncertainty. However, they addressed pseudo-turnover only in an indirect way by comparing several replicate samples made within the probable area of the historical sample.

Therefore, to directly assess the importance of the location uncertainty on result from vegetation resurveys, we compared the vegetation changes on exactly relocated (i.e. permanent) and approximately relocated (i.e. semi-permanent) plots resurveyed after 40 years in České středohoří (*Chapter 1*). Our results suggest that the resurvey of historical vegetation plots is robust to uncertainty in original plot location and, when done properly, provides reliable evidence of decadal changes in plant communities. This provides important background for other resurvey studies, including other chapters included in my thesis.

To relocate semi-permanent plots in the field, researchers most often use historical maps with marked plot locations. To further increase relocation accuracy, only a site with elevation, slope and aspect similar to the historical plot can be resurveyed (Harrison et al., 2010; McCune & Vellend, 2013). Sometimes, researchers use also tree species composition as additional criteria for plot relocation within a forest stand, seeking for comparable composition of tree species forming forest canopy (Chytrý & Danihelka, 1993; Rogers et al., 2008).

Interestingly, in *Chapter 1*, we found that not so often used tree species composition is important for the proper plot re-localization. This approach assumes that the time between the surveys is shorter than the turnover of the canopy trees. However, this is not a problem for most studies as only few resurveys span more than six decades (Keith et al., 2009; Šebesta et al., 2011; Newton et al., 2012). The second assumption is that no major canopy disturbance occurred between the surveys. This is not an important limitation for most studies, either, because such disturbance-affected plots are usually *a priori* discarded from the resurvey to avoid successional young stages with their distinct species composition (Hédl, 2004; Wild et al., 2004; Wiegmann & Waller, 2006). Therefore, I recommend using the historical tree composition as additional criteria for plot re-localization in the field.

In *Chapter 1*, we used data from the Database of Czech Forest Classification System (Zouhar, 2012). This database contains over 30,000 plots sampled with comparable methodology in the Czech Republic since the 1950s. We found that these plots can be successfully relocated and that the coordinates of the plots are highly accurate given the combined uncertainty of the original plot marking in the map and the geographic coordinates of the marked tree measured with a basic GPS receiver (Johnson & Barton, 2004; Piedallu & Gégout, 2005).

The standardised sampling protocols and relatively precise localization of forestry plots contrasts with most vegetation plot data stored in the Czech National Phytosociological Database (Chytrý & Rafajová, 2003) and with other phytosociological data in general. These legacy data from local phytosociological studies have been collected with various research aims and survey designs (Chytrý et al., 2014). Moreover, they usually have only vague descriptions of plot location (Dengler et al., 2011) Therefore I argue that resurveys of plots from forest databases such as the Database of Czech Forest Classification System can be used for vegetation change assessment at a scale that is not possible with legacy data from phytosociological studies.

Management legacies

The historical factors are increasingly recognized as one of the most important drivers of current vegetation patterns (Ricklefs, 1987; Chase, 2003; Dambrine et al., 2007). Even the forest plant

communities traditionally considered as “true nature” are increasingly recognised as systems largely formed by historical human management (Dupouey et al., 2002; Jamrichová et al., 2012; Etienne et al., 2013).

However, historical human management have not been traditionally considered as the important driver of forest vegetation diversity and composition. This is rather surprising because already Heinz Ellenberg in his famous book (Ellenberg 1988) argue at several places that human management was shaping forest vegetation through history. Despite these suggestions, the widespread believe that forest plant communities are determined mostly by local environmental conditions (climate, soil and topography) did not take historical influences into account (Bohn & Neuhäusl 2000).

The human impact in central European forest can be traced at least back to Neolithic (Gardner, 2002; Haneca et al., 2005; Billamboz, 2014) and most probably to Mesolithic (Tinner et al., 2007). At least since the middle-ages, almost all lowland forests have been rationally managed according to codified rules (Szabó, 2010). However, the traditional forest management (mainly coppicing) have been gradually abandoned from the second half of 19th century. Many lowland forests have been managed as coppice or coppice-with-standards up to the WWII (Szabó, 2010; Müllerová et al., 2014). Shortly after the WWII, coppicing completely stopped and traditionally coppiced forest have been either abandoned (mainly in nature reserves) or transformed to high forest.

In one of the first examples of the vegetation resurvey of semi-permanent plots, Milan Chytrý and Jiří Danihelka resampled 46 plots in thermophilous forest plant communities of Milovice Wood in 1992. They found marked shift in species composition and attributed this shift to establishment of two game preserves (Chytrý & Danihelka, 1993). During the 1990s, the density of game has been substantially reduced and this gave us the opportunity to explore the reaction of the forest vegetation. If the game was the primary driver behind the shifts observed by Chytrý and Danihelka, than the vegetation should at least partly recover. In 2006, we repeated the sampling in Milovice Wood and subsequently analyzed the vegetation changes between all three surveys (*Chapter 2*). Surprisingly, the trend found by Chytrý and Danihelka continued and this lead us to the conclusion that the primary driver of the vegetation change was not the game but most probably the change in the forest management from coppicing to high-forest. Since then, the trends found in Milovice Wood have been confirmed also from other lowland forests in the Czech Republic (*Chapter 3*, Veverková, 2013, Pospíšková, 2014).

We also found that the decrease in plant species richness can be dramatic and even worst that the most vulnerable species are also nationally endangered species (*Chapters 2, 3*). Interestingly, parallel conclusions have been reached by entomologists studying frustrating decline of biodiversity, especially of forest butterflies (Bergman, 2001; Benes et al., 2006; Konvicka et al., 2008; Streitberger et al., 2012; Cizek et al., 2013; Fartmann et al., 2013). In series of studies, they showed that recent extinctions of forest butterfly species in the central Europe are closely linked with the changes in forest management, particularly with abandonment of coppicing. Together with the papers included in this thesis (*Chapters 2, 3*), these results showed that nature in central European lowland forest is rapidly changing at large spatial scale. We showed that the vegetation of lowland forests became impoverished of many light-demanding species (*Chapter 3*) and that the distinctness of their species composition gradually faded (*Chapters 2*).

Our results suggest that the most important driver of this vegetation change was the shift in forest management around the half of 20th century. These findings have wide implications for nature conservation and forest management. If forestry and conservation policies continue to prefer closed-canopy stands, many endangered species are likely to pay their extinction debts.

Taxonomic homogenization

Taxonomic homogenization occurs when species assemblages are more compositionally similar than they were before (Olden & Rooney, 2006). It has been recently documented for many taxonomic groups in a wide range of environments and at various spatial and temporal scales (Rahel, 2000; Rooney et al., 2004; Keith et al., 2009). As a consequence, the local distinctness of community composition is gradually lost and the communities are increasingly composed by widespread generalist and often alien species (McKinney, 2004; Qian & Ricklefs, 2006; Winter et al., 2009).

However, taxonomic homogenization is usually inferred only from temporally static data and many published studies suffers from methodological drawbacks (Olden & Rooney, 2006; Baiser et al., 2012). Vegetation resurveys represent temporally replicated data ideal for testing taxonomic homogenization (McCune & Vellend, 2013). The number of studies using vegetation resurvey to test taxonomic homogenization is therefore steadily increasing (Keith et al., 2009; Naaf & Wulf, 2011b). However, at the beginning of my PhD there were no studies from European lowland forests. In this thesis, I filled this knowledge gap and provide the first evidence that taxonomic homogenization occurs also in forest vegetation in central Europe (*Chapters 2, 3*). Interestingly, my thesis also revealed that the story is not so simple.

In *Chapter 3*, we showed that forest vegetation in Děvín Wood became significantly less variable, i.e. underwent taxonomic homogenization. However, in *Chapter 2* using the same methodological approach, we did not find evidence of taxonomic homogenization in Milovice Wood. This pattern is even more striking given the fact that both studied localities (Děvín and Milovice Wood) lie nearby and share largely the same history of management during last centuries (Szabó, 2010; Müllerová et al., 2014). It may be, as we suggest in *Chapter 2*, that the artificially high numbers of game present in two game preserves in Milovice Wood prevented the taxonomic homogenization in the forest understory. While further research is needed to test this hypothesis, our unpublished results from Krumlov Wood showed that this may be the case (Vild, Hédli & Kopecký, unpublished). While explicitly not tested in the paper, Fig. 6 in *Chapter 1* shows that forest vegetation in České středohoří also did not become taxonomically homogenised. And it should be noted that forests in České středohoří have one of the highest densities of ungulates in the Czech Republic.

Together, these contrasting results suggest that the widespread belief that taxonomic homogenization is common (McGill et al., 2014) can be actually wrong. Results presented in this thesis (together with our unpublished results from several others vegetation resurveys) showed that in some regions forest vegetation homogenized, while in other regions vegetation heterogeneity did not change. Currently, the ecological drivers behind this regional variation are not known. Based on our results, I suggest that the regionally variable densities of ungulates can be such driver. However, this hypothesis remains to be tested.

Temporal nestedness

Through ecological time-scales, species composition of the vegetation plot can change either by the species turnover (i.e. replacement of one species by other species), species immigration (i.e. establishment of previously not present species) and species extinction (Olden & Poff, 2003; Vellend, 2010). However, most existing approaches do not allow disentangling of these contrasting processes (Baselga, 2012). For example, widely used compositional dissimilarities, either for presence-absence data (e.g. Sorensen dissimilarity) or cover-abundance data (e.g. percentage (aka Bray-Curtis) dissimilarity), express simultaneously species turnover and differences in number of present species (Baselga, 2010; Barwell et al., 2015).

The differentiation between species turnover and changes in species richness is especially important in the context of vegetation resurveys. While authors of global meta-analyses argued that there is no general changes in species richness (alpha diversity) (Vellend et al., 2013a; Dornelas et al., 2014), the species richness often differ between repeatedly surveyed plots (*Chapters 2; 3*; Rooney et al., 2004; Woods et al., 2012). This can be caused either by real processes like canopy closure (*Chapter 3*), nitrogen deposition (Thimonier et al., 1994; Bernhardt-Römermann et al., 2007), deer browsing (Rooney et al., 2004; Wiegmann & Waller, 2006) or by artificial differences relating to sampling bias (e.g. different taxonomical skills between the observers performing original survey and resurvey (Archaux et al., 2009; Milberg et al., 2009), and in the case of unknown original plot size by sampling plots of different area. As a result, the differences in species richness between surveys are common.

It is therefore necessary to differentiate between species turnover and changes in species richness. In *Chapter 3*, I developed a novel Temporal Nestedness Analysis, which allows differentiation between species turnover and changes in species richness. This method is based on the concept of nestedness, traditionally applied in spatial context (Wright & Reeves, 1992; Ulrich et al., 2009). Spatial nestedness means that species poorer sites are compositionally nested subsets of the more species rich sites (Wright & Reeves, 1992; Worthen, 1996). In Temporal Nestedness Analysis, nestedness is however applied in temporal context, indicating to what degree are recent samples compositionally nested subsets of the older samples.

We used this method to explore the dominant processes behind the vegetation change in Děvín Wood (*Chapter 3*). We used 122 semi-permanent plots originally surveyed shortly after the abandonment of coppicing and again more than 50 years later. Between the surveys, the vegetation composition shifted toward more mesic species, many plant species became locally extinct and overall species composition homogenised. We used Temporal Nestedness Analysis to ask: “Was this change caused by replacement of previously present species or the species replacement was only minor process and more important was species extinction? “.

We found that the dominant process behind observed vegetation change was ecologically non-random extinction of light demanding species (*Chapter 3*). These findings were important not only theoretically but also practically, because they suggest that potential restoration of coppicing for nature conservation is feasible.

Currently, the restoration of coppicing is being implemented in the part of Děvín Wood by local nature conservation authorities. Our results presented in *Chapter 3* have been used as one of the main arguments supporting this restoration project.

Long-term effects of plant invasions

The invasion of alien plant species can change native community structure resulting in biodiversity loss (Levine et al., 2003; Powell et al., 2011; Vilà et al., 2011). However, even the most successful invaders can be passengers rather than drivers of change, having no direct effect on biodiversity (Didham et al., 2005; MacDougall & Turkington, 2005; Davis et al., 2011). To disentangle harmful invaders from harmless ones, we therefore need to know the long-term effects of invasive species (Strayer et al., 2006; Gilbert & Levine, 2013).

Long-term assessment is especially important in ecosystems with slow temporal dynamics, such as temperate forests (Rees et al., 2001; Woods, 2007). Temperate forests are considered resistant against plant invasions as they are currently among habitats with the lowest proportion of alien plant species (Chytrý et al., 2008a, 2008b; Essl et al., 2011). Despite low invasibility, several alien herbs have successfully spread across temperate forests (Martin et al., 2009).

One of the most successful herbaceous invaders is *Impatiens parviflora*. During the last decades, *Impatiens parviflora* invaded both managed and natural forests across Northern Hemisphere (Lambdon et al., 2008; Kalusová et al., 2014). Such massive and rapid invasion led to the common belief that *Impatiens parviflora* reduces native plant diversity and modifies vegetation composition. Indeed, several observational studies reported lower species diversity and altered species composition in invaded stands (Obidziński & Symonides, 2000; Chmura & Sierka, 2007; Vervoort & Jacquemart, 2012). These results sharply contrast with short-term experiments reporting no negative effects of *Impatiens parviflora* (Hejda, 2012; Čuda et al., 2014). A long-term perspective was therefore needed to disentangle this conflicting evidence.

In Chapter 4, we developed a novel approach based on vegetation plot resurveys that allows for the testing of the long-term effects of invasive species. Through this approach, we showed that highly invasive alien herb *Impatiens parviflora* did not reduce diversity and did not disassemble native plant communities even after decades following the invasion. Our long-term data thus challenged the paradigm that all invasive species have negative effects (Davis et al., 2011; Thomas & Palmer, 2015).

The differentiation of invasive species that are driving changes in biodiversity from those that are their passengers is therefore urgently needed. Our approach can provide this differentiation. Moreover, comparable vegetation resurveys are increasingly conducted worldwide and our approach can be readily extended to other species, regions and study systems.

Conclusion and future outlook

My thesis fills the knowledge gap about temporal changes in vegetation of central European lowland forests. Together with my co-authors, I showed that 1) vegetation of several lowland forests substantially changed during last decades, 2) important driver of these changes has been abandonment of traditional coppicing, 3) after the abandonment of coppicing, the main process of vegetation change was the non-random extinction of light-demanding species and 4) at least some highly invasive species are passengers rather than drivers of these changes.

In my thesis, I showed that the most probable driver of decadal vegetation change in several lowland forests was the shift from traditional coppice management toward high forest. However, to provide further support for this hypothesis it would be necessary to i) include more regions with different environmental settings and associated species pools and ii) to compare the importance of the management change to the importance of other potential drivers like climate change, nitrogen deposition and changing number of game.

My results also suggest that taxonomic homogenization of forest understories is not universal process and depends on other factors, such as regional game densities. Again this suggestion needs further testing. However, preliminary results from several other regions confirmed regional variability in taxonomic homogenization. The interesting question is therefore the driver behind this variation. The regional game density is one possibility, however this hypothesis needs to be tested.

Results from Děvín Wood clearly showed that highly even highly invasive species such as *Impatiens parviflora* can simply join other native species without negative impact on invaded community. However, these results can be specific for the species or region studied. Therefore, more studies are needed to assess the generality of this finding. Comparable vegetation resurveys are increasingly conducted across the Northern Hemisphere and the approach developed in our case study can be readily extended to other species, regions and study systems to provide this assessment.

In my thesis, I also present the first published study from resurvey of the vegetation plots stored in the Database of Czech Forest Classification System. The standardised sampling protocols and relatively precise localization of these forestry plots contrasts with most vegetation plot data stored in traditional phytosociological databases. The important result from my thesis is therefore also the finding that resurveys of plots from forest databases can be used for vegetation change assessment at a scale that is not possible with legacy data from phytosociological studies. This would provide large-scale and community-wide insights into decadal changes in plant species diversity and distribution, while maintaining all details of spatially explicit plot data. I plan to explore these exciting possibilities in my future.

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IN A NUTSHELL

Chapter 1: Kopecký, M. & Macek, M. (2015) Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, 21, 322–330.

We explored how important is the uncertainty in original plot location for interpretation of the results from studies of vegetation change based on semi-permanent plots. Surprisingly, we found that the vegetation changes are comparable between exactly and approximately relocated plots. Therefore, we concluded that the vegetation resurvey is robust to uncertainty in original plot location.

Chapter 2: Hédli, R., Kopecký, M. & Komárek, J. (2010) Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity and Distributions*, 16, 267–276.

We used semi-permanent plots sampled three times to explore the vegetation changes in central European oak-forest and discussed the potential role of historical human management on forming and maintaining this forest type. We found that the original species rich communities of thermophilous oak forest have shifted toward mesic and species poorer assemblages. The most probable driver of this change was the abandonment of traditional coppicing, which maintained the thermophilous character of the oak forest for centuries. Interestingly, we have also found that the artificially high number of game probably slowed down the process of vegetation homogenization.

Chapter 3: Kopecký, M., Hédli, R. & Szabó, P. (2013) Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology*, 50, 79–87.

We tried to disentangle simultaneous changes in species richness and composition and identify the main processes behind the vegetation change in abandoned coppices. We found that after the abandonment of traditional coppicing, the main process of vegetation change was ecologically non-random extinction of light demanding species. As a result, current vegetation is substantially species poorer and represents temporally nested subset of previously present species. Interestingly, the most declined species often form persistent seed-bank. Therefore, restoration of coppicing would potentially bring these endangered species back.

Chapter 4: Kopecký, M. & Hédli, R. (2015) Long-term effects of alien herb invasion on forest plant communities. *submitted to the Journal of Ecology*.

We used a resurvey of historical vegetation plots to test the long-term effect of highly invasive herb *Impatiens parviflora* on native forest vegetation. Despite massive invasion, *Impatiens parviflora* did not decrease species richness, evenness and beta diversity and did not change species composition of the invaded stand. Therefore we concluded that, contrary to general belief, *Impatiens parviflora* did not threaten native forest flora. We also encouraged other researchers to use our novel approach to test long-term effect of invasive species to differentiate between harmful and harmless invaders.

Vegetation resurvey is robust to plot location uncertainty

Martin Kopecký & Martin Macek

ABSTRACT

Aim Resurveys of historical vegetation plots are increasingly used for the assessment of decadal changes in plant species diversity and composition. However, historical plots are usually relocated only approximately. This potentially inflates temporal changes and undermines results.

Location Temperate deciduous forests in Central Europe.

Methods To explore if robust conclusions can be drawn from resurvey studies despite location uncertainty, we compared temporal changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots. We hypothesized that compositional changes should be lower and changes in species richness should be less variable on exactly relocated plots, because pseudo-turnover inflates temporal changes on approximately relocated plots.

Results Temporal changes in species richness were not more variable and temporal changes in species composition and compositional heterogeneity were not higher on approximately relocated plots. Moreover, the frequency of individual species changed similarly on both plot types.

Main conclusions The resurvey of historical vegetation plots is robust to uncertainty in original plot location and, when done properly, provides reliable evidence of decadal changes in plant communities. This provides important background for other resurvey studies and opens up the possibility for large-scale assessments of plant community change.

Key-words: pseudo-turnover, resampling, revisitation, semi-permanent plots, temperate forest, temporal vegetation change

INTRODUCTION

Resurveys of historical datasets provide invaluable insights into species distributional shifts and community dynamics in the face of climate and land use change (Leach & Givnish, 1996; Harrison et al., 2010; de Frenne et al., 2014; Grytnes et al., 2014). Essential for any resurvey is the availability of methodologically consistent and spatially explicit historical datasets (Magurran et al., 2010; Vellend et al., 2013). In this respect, historical vegetation plots represent an enormous data source collected by comparable methodology across several continents for over a century (Ewald, 2003; Chytrý et al., 2014; Waller et al. 2012). There are millions of plots already available in electronic databases (Dengler *et al.*, 2011). Vegetation plot resurveys are therefore increasingly used for the assessment of decadal changes in plant communities and subsequent conservation suggestions (Keith et al., 2009; Amatangelo et al., 2011; Verheyen et al., 2012; Kopecký et al., 2013).

Most vegetation plots are, however, non-permanent and their exact locations are not known (Bakker et al., 1996; Chytrý et al., 2014). To relocate such plots, historical maps with plot locations are commonly used (Rooney et al., 2004; Van Calster et al., 2007; Vittoz et al., 2009; Baeten et al., 2010; Naaf & Wulf, 2010). When historical maps are not available, other types of information can be used – e.g. the identification of the forest compartment in which the plot was established (Chytrý & Danihelka, 1993; Hédli, 2004) or the square of the national grid in which the sampling was made (Bennie et al., 2006; Ross et al., 2010). To further increase relocation accuracy, only a site with elevation, slope and aspect similar to the historical plot can be resurveyed (Harrison et al., 2010; Kopecký et al., 2013; McCune & Vellend, 2013). Comparable tree species composition has also been used to relocate the plot within a forest stand, assuming that the time between the surveys is shorter than the turnover of the canopy trees (Chytrý & Danihelka, 1993; Rogers et al., 2008).

Nonetheless, because historical plots are relocated only approximately, resurvey may in fact concern a spatial location with different species composition. This could result in pseudo-turnover – i.e. change in species composition caused by sampling different place (Fischer & Stocklin, 1997). Surprisingly few studies have explored this limitation. Persson (1980) compared temporal vegetation changes on plots resurveyed at the most probable locations of the historical plots with changes on plots shifted five meters apart. Fisher & Stocklin (1997) showed that pseudo-turnover increases with increasing distance between the most probable location of the historical plot and the new relocated plot. Hédli (2004) sampled several new plots for each historical plot and compared vegetation changes observed on the most topographically similar pair of plots with temporal changes of the whole dataset. Finally, Ross et al. (2010) found lower spatial turnover among several new plots established within the probable location of the historical plot than the temporal turnover between all possible pairs of historical and new plots. Collectively these studies indicate that resurvey of non-permanent plots is relatively robust to location uncertainty. However, they addressed temporal pseudo-turnover only in an indirect way by comparing several replicate samples made within the probable area of the historical sample. Their results therefore depend on spatial vegetation heterogeneity within the resurveyed area (Ross et al., 2010).

Here we used a new approach directly comparing vegetation changes between approximately and exactly relocated plots. To explore if robust conclusions can be drawn from resurvey studies despite location uncertainty, we compared temporal changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots in temperate deciduous forests. We hypothesized that compositional changes should be lower and changes in species richness should be less variable on exactly relocated plots, because pseudo-

turnover inflates temporal changes on approximately relocated plots. If this is true, the resurveys of approximately relocated plots will provide biased assessment of vegetation changes and their results should be approached with caution.

METHODS

Study area

We resurveyed historical vegetation plots in the NW part of the Czech Republic (Fig. 1). We selected this area, because of i) high diversity of semi-natural forest vegetation, ii) anecdotal evidence that forest vegetation substantially changed during the last decades, presumably because iii) forests in this area suffer high nitrogen deposition (up to $2 \text{ g.m}^{-2}.\text{y}^{-1}$ - Hůnová et al., 2014).

The climate is temperate, with 6-7 °C mean annual temperature and 550-600 mm of mean annual precipitation (Tolasz et al. 2007). The relief is highly variable (200-800 m a.s.l.), with characteristic volcanic hills rising from the sedimentary plateau (Fig. 1).

The diversity of semi-natural forest vegetation reflects this environmental heterogeneity. Oak-hornbeam forests dominated by *Quercus petraea* and *Carpinus betulus* cover the plateau and the lower parts of the hills, while beech forests (*Fagus sylvatica*) dominate on hill tops and northern slopes. Thermophilous oak forests with *Quercus pubescens* occur mainly on southern slopes, and ravine forests (*Tilia cordata* and *platyphyllos*, *Acer pseudoplatanus* and *platanoides*, *Ulmus glabra*) cover steep slopes and screes. Alluvial forests with *Fraxinus excelsior* and *Alnus glutinosa* occur along the streams.

Data collection

We resurveyed historical vegetation plots stored in the Database of Czech Forest Classification System (Zouhar, 2012). This database contains over 30 000 plots sampled with comparable methodology in the Czech Republic since the 1950s. The aim of the original sampling was to document forest vegetation heterogeneity and to provide a basis for forest type classification. In the field, sampling followed a standardized protocol, which included the permanent marking of the central tree within the plot (Mráz & Samek 1957). Simultaneously, plot location was indicated on a forestry map usually with a spatial resolution of 1:10 000.

We retrieved all plots sampled in the study region before 1980 from the database. For resurvey, we selected plots originally sampled by a single observer (J. Smejkal) in 1972-1973. To relocate these plots, we used: 1) geographic coordinates of plot location on the historical map, 2) plot elevation, slope and aspect and 3) tree species composition. In the field, we navigated to the approximate location of each plot with a GPS receiver and then thoroughly searched for places with corresponding topography and tree species composition. We also searched for the original mark painted on the central tree (Fig. 1). If we found the mark, we resurveyed the same site around the central tree. In other cases, we sampled the most probable site according the information from the original survey.

In 2013, we resurveyed all plots originally established in semi-natural broadleaf forests which were not clear-cut between the surveys. From 69 resurveyed plots, we exactly relocated 24 plots. The remaining 45 plots were relocated only approximately (Fig. 1). We resurveyed the plots in the same season and used the same plot area as in the original survey (450 or 500 m²). Within each plot,

we listed all vascular plant species, assigned them to vertical layers (e.g. tree, shrub, herb) and estimated their cover-abundance according the Zlatník scale used during the original survey (Zlatník 1953). The Zlatník scale has 11 ordinal classes, the first two express species abundance (less than 3 individuals; more individuals but with cover below 1 %), while the rest express species cover (up to 5, 15, 25, 37, 50, 62, 75, 87 and 100 %).

Data analysis

To explore whether the uncertainty in plot location affects the assessment of temporal changes in the forest herb layer, we compared changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots. First, we standardized plant nomenclature according to Kubát et al. (2002). Where species identification was uncertain, we combined taxa at the aggregate or genus level. We also transformed the ordinal classes of the Zlatník scale to species percentage cover. We converted the two lowest classes as 1 and 2 % and all other classes as percentage midpoints of the respective class.

Species richness. To test if the temporal changes in the number of taxa present within the plot differ in magnitude or variance between exactly and approximately relocated plots, we used a two-sample Kolmogorov-Smirnoff test implemented with *ks.test* function in R (R Core Team 2013).

Species frequency. To assess whether relocation uncertainty bias changes at the species level, we correlated temporal changes in species frequency on exactly and approximately relocated plots. From the total species pool (N=243), we selected species which occur in more than one sample in both plot types (N=98). To test whether these species changed comparably between plot types, we used the Pearson correlation coefficient.

Species composition. To explore if species turnover differs between exactly and approximately relocated plots, we tested the interaction between type of plot and survey period. To calculate temporal turnover in species identities, we used the incidence based Simpson index (Lennon *et al.*, 2001). To calculate temporal turnover in species proportions, we used the abundance based Bray-Curtis index calculated from species cover data standardized by sample totals.

We used permutation-based MANOVA (Anderson, 2001) to test the interaction between type of plot and survey period. To correctly partition type III sum of squares, we used *anova.2way.unbalanced* R-function and tested the interaction by permutation of the raw data (Anderson & Legendre, 1999). Following Borcard et al. (2011, pp. 185-188), we checked the test assumption of homogeneity of the variance-covariance matrices with *betadisper* R-function from the *vegan* package (Oksanen et al. 2013).

To visualize compositional changes, we performed non-metric multidimensional scaling (NMDS) in two dimensions. We performed global NMDS separately on Simpson and Bray-Curtis dissimilarity matrices using the *monoMDS* R-function from the *vegan* package.

Compositional heterogeneity. To explore if compositional heterogeneity changes differ between exactly and approximately relocated plots, we compared temporal changes in plot distances to the multivariate centroid of all plots from the same survey (Anderson *et al.*, 2006). First, we projected Simpson and Bray-Curtis dissimilarity matrices into euclidean space and extracted plot distance to the group centroids (spatial medians) using *betadisper* R-function. Then, we tested the interaction between type of plot and survey period using the test for homogeneity in multivariate dispersion (Anderson, 2006) implemented with *anova.2way.unbalanced* R-function.

RESULTS

The resurvey of approximately and exactly relocated plots provided a comparable assessment of temporal vegetation changes (Table 1). The variability and magnitude of species richness changes was not higher on approximately relocated plots (Fig. 2).

The frequency of individual species changed similarly on exactly and approximately relocated plots ($R = 0.72$, $t = 10.04$, $p < 0.0001$; Fig. 3).

Despite considerable species turnover (Fig. 4), the compositional changes were not substantially higher on approximately relocated plots (Fig. 5). The magnitude of changes in compositional heterogeneity was not higher on approximately relocated plots (Fig. 6).

DISCUSSION

Our results suggest that temporal changes inferred from vegetation plot resurveys are robust to uncertainty in original plot location. This is important as resurvey studies are increasingly used to assess decadal vegetation changes and provide management and conservation recommendations (Bergamini et al., 2009; Kopecký et al., 2013; Meyer et al., 2013). The uncertainty in plot relocation - potentially inflating temporal changes - has been frequently used as an argument against resurvey studies. However, our results showed that the resurvey of semi-permanent historical plots can provide vegetation change assessment comparable to permanent plots. This provides important background for other resurvey studies and supports their conclusions. Moreover, our results indicate that permanent plots no longer marked in the field can be successfully relocated. This will allow vegetation change assessment over longer time-period that is usually possible with intensive but short-term data from vegetation monitoring programs (Bakker et al., 1996; Chytrý et al., 2014).

In our study, we assessed the importance of imprecise plot relocation, but it is not the only factor that could cause compositional pseudo-differences between resurveyed plots. The observer is usually not the same for different sampling periods and this can introduce temporal pseudo-differences through subjective cover estimation, plant misidentification or overlooking (Lepš & Hadincová, 1992; Scott & Hallam, 2002; Archaux et al., 2009; Vittoz et al., 2010). Within season vegetation variability and among season fluctuations can also contribute to the compositional pseudo-turnover (Kirby et al., 1986; Brunet & Tyler, 2000; Vymazalová et al., 2012). These biases are nevertheless common to all repeated samples, both from approximately and exactly relocated plots. Our results are therefore not affected by them, because - if they are present within our dataset - they are the same for samples from approximately and exactly relocated plots. However, the issue of these possible pseudo-differences between resurveyed vegetation plots needs to be addressed in the future.

Plot relocation

To relocate the plots, we used geographic coordinates extracted from historical maps, local topography and species composition of the tree layer. While historical maps and terrain morphology have been used frequently, tree species composition has been used only rarely (Chytrý & Danihelka, 1993; Rogers et al., 2008). In the field, we found the historical mark only after close examination of the site with the tree species composition corresponding to the historical one. Especially useful were

admixture tree species in stands with one dominant species (e.g. a single linden in an otherwise oak-dominated forest). We therefore encourage researchers to use tree species composition as an additional criterion for plot relocation in the field.

This of course assumes that the time between the surveys is shorter than the turnover of the canopy trees. However, this is not a problem for most studies as only few resurveys span more than six decades (Keith et al. 2009; Newton et al. 2012; Šebesta et al. 2011). The importance of this limitation will nevertheless increase in the future.

The second assumption is that no major canopy disturbance occurred between the surveys. This is not an important limitation for most studies, either, because such disturbance-affected plots are usually *a priori* discarded from the resurvey to avoid successional young stages with their distinct species composition (Hédl, 2004; Wild et al., 2004; Wiegmann & Waller, 2006).

In line with this common practice, we resampled only stands that were not clear-cut and replanted between the surveys. Theoretically, we should have found marked trees on all plots. In reality, we found the marked tree only on one third of all resurveyed plots. This can be attributed to the surveyor not marking the tree, our failure to find the mark, the death of the marked tree or occasional thinning. We think that in most cases thinning is the probable explanation, because sanitary thinning is often performed within the region and we found some stumps both on exactly and approximately relocated plots.

Datasets for resurvey

Careful selection of historical datasets with sufficient information is essential for any resurvey. Therefore we stress that our results can be specific for our study area, data source or even sample size and we encourage other researchers to carry out similar comparisons. We resurveyed plots scattered over 100 km² of a topographically diverse landscape and this resulted in high species turnover among resurveyed plots. The relocation-driven pseudo-turnover should be lower in regions with less variable vegetation (Ross et al. 2010). Our results therefore suggest that resurveys are robust to relocation uncertainty even in heterogeneous regions.

Another interesting question is the effect of plot size on compositional pseudo-turnover between resurveys. Our plots were larger than the most common size used for sampling forest vegetation in Europe (Chytrý & Otýpková 2009). Many resurveys used substantially smaller plots (Verheyen et al. 2012; Vellend et al. 2014). It is therefore possible that the effect of relocation error will be higher in resurveys of these smaller plots, because smaller plots can capture more fine-scale vegetation variability (Reed et al. 1993).

We resurveyed plots extracted from the Database of Czech Forest Classification System. Most historical plots stored in this database have been collected with comparable sampling protocols. We are therefore confident that the results from our study area can be generalized to other data stored in this database. We found all exactly relocated plots within 60 m from the original coordinates, and the mean distance between original coordinates and the marked tree was only 27 m. This indicates that plot geographic coordinates are surprisingly accurate given the combined uncertainty of the original plot marking in the map and the geographic coordinates of the marked tree measured with a basic GPS receiver (Johnson & Barton, 2004; Piedallu & Gégout, 2005).

The understanding of temporal patterns in biodiversity is limited by the availability of long-term, large-scale and high-resolution data (Dornelas *et al.*, 2013). The data stored in the Database of Czech Forest Classification System have all these characteristics (Zouhar 2012). Moreover, our study

showed that their resurvey provides results robust to location uncertainty. This highlights their potential for resurvey studies on the national scale and we plan to move in this direction in the future.

Contrary to forest plot databases, most vegetation databases are based on legacy data from local phytosociological studies (Dengler *et al.*, 2011). These local datasets have been collected with various research aims and survey designs, which substantially reduce their utility for large-scale studies of vegetation change (Chytrý *et al.*, 2014). Moreover, historical phytosociological relevés usually have only vague descriptions of plot location (Dengler *et al.*, 2011). This is in sharp contrast with the standardized sampling performed in forestry over large regions (Thomas *et al.*, 2009; Bertrand *et al.*, 2011; Zhu *et al.*, 2012). Therefore we argue that resurveys of forest plot databases can be used for vegetation change assessment at a scale that is not possible with legacy data from traditional phytosociological studies. This would provide large-scale and community-wide insights into decadal changes in plant species diversity and distribution, while maintaining all details of spatially explicit plot data.

CONCLUSIONS

Our results suggest that the resurvey of historical plots - despite the uncertainty in original plot location - represents a robust way to infer temporal vegetation changes. This provides important background for other resurvey studies and opens up the possibility for large-scale assessments of plant community change.

ACKNOWLEDGEMENTS

We thank Radim Hédli, Jesse M. Kalwij, Péter Szabó and three anonymous reviewers for useful comments. We thank Péter Szabó also for language revision and Václav Zouhar for his help with the forestry database. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no 278065. Additional funding was provided by projects RVO 67985939 and CZ.1.07/2.3.00/20.0267 with the financial contribution of the EC and the state budget of the Czech Republic.

Author contributions: Both authors conceived the ideas and collected the data; M.K. analysed the data and led the writing.

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TABLES

Table 1 Mean temporal changes in species richness, composition and heterogeneity in exactly and approximately relocated plots. The differences in temporal changes were evaluated by Kolmogorov-Smirnoff test (species richness), permutational MANOVA (species composition) and test of multivariate homogeneity of group dispersions (compositional heterogeneity).

	Plot relocated		Statistics	p-value
	exactly	approximately		
Species richness	-0.83	0.00	0.153	0.82
Composition (Simpson)	0.37	0.41	0.629	0.23
Composition (Bray-Curtis)	0.56	0.59	0.489	0.48
Heterogeneity (Simpson)	0.02	-0.02	0.898	0.17
Heterogeneity (Bray-Curtis)	-0.01	-0.03	0.696	0.28

FIGURES

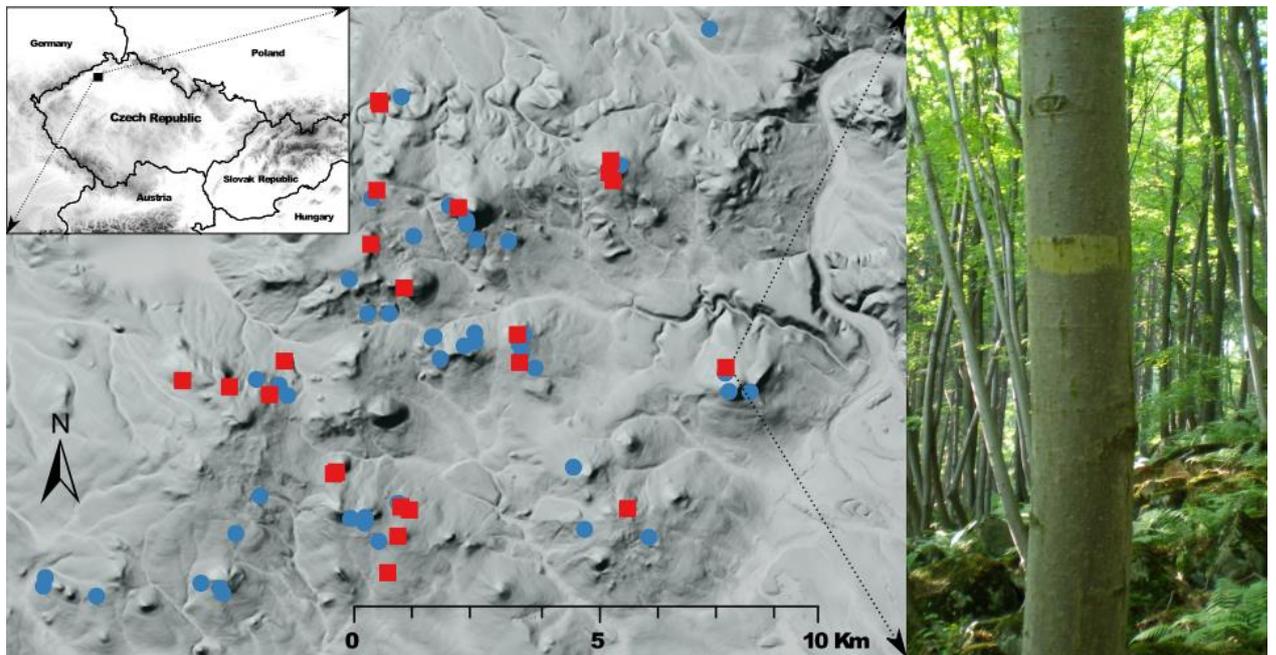


Figure 1 Location of the study area within Central Europe; landscape distribution of exactly (red squares) and approximately (blue dots) relocated plots; and original mark - yellow stripe - on the central tree within the plot.

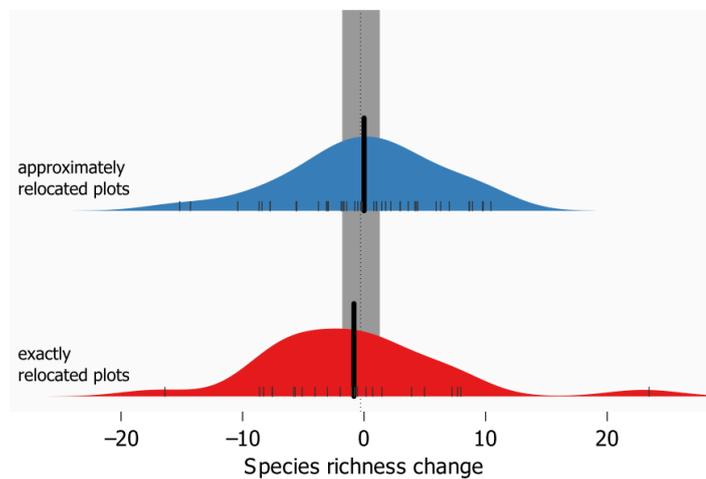


Figure 2 Species richness changes are not more variable on approximately relocated plots. Ridge plots show the density distribution of species richness changes within each plot type, the species richness change on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

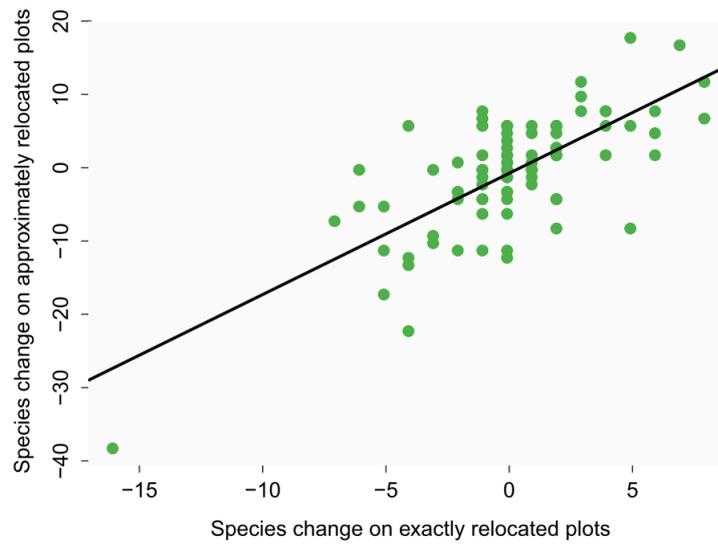


Figure 3 Frequency of individual species changed similarly on exactly and approximately relocated plots. The dots represent temporal change in individual species frequency and the line represents linear relationship fitted to the data.

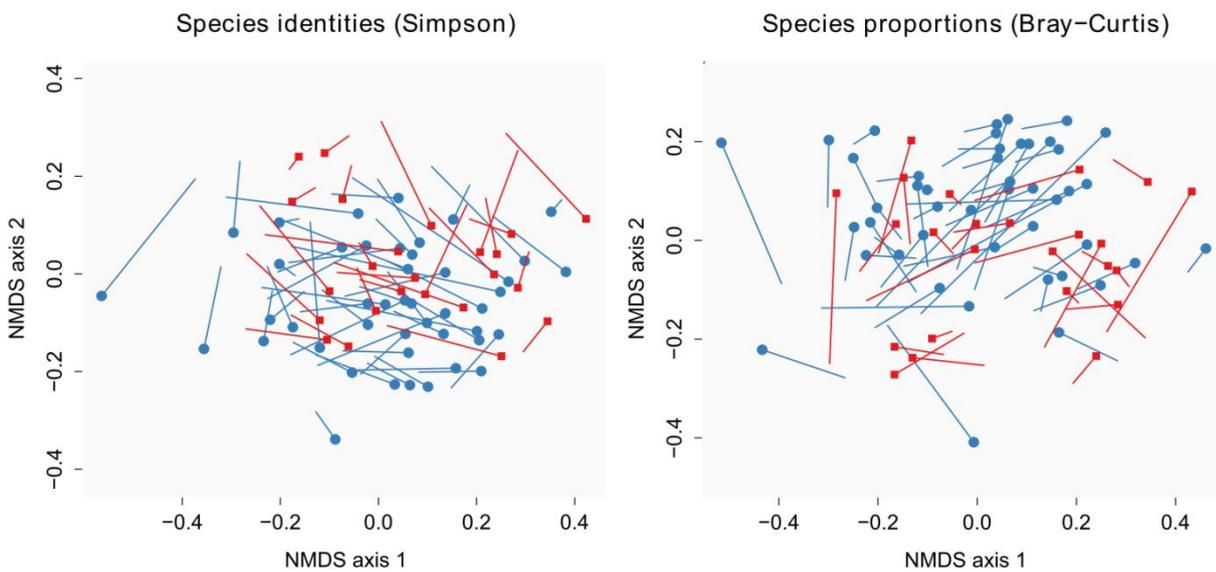


Figure 4 Species composition shifted similarly on exactly (red squares) and approximately (blue dots) relocated plots. The filled symbols represents samples from the original survey, the lines connect both samples from the same plot and the ends of the lines represent samples from the resurvey. The sample configuration from nonmetric multidimensional scaling (NMDS) was centred and rotated by principal component analysis.

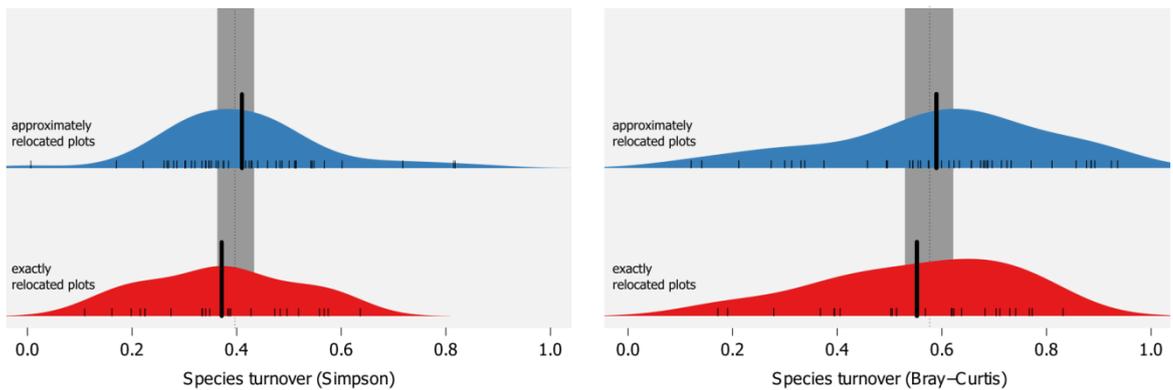


Figure 5 Species composition changed substantially - but comparably - on exactly and approximately relocated plots. Ridge plots show the density distribution of turnover within each plot type, the turnover on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

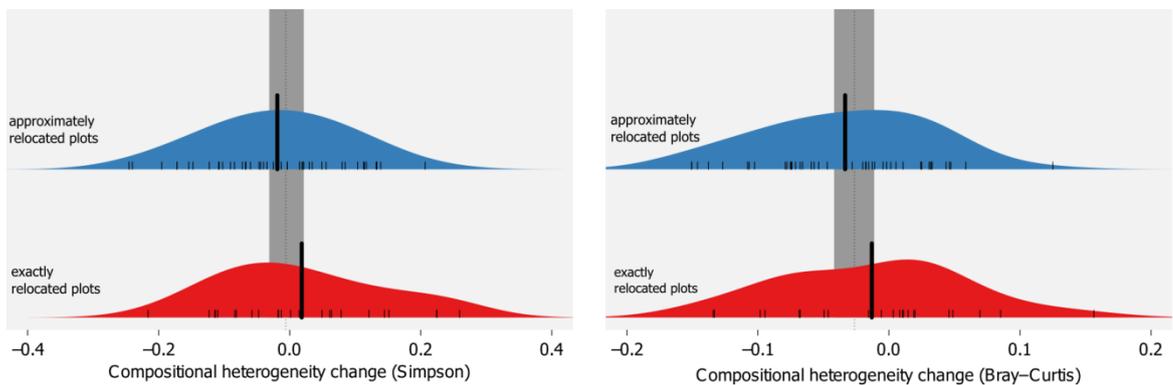


Figure 6 Compositional heterogeneity changes were not higher on approximately relocated plots. Ridge plots show the density distribution of compositional heterogeneity changes within each plot type, the changes on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

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

Radim Hédl, Martin Kopecký & Josef Komárek

ABSTRACT

Aim Lowland woodlands in Europe went through dramatic changes in management in the past century. This paper 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 losing their original character?

Location Czech Republic, Central Europe

Methods The vegetation in forty-six 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 which 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.

Key-words: 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 led to taxonomic impoverishment and homogenization of the woodland vegetation (Keith *et al.*, 2009), which 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, has 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 (Corney *et al.*, 2008; Van Calster *et al.*, 2008a; Baeten *et al.*, 2009), 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; Szabó, 2005; Loidi, 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 paper, 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 due to succession, 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-km² 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 180–324 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 ca. 1300 to the 1940s. The cutting period of the coppice was only 7 years in the Middle Ages (data from 14th and 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 I 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

A 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 m². 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 done in 1953–54 by Jaroslav Horák (1972) before establishing the game preserves, reflecting “the relatively homogeneous structure of a coppice” (personal communication 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, forty-six of Horák’s original plots were re-sampled using the same approach by Milan Chytrý and Jiří Danihelka (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). 22 plots were in the Bulhary preserve, 15 in the Klentnice preserve, and 9 plots remained outside both preserves. In summer 2006, Josef Komárek (2008) sampled the 46 plots again. In total, 138 vegetation records were used in the analyses.

Data analysis

All analyses were done 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 insensitive 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. In order 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 analyzed. 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 non-parametric 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 assess if the dispersions of groups are different, we performed a non-parametric 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 6 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 *Carpinion 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 analyzed 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 to 3 plots, and were subsequently not re-encountered in 1992 and 2006. The same was observed for 6 woody species. Only 15 rare herb species (occurring in 1 to 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 *Carpinion 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. *Carpinion betuli*) showed almost no change at all. For individual species, see Appendix S1.

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 michelii*, *Dictamnus albus*, *Lithospermum purpureocaeruleum*, *Melica picta*, *Melittis melissophyllum*, *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 (*Melittis melissophyllum*) – see Appendix S1. The marked impoverishment of species typical for thermophilous oakwoods and of endangered species clearly indicate 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*, *Carex michelii*, *Dictamnus 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 to 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, *Impatiens parviflora* is a neophyte which 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 *Fraxinus excelsior*, as reported from several other places (Hofmeister *et al.*, 2004; Střešík & 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 due to 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 *Fraxinus excelsior*, *Acer* spp., *Tilia* spp., *Carpinus 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 *T. 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 due to 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 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 which keep the canopy open and understorey disturbed. This finding invokes some older views considering the origins and prehistory 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 prehistory 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 paper 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 would like to 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.

Author contributions: R.H. conceived ideas and led the writing. M.K. conceived ideas, analyzed the data and substantially contributed to the writing. J.K. collected the field data.

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FIGURES

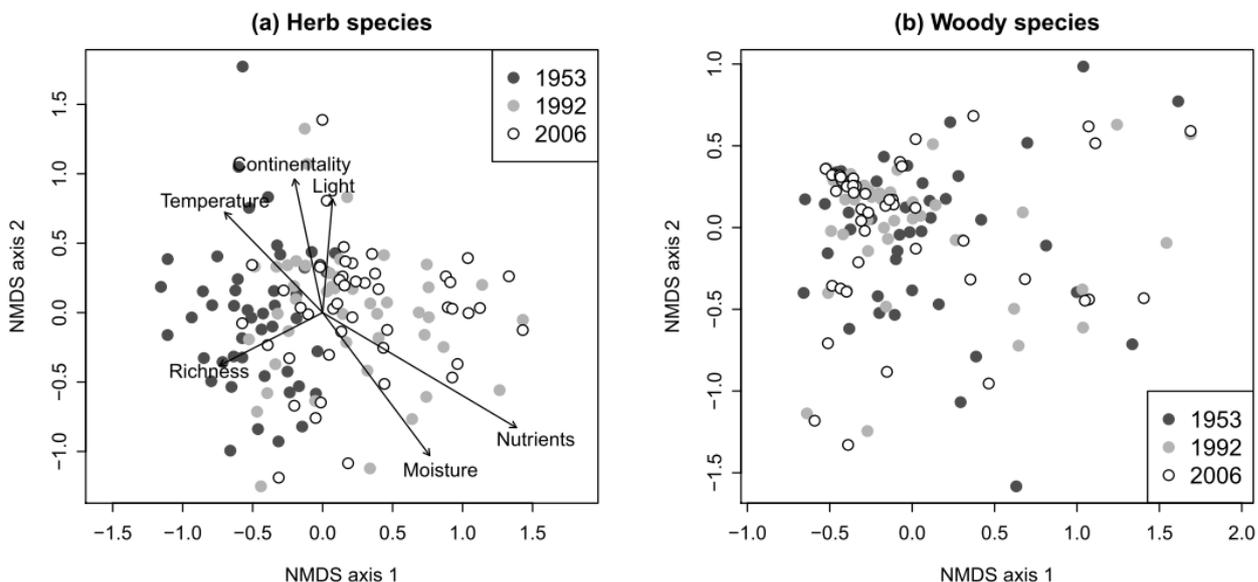


Figure 1 Shift in species composition during last 50 years in Milovice Wood shown in diagrams from non-metric multidimensional scaling (NMDS) for herb (a) and woody (b) species. Symbols represent 46 triplets of plots in three subsequent periods. Vectors of mean Ellenberg indicator values and species 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.

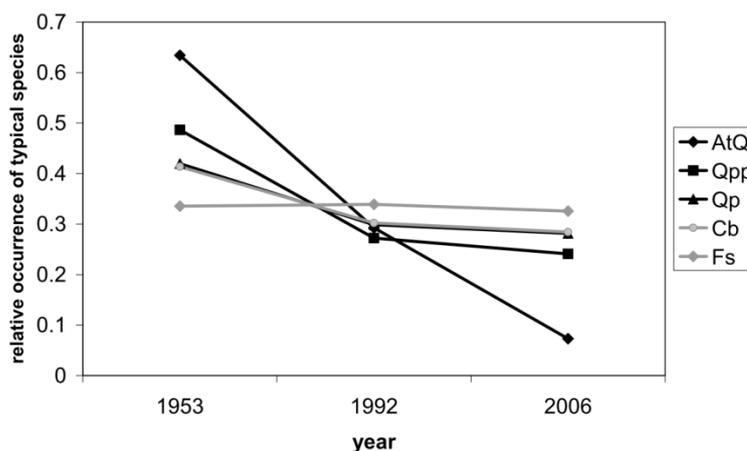


Figure 2 Temporal trends in the relative occurrence of species typical for three thermophilous (black) and two mesic (grey) woodland communities; for full version of the abbreviations in legend see text. A marked decline in the former indicates the loss of the original thermophilous character of the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

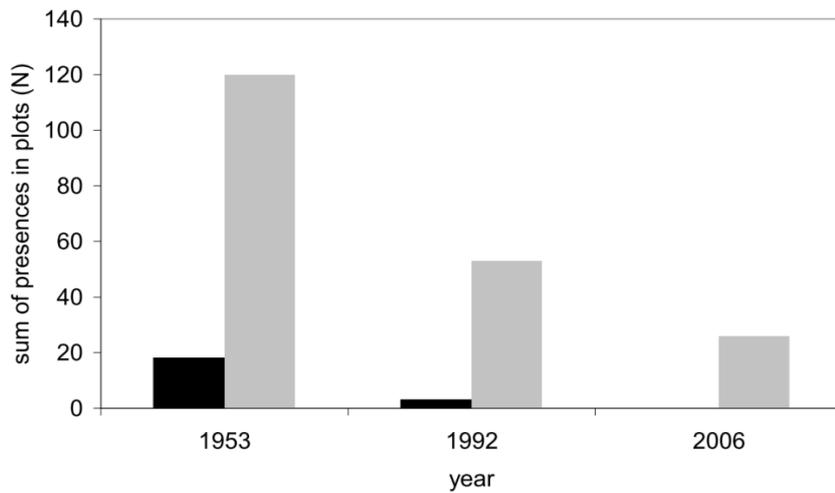


Figure 3 Trends in the occurrence of endangered plant species, sums of the presences in three subsequent records. Occurrences from 1953 were reduced to about one fifth by 2006 in the group of endangered species (C3, grey bars). Critically (C1) and strongly (C2) endangered species (black bars) have completely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

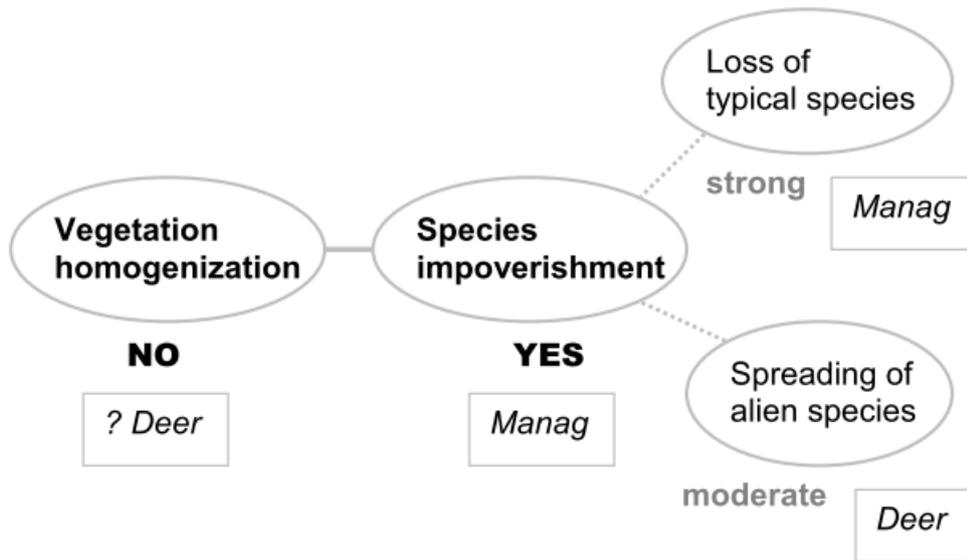


Figure 4 Summary interpretation of the main processes in Milovice Wood in the past half a century. Overall, there has been species impoverishment mainly due to the management shift from coppicing to high forest. This change has strongly affected the light-demanding species of thermophilous oakwoods.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

Non-random extinctions dominate plant community changes in abandoned coppices

Martin Kopecký, Radim Hédl & Péter Szabó

ABSTRACT

- 1.** The plant community structure of European lowland forests has changed dramatically in the 20th century, leading to biodiversity decline at various spatial scales. However, due to methodological difficulties associated with simultaneous changes in species diversity and composition, ecological processes behind the changes are still poorly understood.
- 2.** We analysed temporal changes in forest plant community after the mid-20th century abandonment of coppicing in a typical Central European forest, which had been managed as coppice for centuries. We used 122 semi-permanent plots first surveyed in the 1950s shortly after the last coppicing and again in the 2000s after half a century of natural succession. We used a novel Temporal Nestedness Analysis to disentangle the immigration and extinction processes underlying temporal changes in community structure and tested whether species gains and losses were ecologically random.
- 3.** The studied vegetation has shifted from the species-rich assemblages of a relatively open and low-nutrient forest towards the impoverished flora of a closed-canopy forest dominated by a few shade-adapted species. The significant reduction of beta diversity, i.e. compositional heterogeneity among plots, indicated taxonomic homogenization of the forest understorey. Temporal species turnover was only a minor component of the community change and recent assemblages are nested subsets of the former ones. Ecologically non-random extinctions dominated these changes. Light-demanding species with a persistent seed-bank were the most prone to extinction, while species with high specific leaf area substantially increased in frequency.
- 4. *Synthesis and applications.*** The dominant process after the abandonment of coppicing was the ecologically non-random extinction of light-demanding species leading to an impoverished, temporally nested plant community structure. This development is typical for many abandoned coppices and poses a significant threat to forest biodiversity in Europe. If forestry and conservation policies continue to prefer closed-canopy stands, many endangered species are likely to pay their extinction debts. To restore declining or even locally extinct species, canopy opening in abandoned coppices is urgently needed.

Key-words: community structure, eutrophication, forest management, taxonomic homogenization, life-history traits, long-term changes, resurvey, specific leaf area, semi-permanent plots, temporal nestedness analysis

INTRODUCTION

Disentangling the mechanisms of temporal change in ecological communities, in particular distinguishing between immigration and extinction effects, represents one of the most challenging issues in applied ecology. On ecological time scales, the composition of species assemblages changes through an array of immigration and extinction events (Olden & Poff 2003; Jackson & Sax 2010). If species immigration results in a major compositional turnover or even the creation of a novel community, ecological restoration can be difficult or impossible (Hobbs, Higgs, & Harris 2009). On the other hand, when the resulting assemblage is an impoverished subset of previously present species, the restoration is likely to succeed (Jackson & Hobbs 2009).

These issues are increasingly important because species assemblages change rapidly under human impact. In temperate Europe, lowland forests have gone through dramatic changes since the mid-20th century (Rackham 2008). This has raised many conservation issues because lowland forests are often species rich and host many globally threatened plant and animal species (Ellenberg 1988, Rackham 2006). Substantial changes in plant diversity and composition were recently documented in a number of lowland forests across north-western and central Europe. While there is no common temporal trend in species richness, species composition shifted towards more shade-adapted and nutrient-demanding plant species in most forests (Verheyen *et al.* 2012). Atmospheric deposition and high numbers of ungulates have been widely recognized as principal drivers of these changes (Chytrý & Danihelka 1993; Kwiatkowska 1994; Thimonier *et al.* 1994; Diekmann *et al.* 1999). Recently, these conclusions have been challenged by the hypothesis that the ultimate driver behind the observed changes is the demise of traditional forest management, in particular its most widespread form – coppicing (Decocq *et al.* 2005; Van Calster *et al.* 2007; Hédli, Kopecký, & Komárek 2010).

In contrast to the long periods of uniformly dark conditions in today's forests, coppicing maintained the periodic recurrence of extremely light conditions at short intervals (usually every 7–20 years (Szabó 2010)). These light pulses were a very characteristic feature of European lowland forests, which were managed as short-rotation coppices for centuries (Rackham 2006; Szabó 2010), or even for millennia (Gardner 2002; Haneca, Van Acker, & Beeckman 2005). Due to this long-term influence, the species rich communities of European lowland forests were co-formed by human management (Ellenberg 1988; Decocq 2004a; Rackham 2006).

However, coppicing virtually disappeared from central and north-western Europe by the second half of the 20th century. This was caused by two main factors: 1) traditional management was gradually replaced by high-forest management from the 19th century onwards; and 2) nature conservation policy considered coppicing an undesirable 'human intervention' and banned it in most reserves (Szabó 2010). The demise of coppicing led to substantial changes in forest environments, which in turn resulted in changes both in plant communities (Baeten *et al.* 2009; Hédli, Kopecký, & Komárek 2010) and in invertebrate populations (Benes *et al.* 2006; Freese *et al.* 2006; Konvicka *et al.* 2008).

The changing nature of European lowland forests has been extensively documented, however, the ecological processes behind it are still poorly understood, mainly due to methodological difficulties associated with simultaneous changes in species diversity and composition. Therefore, we developed a novel analytical approach called Temporal Nestedness Analysis, which allows to disentangle processes behind changes in community structure. We used it to analyse changes in forest plant community after the mid-20th century abandonment of coppicing in Central European biodiversity hotspot - Děvín Wood. This site is a typical example of abandoned

coppices; many similar forests can be found throughout Europe. We explicitly focused on three hypotheses: 1) Species composition and diversity changed in response to the abandonment of coppicing. 2) Species turnover was only a minor component of the changes and the recent species assemblages are impoverished subsets of the former ones. 3) Species gains and losses were ecologically non-random.

METHODS

Study site

Děvín (48°52' N, 16°39' E) is a conspicuous limestone crest at 550 m a. s. l. which dominates the flat lowlands in the southeastern corner of the Czech Republic (Fig S1 in Supporting Information). It is located in the meeting zone of the Pannonian, Continental and Alpine biogeographic regions, resulting in species rich assemblages. With 643 species of vascular plants, the site is one of the biodiversity hotspots of central Europe. Climate is sub-continental, relatively warm and dry, with an average annual temperature of 9°C and average precipitation of 550 mm year⁻¹. Carbonate-rich substrates vary from shallow lithosols and rendzinas to loamy-clay luvisols of loess deluvial plateaus. Habitat types range from dry rocky grasslands on south-exposed slopes to ravine forests in north-exposed screes and shady gorges.

The habitats of Děvín have been co-formed by human activities for millennia as continuous human presence can be traced since Neolithic times. Most of Děvín is covered by Děvín Wood, which has had a remarkably stable size of 200-260 ha for at least seven centuries. Management has also been characterised by long-term stability: from the 14th to the 20th century, the Děvín Wood was managed as coppice with varying numbers of standard trees. The coppice cycle was 7 years in 1384 AD and gradually grew to 40 years in the 1940s (Szabó 2010). In 1946 the Wood was included in a non-intervention nature reserve, however, forestry operations continued in some parts. As a result, the present structure of the Wood is dominated by abandoned coppices. It also contains high-forests comprised of singled-out coppice stools, and has some plantations of the alien species *Pinus nigra* and *Quercus cerris*.

The plant communities of Děvín Wood are dominated by Pannonian oak-hornbeam forests (habitat type 91G0 according to NATURA 2000), ravine forests *Tilio-Acerion* (type 9180), and Peri-Alpidic basiphilous thermophilous oak forests (type 91H0). Tree dominants include broadleaved lime *Tilia platyphyllos*, sessile oak *Quercus petraea* agg., European ash *Fraxinus excelsior*, European hornbeam *Carpinus betulus*, and pubescent oak (*Quercus pubescens*). European beech *Fagus sylvatica* and native conifers are completely absent from the site.

Data collection

Between 1953 and 1964 (hereafter 'the 1950s'), J. Horák sampled Děvín Wood in order to describe its forest vegetation (Horák 1967). The plots were placed subjectively and covered the whole vegetation variability of the wood (average plot density was 0.65 plots per hectare). In each plot, Horák recorded a complete list of vascular plant species, estimated their cover-abundance and assigned them to several vertically defined layers.

In 2002–2003 (hereafter 'the 2000s'), one of the authors (RH) repeated Horák's records using the original methodology. Plots were relocated using Horák's original map scaled 1:10,000 with

marked positions of plots and information about slope, aspect and local topography retrieved from Horák's original field sheets. Based on our field experience, we estimated the relocation error to 10 – 20 m for most plots, with occasional maximum error up to 50 m in topographically homogeneous parts. Each plot was re-sampled in the same season as the original record and plot sizes were identical to the originals (200–500 m² for most plots).

Data analysis

In this study, we used 244 paired samples recorded from June to September. After merging species with uncertain determination (see Table S1), the dataset comprised 371 understorey species, defined as specimens lower than 1 m. All statistical analyses were performed with R, version 2.14.1 (R Development Core Team 2011) on incidence matrix with species presence–absence data. Specific methods were performed with R packages *vegan* (Oksanen et al. 2012, functions *metaMDS*, *betadisper*), *indicspecies* (De Cáceres & Legendre 2009, function *signassoc*) and *party* (Hothorn, Hornik & Zeileis 2006, function *ctree*).

Species diversity and composition

To analyse temporal changes in species diversity, we tested if the number of all vascular plant species and the number of forest plant species (see Appendix S1) significantly differ between sampling periods using Wilcoxon signed-rank tests.

To test for temporal changes in compositional heterogeneity (beta-diversity), we used the analysis of multivariate homogeneity of group dispersions (PERMDISP, Anderson et al. 2006). As a measure of compositional dissimilarity, we used the Simpson index for presence–absence data because it is independent from richness differences between samples (Koleff, Gaston, & Lennon 2003). We performed the test with 999 permutations restricted within temporally-paired samples.

To compare the vegetation patterns between the 1950s and the 2000s, we performed non-metric multidimensional scaling (NMDS). For NMDS, we used the same dissimilarity matrix as in PERMDISP. The two-dimensional configuration with the lowest stress after 1000 random starts was centred and rotated by principal components analysis in order to maximize variance along the first ordination axis.

To interpret the main compositional gradients extracted by NMDS, we first calculated unweighted means of Ellenberg indicator values (EIV) of the species present within each sample (Ellenberg et al. 1992). Then, we fitted mean EIVs into NMDS space using generalized additive models (Wood 2006). In accordance with the expected environmental changes, we used EIVs for reaction, nutrients, light and temperature. Furthermore, we tested the change in mean Ellenberg indicator values between the surveys with a permutation test that accounts for non-independence between indicator values and vegetation composition (Zelený & Schaffers 2012).

To identify species that have significantly increased or decreased in frequency, we used permutation tests to investigate whether the proportion of plots occupied by each species changed over time. We used 999 permutations and adjusted the *P*-values through Šidák's correction for multiple testing (De Cáceres & Legendre 2009).

Temporal nestedness

Temporal nestedness expresses the extent to which the recent assemblages are impoverished subsets of older assemblages. It is therefore a temporal analogue of spatial nestedness, which expresses the extent to which the poorer species assemblages are nested subsets of richer assemblages (Ulrich, Almeida-Neto, & Gotelli 2009). The important difference is that temporal nestedness is calculated between subsequent samples from the same plots, while spatial nestedness is calculated among all plots in a dataset, usually sorted in order to maximize nestedness (Elmendorf & Harrison 2009; Ulrich, Almeida-Neto, & Gotelli 2009).

To detect which process dominated the observed vegetation changes, we developed a novel Temporal Nestedness Analysis (TNA), which allows differentiation between immigration and extinction processes. TNA is based on a comparison of the observed temporal nestedness between subsequent samples from the same plots and the nestedness of the same samples whose temporal sequence was randomly reshuffled.

Specifically, we proceeded through the following steps. First, we calculated the nestedness measure based on overlap and decreasing fill for sites ($NODF_{sites}$, Almeida-Neto et al. 2008) between each pair of the temporally sorted old and recent plot samples. Then, we averaged these pairwise $NODF_{sites}$ indexes into temporal nestedness (TN) of the whole dataset. Finally, we compared the observed TN to the distribution of 999 TN values generated by random reshuffling of the survey period between temporally paired samples (see annotated R script in Appendix S2). We reported the difference between the observed TN and the TN values of randomly reshuffled assemblages by standardized effect size (SES), which measures the number of standard deviations that the observed TN value differs from the mean TN value of the simulated assemblages.

Ecology of species loss and gain

To test whether the species gains and losses were ecologically random, we explored how they were related to species life-history traits. First, we selected 18 ecologically relevant species life-history traits from the LEDA (Kleyer *et al.* 2008) and BioFlor (Klotz, Kühn & Durka 2002) databases. We included species traits related to competitive ability (e.g. CSR strategy, canopy height), environmental requirements (e.g. specific leaf area, leaf anatomy) and dispersal (e.g. seed weight, vegetative propagation, full overview in Table S2).

Then we tested whether these traits were useful for partitioning species into homogenous groups with respect to changes in species frequency between the surveys. For partitioning, we used classification and regression trees, because these account for non-linear hierarchical relationships, treat categorical, ordinal and quantitative data simultaneously, and deal with missing values (De'ath & Fabricius 2000). In each split of the tree all species traits are tested and the trait which best discriminates between declined and increased species is selected. The procedure goes on until no trait significantly discriminates between species. We used conditional inference trees as these have several crucial advantages over other approaches (e.g. CART) - the statistical testing of each split through permutation, no need for problematic pruning of over-fitted trees and no selection bias towards variables with many possible splits or missing values (Hothorn, Hornik & Zeileis 2006).

RESULTS

Species diversity and composition

During the second half of 20th century, the forest vegetation of the Děvín Wood became significantly impoverished in vascular plant species (Fig. 1). While the first survey captured 356 species, only 228 species were recorded in the recent survey. The observed decline of gamma diversity was accompanied by a significant reduction in alpha diversity (Fig. 1). Individual plots lost more than one quarter (on average 27.3 %) of their former species richness and this decline was highly significant (Wilcoxon test, $V = 6922$, $P < 0.001$). The richness of forest plant species also declined from 110 species found in the 1950s to 89 in the 2000s. At the plot level, it declined significantly ($V = 5254$, $P < 0.001$) and the temporal pattern was similar to that of all vascular plant species (Fig. 1). Compositional heterogeneity (beta diversity) significantly declined between sampling periods (PERMDISP, $F = 6.77$, $P = 0.001$) indicating taxonomic homogenization of the forest understorey.

Species composition has shifted from the flora of a relatively open, nutrient-poor forest towards mesic, nutrient-rich forest community (Fig. 2). While mean Ellenberg indicator values for light (EIV-L_{old} = 5.3, EIV-L_{new} = 4.9, $P = 0.06$) and nitrogen (EIV-N_{old} = 5.3, EIV-N_{new} = 5.6, $P = 0.10$) changed substantially, indicator values for temperature (EIV-T_{old} = 5.7, EIV-T_{new} = 5.7, $P = 0.33$) and soil reaction (EIV-R_{old} = 7.0, EIV-R_{new} = 7.0, $P = 0.54$) did not change between the surveys.

The community-wide shift was based on substantial changes at the species level. From the pool of 371 species encountered during the surveys, almost a quarter (24.5 %) significantly changed their frequencies between the surveys (Fig.3). While only 15 species occurred significantly more frequently in the 2000s survey, 76 declined or even became locally extinct (for individual species, see Table S3).

Temporal nestedness

We found that species turnover was only a minor component of the community changes, because species assemblages from the 2000s formed temporally nested subsets of those from the 1950s (SES = 10.98, $P = 0.001$). None of the randomly generated assemblages exhibited the high degree of temporal nestedness observed in the real dataset (Fig. 4). Assemblages from the 2000s therefore represented highly impoverished subsets of the assemblages present in the 1950s and the prevailing mechanism underlying the community change was the plot-level extinction.

Ecology of species loss and gain

Species gains and losses were not ecologically random because specific leaf area and the ability to form a persistent seed bank significantly discriminate between increased and decreased species (Fig. 5). The species most prone to local extinction were light-demanding species with low specific leaf area. This group was further divided according the ability of species to form a persistent seed bank (Fig. 5). Species with a persistent seed bank were more susceptible to local extinction than species without persistent seed bank. Shade-tolerant species with relatively high specific leaf area significantly increased between the sampling periods (Fig. 5). Other life-history traits did not discriminate significantly between increased and decreased species.

DISCUSSION

Driving forces of community changes

The studied vegetation has shifted from the species-rich assemblages of a relatively open and low-nutrient forest towards the impoverished flora of a closed-canopy forest dominated by shade-adapted species. A similar scenario was observed in nearby Milovice Wood, whose management history has been almost identical (Hédli, Kopecný, & Komárek 2010). Both sites belonged to the same owners, who utilized the forests as short-rotation coppices continuously from at least 14th to the early 20th century (Szabó 2010). Moreover, the changes observed at both sites are in line with other studies conducted across European lowland forests which were previously managed as coppices (Van Calster *et al.* 2007; Corney *et al.* 2008; Baeten *et al.* 2009). Management changes and nitrogen deposition are the most commonly identified drivers of this pan-European trend (Verheyen *et al.* 2012).

We argue that the demise of coppicing in the mid-20th century was the ultimate driver behind the community changes observed in Děvín Wood. The species that suffered the most significant losses are plants typical of open woodlands characterized by low specific leaf area. The prolonged period of canopy closure is therefore the most probable cause of their decline (Dahlgren *et al.* 2006). The increased frequency of nutrient demanding species was the consequence of forest succession rather than effect of nitrogen deposition, because the abandonment of coppicing has led to biomass accumulation and alteration of soil nutrient status (Hölscher, Schade, & Leuschner 2001). The increasing proportion of trees requiring high levels of soil nutrients and having base nutrient-rich litter (mainly *Fraxinus excelsior*, *Ulmus glabra* and *Acer platanoides*) further contributed to soil eutrophication, leading to a positive feedback between soil chemistry and changes in tree species composition (Hofmeister, Mihaljevic, & Hosek 2004; Hédli, Kopecný, & Komárek 2010; Verheyen *et al.* 2012).

During the coppicing cycle, plant species richness first increases and then, after several years, slowly declines to levels before the last coppicing (Ash & Barkham 1976; Mason & Macdonald 2002). However, stand-scale survival of light demanding species and their co-existence with shade-tolerant species is ensured by the shifting mosaic of differently aged patches created by coppicing (Decocq *et al.* 2004a). After the abandonment of coppicing, lowland forests became structurally homogenized and light demanding species gradually disappeared from the local species pool. The significant taxonomic homogenization detected in our study was most likely caused by the structural homogenization of the forest. In the long run, this unification of vegetation structure and plant species composition can be detrimental to other organisms requiring a fine-scale mosaic of specific habitat patches (Freese *et al.* 2006; Spitzer *et al.* 2008).

Biodiversity threats

Compositional changes observed in abandoned coppices are driven by the population dynamics of species, which react to changing environmental conditions. Unfortunately, these natural changes have significant consequences for biodiversity conservation. The most sensitive indicators of biodiversity change are species with a high population turnover, which react to changing conditions relatively quickly. Butterflies are organisms which possess these characteristics, with the additional benefit of having a well-known ecology and distribution (Beneš *et al.* 2002). Nation-wide extinctions

of butterflies confined to traditionally managed woodlands have already been reported (Van Swaay & Warren 1999; Beneš *et al.* 2002) and the last remaining populations of other endangered species survive in the few fragments of former coppices (Freese *et al.* 2006; Konvička *et al.* 2008). As butterflies are among the most intensively studied organisms, their decline may indicate declines of other, less known species groups (Thomas *et al.* 2004).

Furthermore, the documented extinctions can be vanguards of future developments, because of extinction debt. Extinction debt occurs when a population persists at a formerly suitable site where the conditions have meanwhile become unfavourable, the population growth rate is negative, and the population is doomed to extinction (Tilman *et al.* 1994). Long-lived organisms are especially prone to extinction debt because they are able to persist at a site even without successful reproduction (Kuussaari *et al.* 2009). Recent extinctions of woodland butterflies may be the first signs of future extinctions of other species with slower population turnover, such as forest plants (Krauss *et al.* 2010). If forestry and management policy continues to prefer closed-canopy forests, many species characteristic for European lowland forests will have to pay their debts and will become extinct.

Management restoration

Restoration of traditional woodland management has been suggested in order to ensure the long-term survival of light demanding forest species (Benes *et al.* 2006, Freese *et al.* 2006, Spitzer *et al.* 2008). Based on our results, we argue that opening the forest canopy is the first step required for successful restoration as the species most declined were light demanding and formed persistent soil seed banks. Canopy opening could increase the populations of such species on sites where they still survive, or initiate their establishment from the seed bank on sites where they became locally extinct (Decocq *et al.* 2004b; Van Calster *et al.* 2008a).

In the lowland forest of Białowieża (Poland), the removal of strongly shading *Carpinus betulus* led to the successful restoration of a species rich community with characteristic light demanding plant species (Kwiatkowska & Wyszomirski 1990). Similarly, Van Calster *et al.* (2008b) reported increased performance of several forest species after experimental canopy opening in a Belgian lowland forest. Increased irradiance on the forest floor could also increase the diversity of other organisms living in lowland forests, such as butterflies (Benes *et al.* 2006), ants (Dolek *et al.* 2008), xylophagous beetles (Vodka, Konvicka, & Cizek 2009) and epigeic invertebrates (Spitzer *et al.* 2008).

However, as frequently pointed out by conservation practitioners, a possible negative effect of canopy opening in abandoned coppices is the expansion of ruderal and exotic species. These are frequently nutrient-demanding and would benefit from the faster decomposition of accumulated organic matter after canopy opening. In addition to the internal source of nutrients in accumulated biomass, large amounts of nitrogen have accumulated through atmospheric deposition. Verheyen *et al.* (2012) suggested that the effect of nitrogen accumulation is not yet apparent in lowland forests because of canopy shading. The authors called this situation the “nitrogen time bomb” and warned against future canopy opening, which could suddenly release all accumulated nitrogen. The N-bomb “explosion” is certainly possible, but we argue that its effect would be reduced by soil phosphorus, which became the limiting resource in many terrestrial ecosystems (Vitousek *et al.* 2010; Peñuelas *et al.* 2012), including European lowland forests (Hofmeister *et al.* 2002; Axmanová *et al.* 2011). In contrast to nitrogen, soil phosphorus is related to substrate weathering rather than atmospheric

deposition and its turnover is much slower (Vitousek *et al.* 2010; Peñuelas *et al.* 2012). Limited phosphorus availability is therefore likely to block any effects of nitrogen eventually released by canopy opening.

However, to our knowledge, no papers have been published on long-term responses of plant communities to restoration of coppicing. We therefore encourage ecologists to focus on this applied issue and experimentally explore the consequences of canopy opening in abandoned coppices. This kind of research is urgently needed because of the fast and often irreversible changes in endangered biota of the European lowland forests.

CONCLUSION

In this paper, we applied a novel Temporal Nestedness Analysis, which successfully disentangled the effects of species immigration and extinction on temporal changes in abandoned coppices. We found that the dominant process after the abandonment of coppicing was the ecologically non-random extinction of light-demanding species. This process has led to impoverished assemblages, which constitute compositionally nested subsets of the former ones. Moreover, compositional heterogeneity among plots significantly decreased and the present vegetation is taxonomically more homogenous. This development is typical for many lowland forests previously managed as coppices and poses a significant threat to forest biodiversity in Europe. If management policy continues to prefer closed-canopy forests, many species characteristic for European lowland forests will become extinct. To restore declining or locally extinct species, canopy opening in abandoned coppices is urgently needed.

ACKNOWLEDGEMENTS

We thank J. Horák for historical vegetation samples, J. Danihelka for field support, M. Chudomelová for the help with species life-history traits and M. Chytrý for providing the dataset for forest species delimitation. We also thank the reviewers for useful comments.

The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC Grant agreement n° 278065. Additional funding was provided by grant IAA600050812 and long-term research project RVO 67985939, both from the Academy of Sciences of the Czech Republic.

Author contributions: M.K. conceived ideas, analyzed the data and led the writing. R.H. conceived ideas, collected the field data and contributed to the writing. P.S. conceived ideas and contributed to the writing.

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Chapter 3

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FIGURES

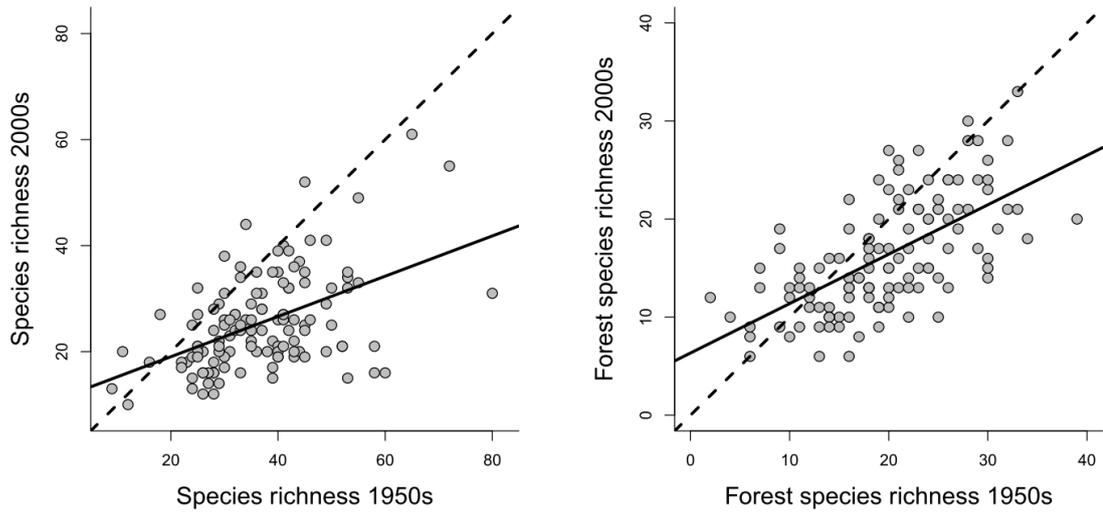


Figure 1 Relationship between species richness observed in 244 paired samples surveyed in the 1950s and the 2000s. The left diagram shows the relationship for all vascular plant species, the right diagram only for forest plant species (note different scales). The dashed line represents the null hypothesis of no change in species richness between surveys and the solid line is a linear relationship fitted to the data.

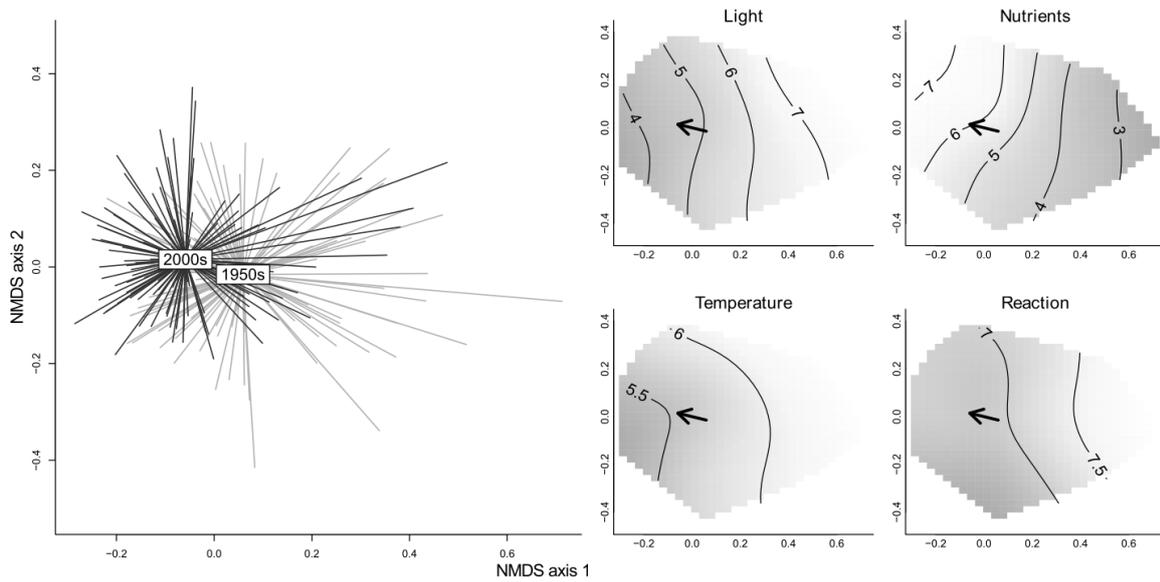


Figure 2 Non-metric multidimensional scaling of temporal change in the understory species composition. **Left:** Compositional turnover between 244 paired samples. Each spider connects individual samples with the average score for the 1950s (grey) and the 2000s surveys (black). The species composition in the 1950s was more heterogeneous than in the 2000s indicating taxonomic homogenization of the forest understory. **Right:** Smoothed surfaces of mean Ellenberg indicator values fitted into the NMDS space. The arrows show the direction of the compositional change connecting the centroids of the sampling periods. The species composition shifted toward flora of shade adapted and nutrient demanding species, while the species indication of temperature and soil reaction did not change.

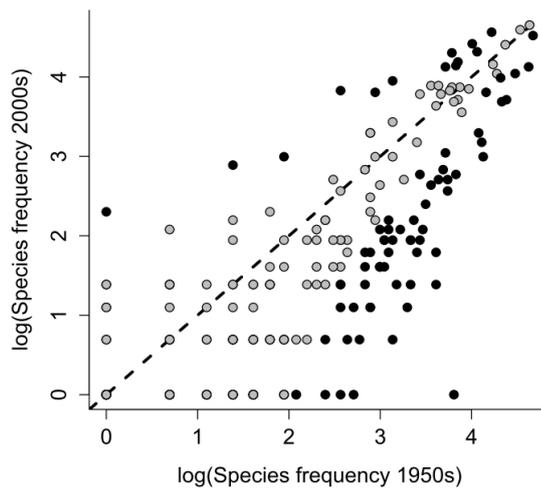


Figure 3 Relationship between species frequency in the 1950s and the 2000s. The dashed line separates species, which increased (above the line) or decreased (below the line). The black symbol marks species whose frequency changed significantly. Note that many species declined, while just a few increased.

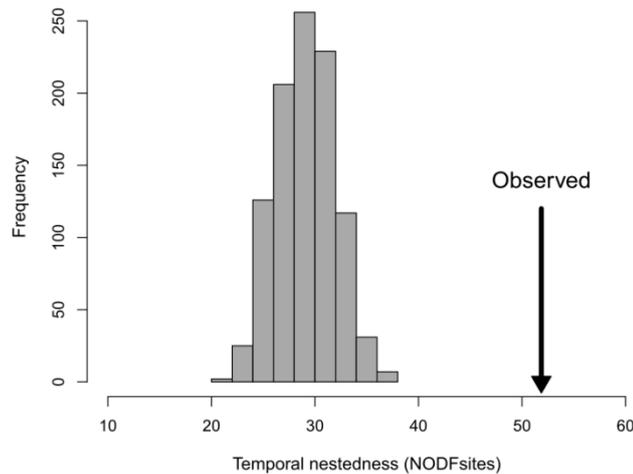


Figure 4 Comparison of the observed temporal nestedness and distribution of 999 nestedness values of species assemblages generated by random reshuffling of the survey period between paired samples. To observe such temporal nestedness by chance is highly improbable, therefore, species turnover was only a minor component of the community change and present assemblages are mainly impoverished subsets of the former ones.

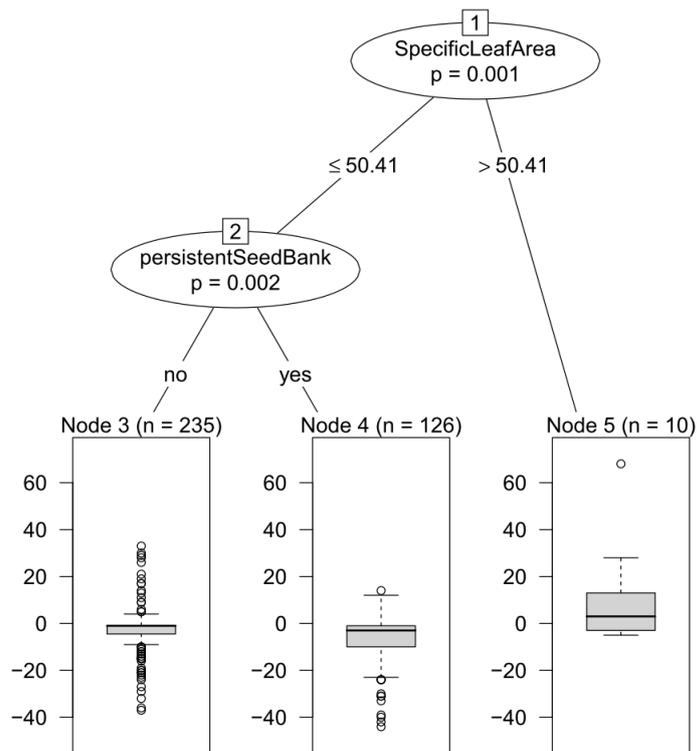


Figure 5 Life-history traits predicting species gains and losses displayed by conditional inference tree. In each split of the tree all species traits are tested and the trait which best discriminate between declined and increased species is selected. The procedure goes on until no trait significantly discriminate between species. The response variable (summarized as box-plots) is the difference in the number of plots occupied by each species in the 2000s and the 1950s. Values below zero indicate declining species and values above zero indicate expanding species. Each split of the tree is described by the life-history trait used at the split, the permutation-based significance of the split (P -value) and the trait values at which the split occurs. The number of species (n) is given at each terminal node.

SUPPORTING INFORMATION

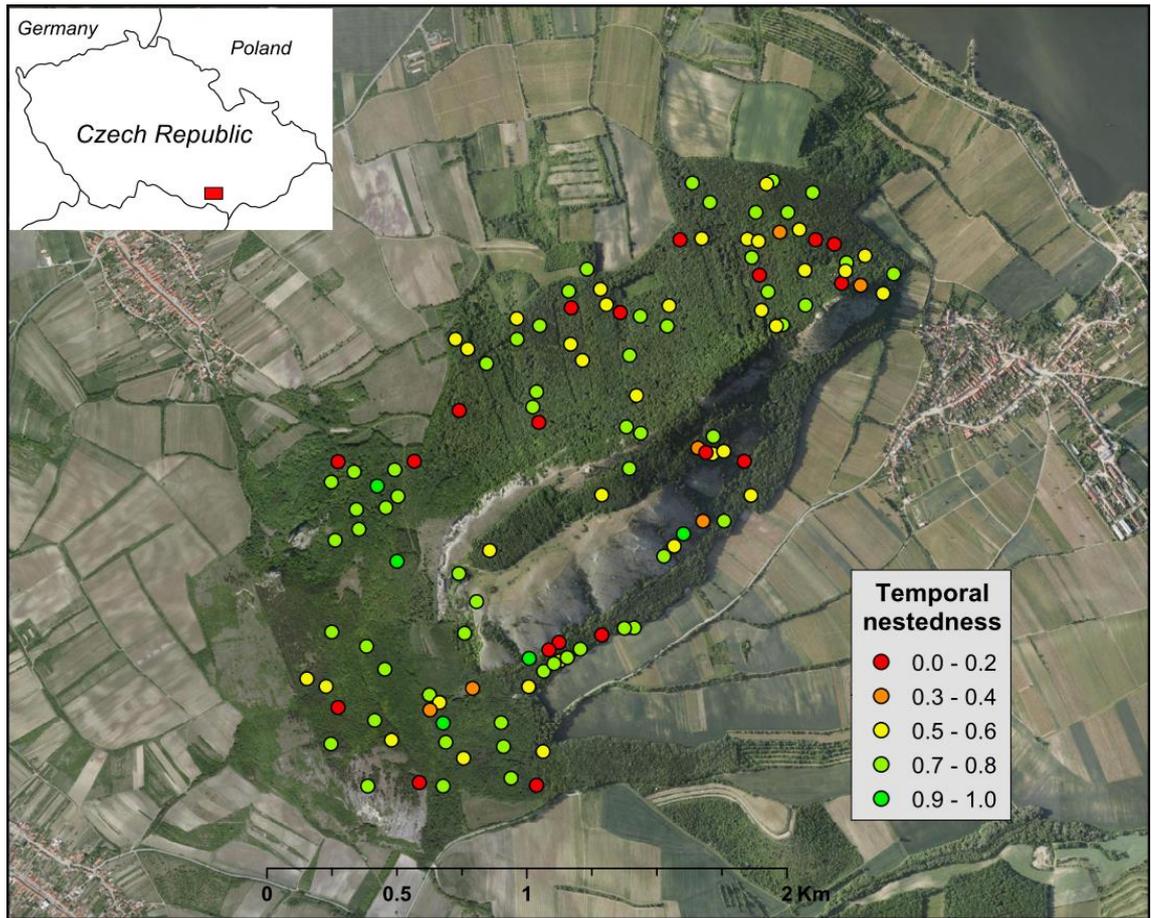


Figure S1 Map of Děvín Wood with temporal nestedness of individual plots.

Table S2 Species life-history traits used for prediction of species gains and losses.

Life-history trait	Source	Data type	Missing values (N/%)
CSR strategy	BiolFlor	categorical	6/2
Canopy height	LEDA	continual	81/22
Life form	BiolFlor	categorical	0/0
Life span	BiolFlor	categorical	0/0
Phenological phase	BiolFlor	ordinal	32/9
Persistent soil seed bank	LEDA	categorical	44/12
Seed weight	BiolFlor	continual	25/7
Seed number per shoot	LEDA	ordinal	126/34
Terminal velocity	LEDA	continual	130/35
Type of dispersal	LEDA	categorical	37/10
Vegetative propagation	BiolFlor	categorical	159/43
Reproduction type	BiolFlor	categorical	2/1
Pollen vector	BiolFlor	categorical	5/1
Fruit type	BiolFlor	categorical	5/1
Floral UV-reflection	BiolFlor	ordinal	141/38
Specific leaf area	LEDA	continual	65/18
Leaf dry matter content	LEDA	continual	80/22
Leaf persistence	BiolFlor	categorical	10/3

Table S3 Species that have significantly decreased (loser species) or increased (winner species) in frequency between the surveys. Species are sorted according to the number of plots in which they decreased or increased. Species with uncertain determination were merged. This is indicated in case of two related species with "+", in case of one or more species within a taxonomical aggregate with "agg.". Species nomenclature follows Kubát, K., Hrouda, L., Chrtek, J. Jr., Kaplan, Z., Kirschner, J. & Stěpánek, J. (eds.) (2002) *Key to the flora of the Czech Republic*. Academia, Prague, CZ.

Species	frequency 1950s	frequency 2000s	adjusted p-value
Loser species			
<i>Veronica vindobonensis</i>	45	1	0.002
<i>Carex muricata</i> agg.	62	20	0.002
<i>Clinopodium vulgare</i>	37	4	0.002
<i>Dactylis polygama</i>	102	62	0.002
<i>Alliaria petiolata</i>	37	6	0.002
<i>Campanula trachelium</i>	80	41	0.002
<i>Quercus petraea+robur</i>	61	24	0.002
<i>Hypericum perforatum</i>	27	3	0.002
<i>Rosa canina</i> agg.	76	40	0.002

Non-random extinctions in abandoned coppices

<i>Festuca rupicola</i>	28	4	0.002
<i>Epipactis helleborine</i>	42	13	0.002
<i>Carex michelii</i>	23	2	0.002
<i>Fragaria vesca</i>	46	16	0.002
<i>Hypericum hirsutum</i>	30	6	0.002
<i>Carpinus betulus</i>	59	27	0.002
<i>Lapsana communis</i>	31	7	0.002
<i>Hylotelephium maximum</i>	32	8	0.002
<i>Ulmus minor</i>	42	15	0.002
<i>Poa nemoralis</i>	88	57	0.002
<i>Securigera varia</i>	24	4	0.002
<i>Astragalus glycyphyllos</i>	28	7	0.002
<i>Brachypodium pinnatum</i>	28	7	0.002
<i>Ajuga genevensis</i>	13	0	0.002
<i>Euonymus verrucosa</i>	33	11	0.002
<i>Scrophularia nodosa</i>	15	1	0.002
<i>Cornus mas</i>	38	15	0.002
<i>Cornus sanguinea</i>	29	9	0.002
<i>Galium mollugo</i> agg.	40	17	0.002
<i>Valeriana stolonifera</i>	16	2	0.002
<i>Achillea millefolium</i> agg.	18	3	0.002
<i>Milium effusum</i>	18	3	0.002
<i>Taraxacum</i> sect. <i>Ruderalia</i>	35	14	0.002
<i>Teucrium chamaedrys</i>	21	5	0.002
<i>Fallopia convolvulus+dumetorum</i>	13	1	0.004
<i>Euonymus europaea</i>	10	0	0.004
<i>Campanula persicifolia</i>	22	6	0.004
<i>Poa angustifolia</i>	25	8	0.004
<i>Ranunculus polyanthemos</i>	20	5	0.004
<i>Torilis japonica</i>	20	5	0.004
<i>Bupleurum falcatum</i>	20	5	0.004
<i>Cirsium arvense</i>	23	7	0.004
<i>Lathyrus niger</i>	14	2	0.004
<i>Verbascum chaixii</i> ssp. <i>austriacum</i>	17	4	0.006
<i>Prunus mahaleb</i>	11	1	0.006
<i>Clematis vitalba</i>	41	21	0.006
<i>Melica nutans picta</i>	15	3	0.008
<i>Silene nutans</i>	8	0	0.008
<i>Veronica teucrium</i>	8	0	0.008
<i>Crataegus species</i>	21	7	0.008
<i>Dictamnus albus</i>	21	7	0.010
<i>Viola hirta+collina</i>	22	8	0.010
<i>Lotus corniculatus</i>	75	54	0.010
<i>Origanum vulgare</i>	7	0	0.012
<i>Arrhenatherum elatius</i>	7	0	0.012

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<i>Brachypodium sylvaticum</i>	7	0	0.014
<i>Carex digitata</i>	7	0	0.014
<i>Lonicera xylosteum</i>	17	5	0.014
<i>Fraxinus excelsior</i>	13	3	0.014
<i>Falcaria vulgaris</i>	18	6	0.016
<i>Festuca pseudovina</i>	11	2	0.018
<i>Pimpinella saxifraga</i>	22	9	0.018
<i>Sorbus torminalis</i>	6	0	0.018
<i>Euphorbia cyparissias</i>	6	0	0.018
<i>Rhamnus cathartica</i>	6	0	0.020
<i>Silene vulgaris</i>	6	0	0.020
<i>Hypericum montanum</i>	6	0	0.022
<i>Euphorbia epithymoides</i>	107	92	0.028
<i>Linaria vulgaris</i>	64	45	0.028
<i>Silene latifolia</i>	31	16	0.028
<i>Pyrethrum corymbosum</i>	20	8	0.028
<i>Medicago lupulina</i>	17	6	0.030
<i>Fumaria vaillantii</i>	8	1	0.034
<i>Elytrigia intermedia</i>	8	1	0.034
<i>Vicia dumetorum</i>	13	4	0.036
<i>Stachys recta</i>	13	4	0.036
<i>Melilotus officinalis</i>	5	0	0.040

Winner species

<i>Impatiens parviflora</i>	0	68	0.002
<i>Chaerophyllum temulum</i>	13	46	0.002
<i>Arum maculatum</i>	23	52	0.002
<i>Ulmus glabra</i>	44	74	0.002
<i>Galium odoratum</i>	68	96	0.002
<i>Galeobdolon montanum</i>	19	45	0.002
<i>Acer platanoides</i>	55	83	0.002
<i>Elytrigia repens</i>	0	12	0.004
<i>Convolvulus arvensis</i>	4	18	0.004
<i>Viola odorata+suavis</i>	1	10	0.008
<i>Parietaria officinalis</i>	41	62	0.012
<i>Pulmonaria officinalis</i>	7	20	0.020
<i>Acer pseudoplatanus</i>	47	66	0.024
<i>Omphalodes scorpioides</i>	46	63	0.026
<i>Asarum europaeum</i>	58	75	0.040

Appendix S1 The definition of forest plant species and the method used for their delimitation.

We derived a national list of forest plant species through the analysis of an extensive dataset of 20467 relevés representing a stratified selection from Czech National Phytosociological Database and covering the whole vegetation variability of the Czech Republic (detailed description can be found in Chytrý et al. 2005). We divided the relevés into forest (N = 3134) and non-forest vegetation types according to the classification given in Table 1 in Chytrý et al. (2005). We excluded 1054 relevés from EUNIS habitat types E5.2, F2, F3, F9.1, F9.2, G5, as these habitats represent a transition from forest to non-forest vegetation. Furthermore, we excluded all tree and shrub species and removed insufficiently covered species with less than 10 occurrences within the dataset. Even after this reduction, our final dataset included 19413 relevés with 1262 plant species.

With this dataset, we tested if the proportion of plots occupied by each species is significantly different between forest and non-forest plots. We used permutation test with 999 permutations implemented in the *indispecies* package for R (De Cáceres & Legendre 2009). We regarded all 268 species with significantly ($p < 0.05$) higher frequency in forests as forest species. The resulting national list of forest plant species can be obtained from the first author.

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- De Cáceres, M. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574.

Appendix S2 R script used for calculation of Temporal Nestedness Analysis.

```
##### This script calculates TEMPORAL NESTEDNESS ANALYSIS (TNA) as
described in

# Kopecký M., Hédli R. & Szabó P. (2012) Non-random extinctions
dominate plant community changes in abandoned coppices. Journal of
Applied Ecology.

# It was written by Martin Kopecký as an illustration of the
proposed method during July 2012.
# It is not computationally efficient or elegantly written and I
make no claims that it will work with your data.
# Any comments or suggestions are welcomed at ma.kopecky@gmail.com

#####

# set your working directory

setwd("YourWorkingDirectory")

# load needed libraries

library(vegan)
library(permute)

# load your data matrix with species as columns and samples as rows
# the script assumes that your data are temporally sorted paired
samples (e.g. Plot_1.old, Plot_1.new, Plot_2.old, Plot_2.new, ...)

data.spec <- read.csv2("YourData.txt", row.names=1)

data.pa <- data.spec

data.pa[data.pa>0] <- 1
  # convert species cover-abundance data into presence-absence
  data

pairs <- 122
  # Number of temporal pairs of plots in the analyzed data set

### This loop calculates NODFsites measure for each temporal pair

NODFsites <- rep(1, pairs)

for(i in seq(1, (2*pairs), 2)) {

  print(i)

  data.pairs <- data.pa[i:(i+1),]
  colS <- colSums(data.pairs)
  data.pairs <- data.pairs[colS > 0]

  NODF <- nestednodf(data.pairs, order = F)
```

```

# uses function nestednodf() from vegan package, see vegan help
for details

NODFsites[i]<- NODF$statistic[[2]]
# extracts NODFsites from the nestednodf() output
}

# produce vector of NODFsites for each temporal pair of plots
NODFsites.pairs <- NODFsites[seq(1,2*pairs,2)]

# calculate temporal nestedness (i.e. mean NODFsites) for the whole
data set

TemporalNestedness <- mean(NODFsites.pairs)

# store file with temporal nestedness of individual plots into
working directory

write.csv(NODFsites.pairs, file = "NODFsites.csv")

### This loop calculates Temporal nestedness value for N
(=permutations) assemblages
### generated by random reshuffling of survey periods between
samples from the same plots

permutations <- 999 # set the desired number of permutations

# create vector of Plot IDs for restricted permutation
PlotID <- rep(c(1:pairs), each = 2)

perm.meanNODFsites <- rep(0,permutations)

for(i in 1:permutations) {

  print(i)

  r.shuffle <- shuffle(2*pairs, permControl(strata = PlotID))
  # uses shuffle() function from permute package, see permute
  help for details

  data.temp <- data.pa[r.shuffle,]
  # create dataset with randomized survey periods

# this loop calculate the temporal nestednes for each randomly
created dataset

  NODFsites.perm <- rep(1,pairs)

  for(j in seq(1,(2*pairs),2)) {

    data.pairs.temp <- data.temp[j:(j+1),]
    colS <- colSums(data.pairs.temp)

```

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```
data.pairs.temp <- data.pairs.temp[cols > 0]

NODF.perm <- nestednodf(data.pairs.temp, order = F)
NODFsites.perm[j] <- NODF.perm$statistic[[2]]
}
perm.meanNODFsites[i] <- mean(NODFr.perm[seq(1,2*pairs,2)])
}

# calculate p.value as a proportion of nestednes values of randomly
generated assemblages
# which shows equal or higher temporal nestedness than was observed
in the real dataset

p.val <- (1+sum(perm.meanNODFsites >=
TemporalNestedness))/(1+permutations)

p.val

# calculate standardized effect size (SES), which measures the
number of standard deviations
# that the observed TN value differs from the mean TN value of the
randomly generated assemblages

SES = (mean(NODFsites.pairs) - mean(perm.meanNODFsites)) /
sd(perm.meanNODFsites)

SES
```

Long-term effects of alien herb invasion on forest plant communities

Martin Kopecký & Radim Hédľ

ABSTRACT

1. Even the most invasive species can be passengers rather than drivers of temporal change in biodiversity. To distinguish harmless from harmful invaders, one needs to know the long-term effects of their invasion. However, so far no suitable approach exists to do so.
2. We developed a novel approach comparing vegetation changes between invaded and uninvaded plots resurveyed after several decades. We used it to test the long-term effects of the highly invasive annual herb *Impatiens parviflora* on plant communities in a temperate broadleaved forest.
3. After five decades, *Impatiens parviflora* became the fourth most dominant understory plant. Despite massive invasion, it did not affect species richness, composition and beta diversity, nor disassemble species co-occurrence structure. Contrary to general belief, *Impatiens parviflora* did not threaten native plant communities.
4. *Synthesis.* Our data show that not all invasive species disassemble native communities. Therefore, the effects of individual invasive species should be tested with long-term data. The resurvey of historical vegetation plots can provide such data and our approach can be used to separate invasive species driving the changes from harmless invaders. Wider application of our approach can help to concentrate resources on the management of the most harmful invasive species.

Key-words: alien species impact, community disassembly, invasion ecology, native species richness, nestedness, non-native plant, plant species invasion, resurvey of semi-permanent plots, species composition, temperate forest

INTRODUCTION

The invasion of alien plant species can change native community structure resulting in biodiversity loss (Levine *et al.* 2003; Vilà *et al.* 2011; Powell, Chase & Knight 2011). However, even the most successful invaders can be passengers rather than drivers of change, having no direct effect on biodiversity (Didham *et al.* 2005; MacDougall & Turkington 2005; Davis *et al.* 2011). To concentrate limited resources on the management of the most detrimental invasions, we need to separate harmful invaders from harmless ones.

The effects of invasive species are usually evaluated only with snapshot data from spatially separated invaded and uninvaded plots (Chmura & Sierka 2007; Hejda, Pyšek & Jarošík 2009; Powell, Chase & Knight 2013). However, the assumption underlying this approach - that invaded and uninvaded plots are fully comparable - is hard to meet and the results can be seriously biased (Gurevitch & Padilla 2004; Didham *et al.* 2005; Stohlgren & Rejmánek 2014).

Another approach, replicated field experiments, can better reveal the true effects of invasive species (HilleRisLambers *et al.* 2010; Meffin *et al.* 2010). However, while most field experiments last only a few years (Strayer *et al.* 2006; Stricker, Hagan & Flory 2015), the effects of invasive species can lag decades behind the invasion (Crooks 2005; Bauer 2012). To disentangle harmful invaders from harmless ones, we therefore need to know the long-term effects of invasive species (Strayer *et al.* 2006; Gilbert & Levine 2013).

Long-term assessment is especially important in ecosystems with slow temporal dynamics, such as temperate forests (Rees *et al.* 2001; Woods 2007). Temperate forests are considered resistant against plant invasions as they are currently among habitats with the lowest proportion of alien plant species (Chytrý *et al.* 2008; Essl, Milasowszky & Dirnböck 2011). Despite low invasibility, several alien herbs have successfully spread across temperate forests (Martin, Canham & Marks 2009).

One of the most successful herbaceous invaders is *Impatiens parviflora*. During the last decades, *Impatiens parviflora* invaded both managed and natural forests across Northern Hemisphere (Lambdon *et al.* 2008; Kalusová *et al.* 2014). Such massive and rapid invasion led to the common belief that *Impatiens parviflora* reduces native plant diversity and modifies vegetation composition. Indeed, several observational studies reported lower species diversity and altered species composition in invaded stands (Obidziński & Symonides 2000; Chmura & Sierka 2007; Vervoort & Jacquemart 2012). These results sharply contrast with short-term experiments reporting no negative effects of *Impatiens parviflora* (Hejda 2012; Čuda *et al.* 2014). A long-term perspective is therefore needed to disentangle this conflicting evidence.

To explore the long-term effects of *Impatiens parviflora* on native plant communities, we developed a novel approach based on the idea that if *Impatiens parviflora* affects the invaded vegetation, long-term changes should differ between invaded and uninvaded plots. To test this, we resurveyed 122 semi-permanent forest plots after five decades. While *Impatiens parviflora* was absent during the original survey, it occurred in more than half of the plots during the resurvey. Between the surveys, many plant species became locally extinct and overall species composition homogenised (Kopecký, Hédli & Szabó 2013). Here we tested whether *Impatiens parviflora* was the driver or the passenger of these vegetation changes.

METHODS

Invasion of *Impatiens parviflora*

Impatiens parviflora DC. (Balsaminaceae) is an annual, shade-tolerant herb native in the Central Asia, where it grows along streams and forested mountain slopes (Coombe 1956). It was introduced and widely spread in Europe, Africa, North America and Asia. The first record in Europe is from 1831 from a botanical garden in Geneva (Coombe 1956). Since that time, it has got permanently established in wide range of forest types across Europe.

In the Czech Republic, *Impatiens parviflora* was first recorded in 1844 in a botanical garden in Prague, and around 1870 in the wild (Slavík 1995). However, the massive invasion into forests appeared much later, mainly in the 1970s and 1980s (Slavík 1995). Since then, *Impatiens parviflora* has become common and often dominates the herb layer in both natural and cultivated forests over the entire Czech Republic.

The successful invasion of *Impatiens parviflora* is probably related to late germination reducing danger of frost damage and to its fast growing seedlings (Skálová, Moravcová & Pyšek 2011; Skálová *et al.* 2013). However, competitively strong clonal species or dense understory vegetation can effectively prevent its establishment (Obidziński & Symonides 2000; Hejda 2012).

In invaded stands, *Impatiens parviflora* grows even in deep shade under dense tree canopy (Coombe 1956; Peace & Grubb 1982; Čuda *et al.* 2014). When exposed to full sunlight, *Impatiens parviflora* readily wilts, as it has high moisture content but only a limited root system (Coombe 1956). It is also sensitive to climatic extremes, especially late frosts (Coombe 1956; Skálová *et al.* 2011).

Study site

We studied the effects of *Impatiens parviflora* invasion in Děvín Wood (Fig. 1). Děvín Wood covers a limestone hill rising to 550 m a. s. l. from the flat lowlands in the south-eastern part of the Czech Republic. It is located in the meeting zone of the three biogeographic regions and provides a wide gradient of environmental conditions, resulting in species-rich assemblages on a relatively small area of 260 ha.

Climate is sub-continental, relatively warm and dry, with an average annual temperature of 9°C and average precipitation of 550 mm per year. Carbonate-rich soils vary from shallow lithosols and rendzinas on upper slopes to loamy-clay luvisols on the lower slopes. The forest vegetation reflects a gradient of substrate and topographic conditions, from dry open oak forests with *Quercus pubescens*, through mesic oak-hornbeam forests with *Carpinus betulus* and *Quercus petraea* to moist and shady ravine forests with *Tilia platyphyllos*.

Děvín Wood is an ancient forest which was managed for centuries as coppice-with-standards (Szabó 2010). Since late 19th century, coppicing was gradually abandoned and the last regular cut was done in the 1930s (Müllerová, Szabó & Hédli 2014). In 1946 the Wood was included in a non-intervention nature reserve. During the following decades, the forest became impoverished of many light-demanding species, vegetation composition shifted toward mesic and nutrient-demanding species and compositional variability among plots decreased (Hédli, 2005; Kopecký *et al.*, 2013).

The invasion of *Impatiens parviflora* into Děvín Wood started most probably in the 1960s. It was first recorded in Děvín Wood in 1963 (Neuhäusl & Neuhäuslová 1968). Since then, the *Impatiens parviflora* has become common.

Data collection

Between 1953 and 1964 (hereafter ‘the 1950s’), J. Horák sampled forest vegetation in Děvín Wood (Horák 1967). He distributed the plots according to the variability of natural conditions and vegetation types resulting in a mean plot density of ca. one plot per two hectares of the Wood (Fig. 1). In each plot, Horák recorded a complete list of vascular plant species, estimated their cover-abundance and assigned them to several vertically defined layers. In 2002–2003 (hereafter ‘the 2000s’), R. Hédl resurveyed Horák’s plots (Hédl 2005). To relocate the plots, Hédl used the plot positions marked on Horák’s original map scaled 1:10 000 supplemented with data about plot slope, aspect and local topography available from Horák’s field protocols.

Data editing

For the analyses, we used only vegetation samples originally recorded between June and September. The dataset represents 244 paired reference and resurvey samples from 122 plots distributed over Děvín Wood (Fig. 1). In the 1950s survey, *Impatiens parviflora* was completely absent. In the 2000s survey, *Impatiens parviflora* was recorded in 68 plots. The 1950s survey therefore recorded plant communities shortly before the start of the invasion in the 1960s, while the 2000s resurvey recorded plant communities decades after the invasion.

Since *Impatiens parviflora* is an annual herb, its invasion may affect only specimens growing in the forest understory. We therefore removed all specimens growing in the tree and shrub layers from the dataset. Because invasive herbs can affect also tree regeneration (Stinson *et al.* 2006; Flory & Clay 2010), we analysed all herbaceous species and tree and shrub saplings lower than 1 m.

Further, we removed *Impatiens parviflora* from the analysed dataset because we used its presence to classify plots as invaded. We also standardized plant nomenclature between the surveys and where species identification was uncertain, we combined taxa at the aggregate or genus level. We transformed the ordinal classes of the Zlatník (1950s survey) or the Braun-Blanquet (2000s survey) cover-abundance scales to species percentage cover. We converted the two lowest classes as 1 and 2% and all other classes as percentage midpoints of their respective classes.

After these treatments, the final dataset had 370 vascular plant species. 356 occurred in the 1950s survey and 227 in the 2000s survey.

Data analysis

To test the hypothesis that *Impatiens parviflora* invasion affected native plant communities, we compared temporal changes in species richness, evenness, composition and heterogeneity between invaded and uninvaded plots. In accordance with the literature, we hypothesized that *Impatiens parviflora* decreased species richness and evenness, increased species turnover and decreased compositional heterogeneity on the invaded plots.

These changes can however lag behind the invasion because plants can survive at unsuitable sites for decades (Kuussaari *et al.* 2009). In such cases, the effects of invasive species can be detected as changes in species co-occurrence structure (Sanders *et al.* 2003). Therefore, we also tested whether *Impatiens parviflora* modified the species co-occurrence structure of the invaded communities.

Species richness To test if the invasion affected species richness, we compared changes in the number of species between invaded and non-invaded plots. We tested the differences between invaded and non-invaded plots through a 2-sample permutation test implemented with the *oneway_test* function from the coin package (Hothorn *et al.* 2006) for R (R Core Team, 2015). This test is based on a conditional inference framework (Hothorn *et al.* 2006) and represents a non-parametric alternative to the classical t-test (Hollander & Wolfe 1999). The statistical significance of the difference between invaded and uninvaded plots was calculated by a Monte Carlo permutation test with 9999 permutations.

Species evenness To test if the invasion affected species evenness, we compared changes in species evenness between invaded and non-invaded plots. To calculate evenness, we used Pielou's index defined as Shannon–Weaver diversity index divided by the natural logarithm of species richness of the sample. We tested the differences between invaded and non-invaded plots through a 2-sample permutation test from the coin R-package (9999 permutations).

Species composition To test if the invasion affected species composition, we compared temporal species turnover on invaded and uninvaded plots. We calculated species turnover as percentage (Bray-Curtis) dissimilarity between the 1950s and the 2000s sample from the same plot. To reduce the effects of dominant species, we square-rooted species percentage cover data before the calculation (hereafter 'Bray-Curtis matrix'). We tested whether the species turnover differed between invaded and non-invaded plots with a 2-sample permutation test from the coin R-package (9999 permutations).

To visualize compositional changes on invaded versus non-invaded plots, we performed non-metric multidimensional scaling (NMDS) on Bray-Curtis matrix. We run global NMDS in two dimensions with 100 random starts using the *monoMDS* function from the vegan R-package (Oksanen *et al.*, 2015).

Compositional heterogeneity To test if the invasion affected compositional heterogeneity among plots, we compared differences in plot distance to multivariate centroids in the 1950s and the 2000s between invaded and uninvaded plots. The distance to multivariate centroid expresses how dissimilar the plot species composition is from the multivariate centroid of all plots (Anderson, Ellingsen & McArdle 2006). It is therefore the measure of compositional heterogeneity – the higher the mean dissimilarity of the plots to the multivariate centroid, the higher the heterogeneity of species composition on these plots.

For each plot, we first calculated its distance to the multivariate centroid of all samples from the 1950s and all samples from the 2000s. To calculate plot distances to multivariate centroids, we used the *betadisper* function from the vegan R-package applied to the Bray-Curtis matrix. To get the temporal change in distance to centroid for each plot, we subtracted plot distances to centroids in the 1950s and the 2000s. Finally, we tested whether these changes differ between invaded and non-invaded plots through a 2-sample permutation test from the coin R-package (9999 permutations).

Species co-occurrence structure To test the hypothesis that *Impatiens parviflora* disassembled the invaded communities, we compared temporal changes in species co-occurrence between invaded and uninvaded plots (Sanders *et al.* 2003). As a measure of species co-occurrence, we used the

$NODF_{species}$, which quantifies how often less frequent species are found in subsets of sites where more frequent species occur (Almeida-Neto *et al.* 2008).

To get the temporal change in species co-occurrence (change- $NODF_{species}$) on invaded plots, we first calculated the $NODF_{species}$ for that subset of plots from the 1950s survey which were later invaded by *Impatiens parviflora*. Then, we calculated the $NODF_{species}$ for the same set of plots from the 2000s resurvey. Finally, we subtracted the $NODF_{species}$ of the 1950s subset from the $NODF_{species}$ of the 2000s subset. To get the change- $NODF_{species}$ also on uninvaded plots, we repeated the same procedure for the uninvaded subset of plots.

To test the significance of the difference in change- $NODF_{species}$ between invaded and uninvaded plots, we compared the observed difference to the null distribution. To calculate the null distribution, we randomly shuffled pairs of old and new samples among invaded and uninvaded plot subsets. After each reshuffling, we recalculated the change- $NODF_{species}$ between randomly assigned invaded and uninvaded plots. We repeated the reshuffling procedure 999 times. Finally, we calculated the p-value as the proportion of null model values that were higher or equal to the observed one.

We reported the difference between the observed change- $NODF_{species}$ and the null distribution by standardized effect size (SES), which measures the number of standard deviations that the observed value differs from the mean value of the simulated assemblages. To calculate $NODF_{species}$, we used the *nestednodf* function from the vegan R-package. For the randomization, we used the *shuffle* function from the permute R-package (Simpson, 2013).

RESULTS

During fifty years, *Impatiens parviflora* became the fourth most dominant understory plant in Děvín Wood (Fig. 2). Surprisingly, this massive invasion did not affect long-term changes in species richness ($Z = -0.62$, p-value = 0.55) and evenness ($Z = 0.27$, p-value = 0.79; Fig. 3).

Moreover, the general pattern of vegetation change was similar on invaded and uninvaded plots (Fig. 4). The invasion did not increase species turnover ($Z = 0.77$, p-value = 0.44) and did not decrease compositional heterogeneity among invaded plots ($Z = -0.46$, p-value = 0.65; Fig. 5)

Impatiens parviflora did not disassemble invaded communities, either. The change in species co-occurrence structure was comparable between invaded (change- $NODF_{species} = -9.22$) and uninvaded (change- $NODF_{species} = -6.48$) plots and the difference between invaded and uninvaded plots was not statistically significant (SES = -1.08, p-value = 0.18)

DISCUSSION

***Impatiens parviflora*: driver or passenger of vegetation change?**

The massive invasion of *Impatiens parviflora* has led to the widespread belief that it threatens native plant communities. However, we did not find any evidence that it affects species diversity or composition even after decades following invasion.

Our findings thus contradict several observational studies, attributing lower diversity and different species composition on invaded plots directly to *Impatiens parviflora* (Obidziński & Symonides 2000; Chmura & Sierka 2007; Vervoort & Jacquemart 2012). However, these studies were based on temporally non-replicated, 'snapshot' data. Other factors than *Impatiens parviflora* could

be responsible for the observed differences between invaded and uninvaded plots and snapshot data do not allow for the separation of these factors from the direct effects of the invasion (Gurevitch & Padilla 2004; Didham *et al.* 2005; Stohlgren & Rejmánek 2014).

To overcome limitations of temporally non-replicated observational studies, we compared *temporal changes* between invaded and uninvaded plots. While the reference survey captured plant communities before the invasion, the resurvey captured them after decades following the invasion. If the invasive species really disassemble local communities, temporal changes should differ between invaded and uninvaded plots. However, this was not a case. We therefore concluded that *Impatiens parviflora* was a passenger, not the driver of vegetation change.

This conclusion is supported by several experimental studies. In a one-year experiment, the weeding of *Impatiens parviflora* did not increase species richness on invaded forest plots (Hejda 2012). In a replicated field experiment lasting three years, *Impatiens parviflora* was not even able to outcompete its native congener *Impatiens noli-tangere* (Čuda *et al.* 2014). The two species occupy partly different niches and their competition in mixed stands is probably limited (Godefroid 2010; Čuda *et al.* 2014).

Did *Impatiens parviflora* find an unoccupied niche?

In forests, *Impatiens parviflora* quickly colonizes patches with disturbed soil and can therefore be considered an indicator of anthropogenic disturbance (Obidziński & Symonides 2000; Chmura & Sierka 2006, 2007). However, we found that after establishment and subsequent population increase, *Impatiens parviflora* did not outcompete native species. It seems that *Impatiens parviflora* is able to quickly utilize the available resources and to persist within the site when established, but without negative effects on other plant species.

To explain this observation, we propose two hypotheses. The first hypothesis suggests that *Impatiens parviflora* filled an unoccupied temporal niche critical for its regeneration. In central European forests, *Impatiens parviflora* use a relatively short temporal niche between the development of spring and summer vegetation aspects (Piskorz & Klimko, 2002, Piskorz, 2005). In Děvín Wood, the spring aspect lasts from March until April and is characterized by a luxuriant cover of flowering geophytes, such as *Corydalis* spp., *Galanthus nivalis*, *Anemone ranunculoides* or *Adoxa moschatellina*. *Impatiens parviflora* is not visible until late April and develops from seed only after that period. At this time, species of the full summer aspect are already present but have not yet developed much vegetative biomass. These species, most notably *Galium odoratum*, *Mercurialis perennis*, *Galeobdolon montanum* and *Melica uniflora*, start to dominate the understory vegetation from June to August. The time window from May to June is therefore characterized by the fast development of *Impatiens parviflora*, which quickly accumulates resources to produce flowers (from May to September) and seeds (July to September) to be able to regenerate the next year.

The second hypothesis suggests that the invasion potential of *Impatiens parviflora* is suppressed by water stress. Although *Impatiens parviflora* is the most tolerant to low soil moisture from all three *Impatiens* species present in the Czech Republic (Skálová *et al.* 2013; Čuda *et al.* 2014), many forest sites are simply too dry for this species. In Děvín Wood, *Impatiens parviflora* invaded plots that had significantly higher soil moisture than uninvaded plots (Supporting Information Notes S1). Seasonal drought can therefore be a limiting factor, preventing further invasion in drought-prone sites. Soil moisture can drop fast already in May in the subcontinental climate of Děvín Wood (unpublished measurements) and *Impatiens parviflora* is among the first species to wither and die off

after rainless periods lasting two weeks and longer. In the future, *Impatiens parviflora* may even withdraw from the invaded forests if precipitation frequency shifts and early summer drought becomes more frequent due to ongoing climate change.

Not all invasions are harmful

The widespread belief that alien invasion will necessarily result in biodiversity loss is closely connected with the theory that species communities are saturated (Sax & Gaines 2008; Martin *et al.* 2009). According to the theory, when an invasive species enters a saturated community, the species co-occurrence structure and species diversity should change (Mac Arthur & Wilson, 1967).

However, saturated plant communities are more of a myth than reality (Stohlgren *et al.* 2008; Harmon & Harrison 2015). Our results fully support this opinion, as non-native *Impatiens parviflora* simply joined the community and did not modify its structure. In other words, the establishment of a new species does not necessarily result in community reorganisation and subsequent species extinction (Sax & Gaines 2008). Currently we do not know how typical this scenario may be. Our results could be specific for our species or study system. Nevertheless, a recent analysis of native and alien plant species from Great Britain showed that this scenario could actually be much more common than previously thought (Thomas & Palmer 2015). To provide more efficient management of invasive species, individual species impact assessment is needed (Hulme *et al.* 2013; Blackburn *et al.* 2014). To provide this assessment, one needs to complement short-term experiments with a long-term perspective.

Long-term perspective through vegetation resurvey

A long-term perspective on the effects of invasive species is essential for the prediction of future biodiversity. The crucial limitation to this perspective is the availability of suitable data (Strayer *et al.* 2006). In this paper, we showed that the resurvey of historical vegetation plots can provide an assessment of the long-term effects of invasive species. Vegetation resurveys are increasingly used to explore temporal changes in species diversity and composition and their potential drivers (Verheyen *et al.* 2012; Vellend *et al.* 2013; Kopecký & Macek 2015).

Our study highlighted the so far overlooked potential of vegetation resurveys for the assessment of the long-term effects of invasive species. As we showed, data from vegetation resurveys often capture plant communities before and after invasion and can serve as natural long-term experiments. While literature is stacked with studies exploring short-term and often transient effects of plant invasions, the studies of long-term and probably persistent effects are extremely scarce (Dostál *et al.* 2013; Stricker *et al.* 2015).

We think our approach can be used to partly fill this knowledge gap. Suitable data from many vegetation resurveys are at hand and the amount of such data is already impressive (Verheyen *et al.* 2012; Vellend *et al.* 2013). Therefore, we encourage researchers to adopt our approach and use vegetation resurvey for the assessment of the long-term effects of invasive species.

CONCLUSION

In contrast with the generally negative perception of invasive species, *Impatiens parviflora* is not a serious threat to the diversity and composition of native plant communities. Our results thus support

the growing evidence that not all invasive species have negative effects (Davis 2003; Didham *et al.* 2005; Thomas & Palmer 2015). This underscores the immense importance of long-term, temporally replicated data allowing for the separation of harmful invasive species from harmless ones. The resurvey of historical vegetation plots originally recorded before invasion can provide such data. We therefore encourage other researchers to use a similar approach as we used here to differentiate between drivers and passengers of vegetation change. Such differentiation is badly needed to concentrate limited resources on the control of the most harmful invasions.

ACKNOWLEDGEMENTS

We thank J. Horák for providing us with his original field forms and J. Danihelka for his help during the resurvey. We thank Péter Szabó for language revision and useful comments. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC Grant agreement no 278065) and institutional project RVO 67985939.

Author contributions: M.K. conceived ideas, analysed the data and led the writing. R.H. conceived ideas, collected the field data and contributed to the writing.

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Chapter 4

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FIGURES

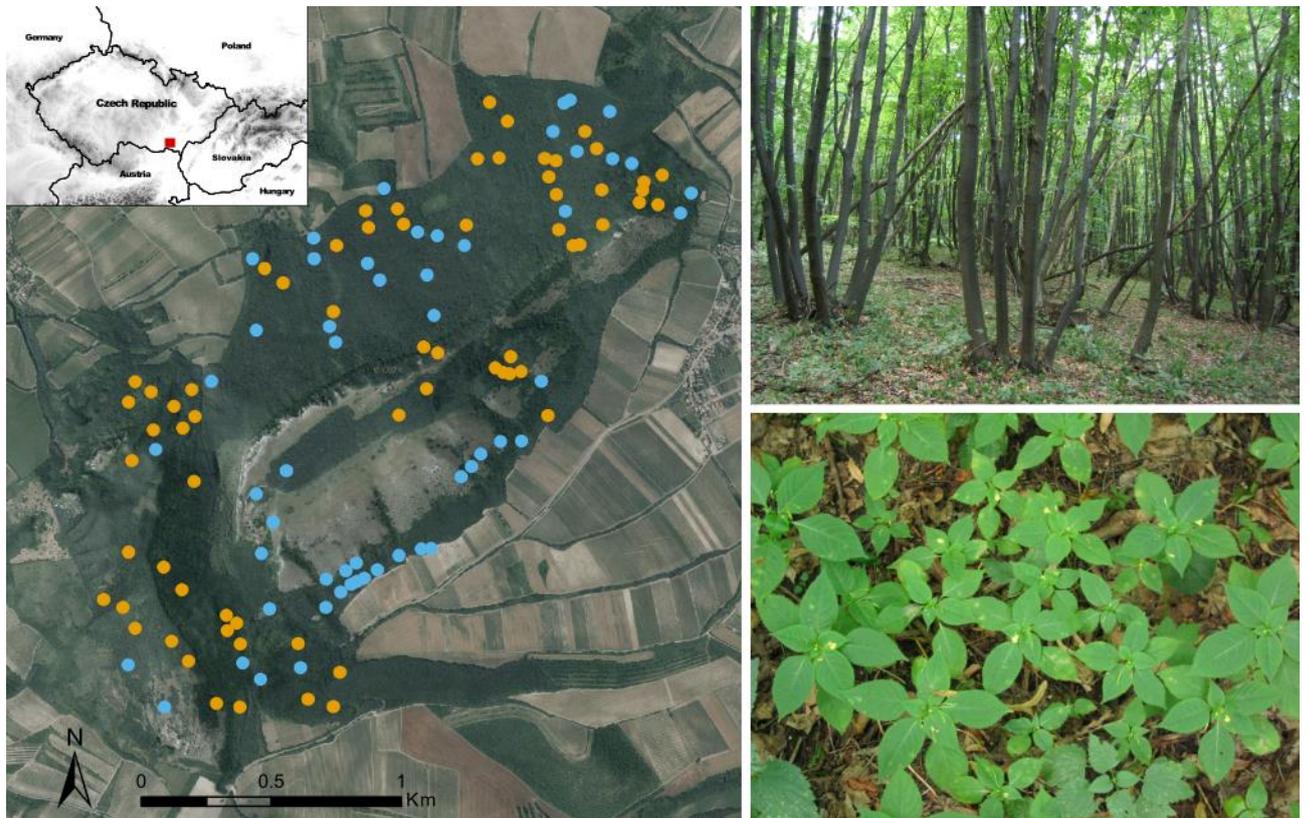


Figure 1 Location of Děvín Wood in the Czech Republic and the distribution of resurveyed plots within the Wood. The yellow dots represent plots invaded during the last 50 years by the alien shade-tolerant herb *Impatiens parviflora*, while the blue dots represent uninvaded plots. The photos taken during plot resampling in 2003 show the structure of the abandoned coppice (top right) and the invasive herb *Impatiens parviflora* growing in the understory (bottom right).

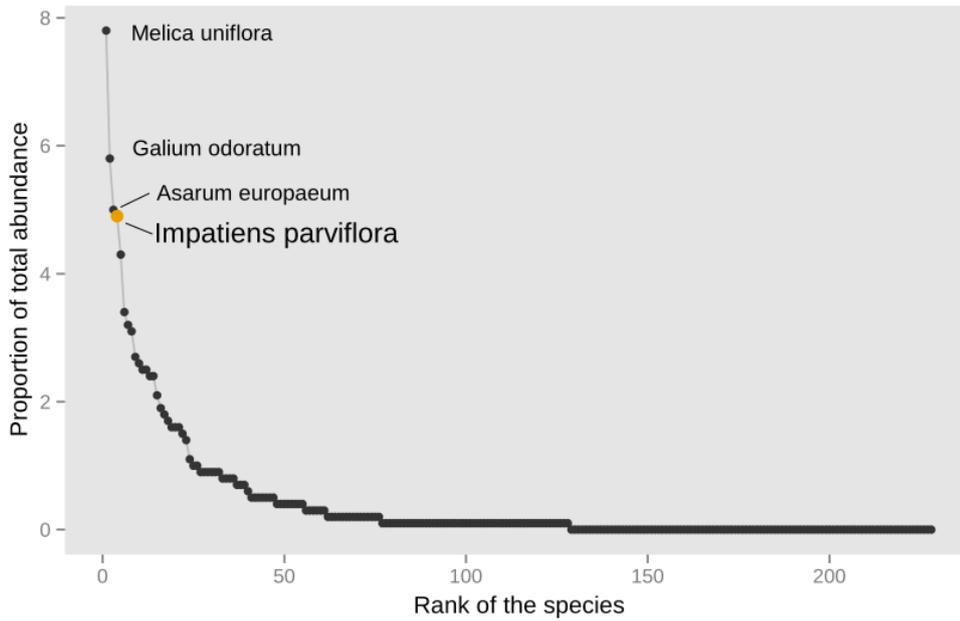


Figure 2 Rank-abundance curve showing the proportion of total abundance attained by individual understory species in the 2000s resurvey of 122 semi-permanent plots. While the invasive herb *Impatiens parviflora* was completely absent in the 1950s survey, it became the fourth most dominant understory plant in the 2000s resurvey.

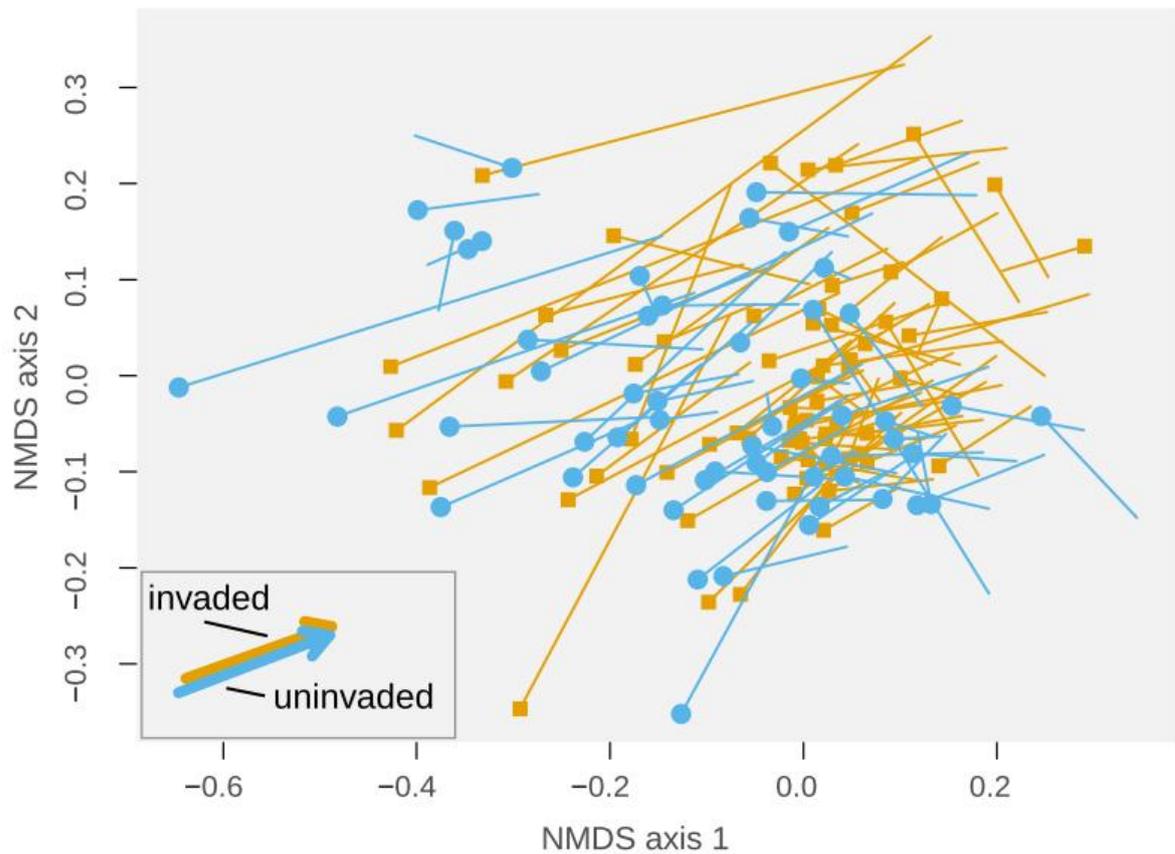


Figure 3 Invasion by the alien herb *Impatiens parviflora* did not affect long-term changes in forest vegetation. Species composition changed similarly on plots invaded by *Impatiens parviflora* (yellow squares) and on uninvaded plots (blue dots). The filled symbols represent samples from the 1950s survey, the lines connect samples from the same plot, and the ends of the lines represent samples from the 2000s resurvey. The thick arrows in the bottom left corner show temporal shifts in multivariate centroids of 68 invaded (yellow) and 54 uninvaded (blue) plots. The Non-Metric Multidimensional Scaling (NMDS) was run on a percentage (Bray-Curtis) dissimilarity matrix and the ordination was centred and rotated by principal component analysis.

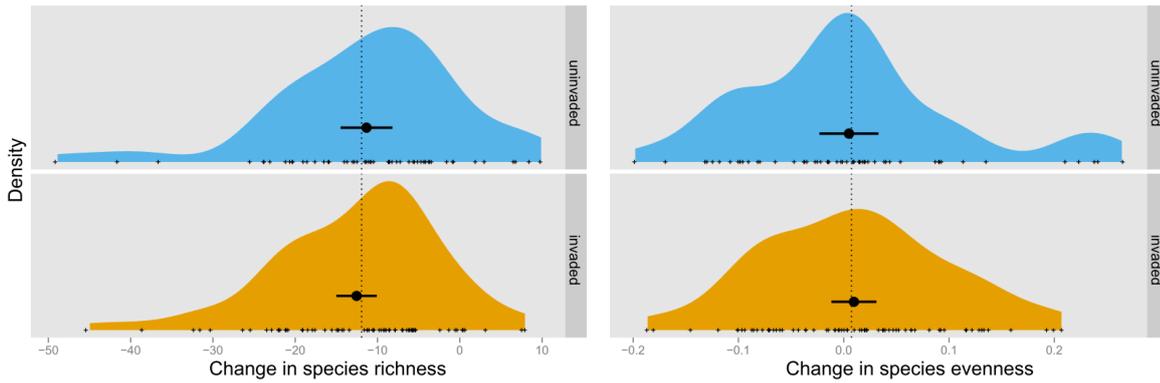


Figure 4 Invasion by the alien herb *Impatiens parviflora* did not decrease species richness and evenness on invaded plots. Ridge plots show the density distribution of temporal changes on invaded (yellow) and uninvaded (blue) plots, changes on individual plots (small black crosses), the mean \pm 95 % CI for each plot type (black dot and horizontal lines) and the overall mean (dashed line).

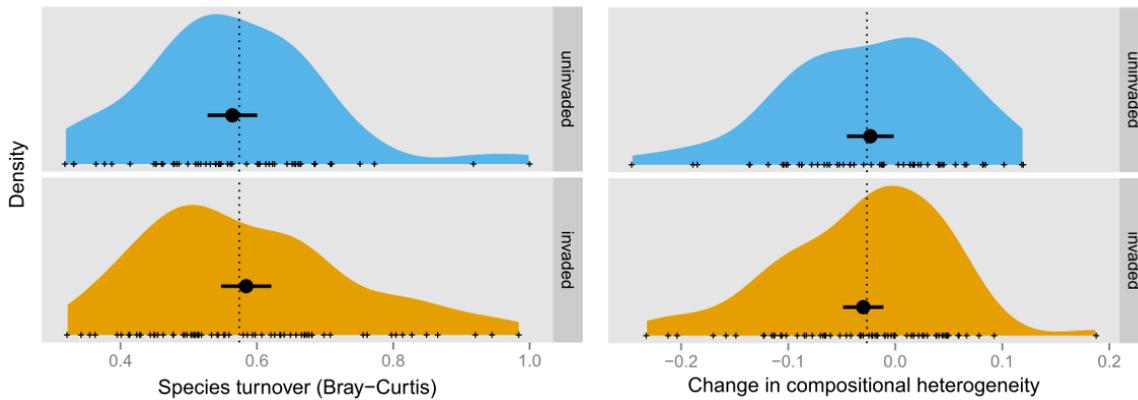
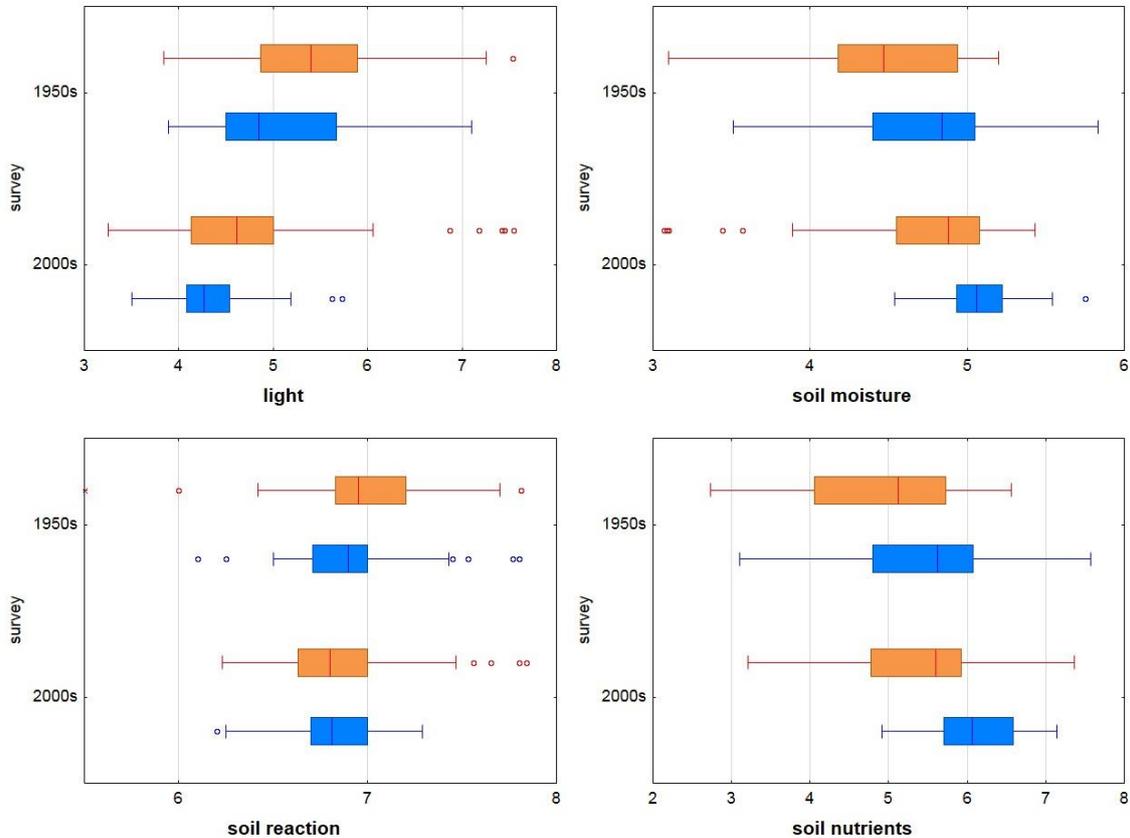


Figure 5 Invasion by the alien herb *Impatiens parviflora* did not increase species compositional turnover on invaded plots. It did not increase temporal changes in compositional heterogeneity among invaded plots, either. Ridge plots show the density distribution of temporal changes on invaded (yellow) and uninvaded (blue) plots, changes on individual plots (small black crosses), the mean \pm 95 % CI for each plot type (black dot and horizontal lines) and the overall mean (dashed line).

SUPPORTING INFORMATION

Appendix S1 Mean Ellenberg indicator values in plots uninvaded (orange) and invaded (blue) by *Impatiens parviflora*, in the 1950s survey and the 2000s resurvey. Medians, interquartile range, non-extreme range and outliers are displayed.



Environmental conditions in plots were calibrated using means of unweighted Ellenberg indicator values for herbaceous species present in the plots. All woody species were excluded. Testing the differences between the invaded and uninvaded plots (Kolmogorov-Smirnov two-sample test), all comparisons were significant at $p < 0.05$ except for light, where the two surveys had no significant differences between uninvaded and invaded plots. In the three other parameters, the patterns were as follows:

Light: invaded plots (blue) were significantly darker than uninvaded plots (orange) both in the 1950s and 2000s, and became generally darker between the surveys. This pattern confirms the knowledge of the ecology of the species – it prefers shady forest sites and probably avoids permanently sunlit places because of its sensitivity to desiccation.

Soil moisture: invaded plots were significantly moister than uninvaded plots in both surveys, and became generally moister in time. Based on studies comparing the species of *Impatiens* in central Europe, *I. parviflora* is the most tolerant to low soil moisture. However, it cannot stand too dry soils. It prefers microsites with topography retaining soil moisture and can be limited by seasonal drought.

Soil nutrients: invaded plots were significantly nutrient-richer than uninvaded plots and nutrient enrichment can be observed through time. *I. parviflora* is selective towards sites with high levels of nutrients, probably mainly nitrogen.

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