

Long-term shift towards shady and nutrient-rich habitats in Central European temperate forests

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Summary

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- Biodiversity world-wide has been under increasing anthropogenic pressure in the past century. The long-term response of biotic communities has been tackled primarily by focusing on species richness, community composition and functionality. Equally important are shifts between entire communities and habitat types, which remain an unexplored level of biodiversity change.
- We have resurveyed > 2000 vegetation plots in temperate forests in central Europe to capture changes over an average of five decades. The plots were assigned to eight broad forest habitat types using an algorithmic classification system. We analysed transitions between the habitat types and interpreted the trend in terms of changes in environmental conditions.
- We identified a directional shift along the combined gradients of canopy openness and soil nutrients. Nutrient-poor open-canopy forest habitats have declined strongly in favour of fertile closed-canopy habitats. However, the shift was not uniform across the whole gradients.
- We conclude that the shifts in habitat types represent a century-long successional trend with significant consequences for forest biodiversity. Open forest habitats should be urgently targeted for plant diversity restoration through the implementation of active management. The approach presented here can be applied to other habitat types and at different spatio-temporal scales.

Introduction

The world's ecosystems are experiencing unprecedented changes in biodiversity. These are observed not only as species losses (Pimm *et al.*, 1995) but also as changes in community composition (Dornelas *et al.*, 2014). The main drivers of these changes are habitat loss, overexploitation, invasive species, climate change and pollution (Pereira *et al.*, 2012). These drivers affect most taxonomic groups, including amphibians, insects and vascular plants (Hoffmann *et al.*, 2010; Dornelas *et al.*, 2014; Outhwaite *et al.*, 2022).

In temperate forests, studies of long-term changes in plant communities have revealed biotic homogenisation and an increase in nutrient-demanding species (Hédl *et al.*, 2010; Verheyen *et al.*, 2012; Prausová *et al.*, 2020). However, the magnitude of changes differs in individual sites. Some studies have found that nutrient-poor sites experience greater compositional

changes compared with mesophilous or nutrient-rich sites (Heinrichs & Schmidt, 2016; Dittmann *et al.*, 2018). This variability underscores the importance of long-term resurveys covering broad community and environmental gradients. Such studies can help determine how different factors, including climate and soil conditions, impact anthropogenic biodiversity changes (Perring *et al.*, 2018b; Vandvik *et al.*, 2020; Lynn *et al.*, 2021).

The main drivers of understory changes in temperate forest communities include nitrogen deposition, forest management and large herbivores (Bernhardt-Römermann *et al.*, 2015). However, none of the many factors driving ecosystem dynamics act independently, but rather in mutual and often complex interactions (Tylianakis *et al.*, 2008; Perring *et al.*, 2018b; for contrary evidence see Koerner *et al.*, 2023). Several studies have investigated the spatial variability of understory changes in the context of the interaction between nitrogen deposition and other factors. Nitrogen deposition was found to have a greater effect on species

composition on oligotrophic sites than on sites with higher fertility (Ewald *et al.*, 2013; Roth *et al.*, 2021). The historical context of management also plays a role, where a decrease in understorey species richness was observed on sites with former coppice management, while the opposite was found in forests historically managed as high forests (Perring *et al.*, 2018a).

Differences in the sensitivity of forest habitats to global change drivers have conservation implications. While climate change-induced drought is the main threat to beech forests in Europe (Martinez del Castillo *et al.*, 2022), oak and other open forest habitats are mostly threatened by the abandonment of traditional coppice management combined with atmospheric nitrogen deposition (Chudomelová *et al.*, 2017). Effective conservation of forest habitats therefore requires tailored strategies, in which a detailed understanding of habitat-specific vulnerabilities becomes crucial.

In order to understand long-term biodiversity changes at the level of biotic communities, most assessments focus on species richness (Vellend *et al.*, 2013; Dornelas *et al.*, 2014), more recently also including relative species abundance (Jandt *et al.*, 2022). Recent critical assessment of the reliability of time series data has shown that estimates of species richness change are sensitive to the combination of data sets of different origins, which can lead to erroneous results (Douda *et al.*, 2023; Valdez *et al.*, 2023). Compared with conventional approaches to assessing biodiversity change, here we bring a new perspective based on the classification of vegetation types according to their characteristic species composition. We analyse qualitative changes in plant biodiversity by taking into account changes in the assignment of samples to individual habitat types. This approach builds on a robust and widely used system of vegetation classification developed over the past century (Mucina *et al.*, 2016). An elaborate system for classifying vegetation into hierarchically arranged types provides an excellent framework for understanding changes in plant biodiversity. In addition to its scientific importance, this approach also has practical applications as the habitat level is often used as a framework in conservation policy and decision-making. In particular, the system of natural habitats that forms the backbone of the EU's Natura 2000 framework (Habitats Directive) directly follows the vegetation classification approach (Loidi, 1999; Evans, 2006).

We used a large, original, nationwide dataset of forest vegetation plots resurveyed on average after five decades. The plots represent a wide range of environmental conditions and forest types. We aimed to test our hypothesis that there was a long-term trend detectable as shifts between forest habitats. Based on evidence from existing studies in temperate ecosystems, we predicted that this trend reflects a succession towards more fertile and shady habitats.

Materials and Methods

Data source

We resurveyed 2292 vegetation plots in temperate forests in the Czech Republic. The plots cover a wide range of climatic and substrate gradients in the region. They are situated at elevations ranging from 145 to 1250 m above sea level (asl) with a median

of 399 m. The size of most plots is 400 or 500 m², which allows for a standardised record of the local diversity of the plant communities studied (Supporting Information Fig. S1). The plots are located mainly in ancient forests, which have had a continuity of forest land use since at least the mid-19th century (Hermy, 1999). However, nearly all the plots have been and still are influenced by human activities of various intensities. This also applies to nature reserves with former traditional management (often coppicing) and commercial forests with a rotation period of at least 80 yr or longer. The forests surveyed mostly represent natural to semi-natural vegetation. Clearings and young stands were not included.

Two sampling surveys of each plot were conducted to study the composition and structure of the plant community. The first sampling (baseline survey) took place mainly in the 1950s to 1970s (Fig. S1). The datasets included various sources and authors, but by far the largest source is the standardised forest typology monitoring plots carried out by today's Forest Management Institute (Ministry of Agriculture of the Czech Republic). The second sampling (resurvey) was carried out mostly by the authors of this study between 2002 and 2018. The average interval between the two surveys was 52 yr, mostly 45–60 yr. For the resurvey, plots were relocated using a combination of information from contemporary maps, site descriptions with local topography, tree species composition and occasionally the remains of soil sampling pits or paint markings on trees. The plots are therefore typically quasi (or semi)-permanent (Kapfer *et al.*, 2017). This approach is relatively robust in terms of locating historical vegetation plots (Kopecký & Macek, 2015; but see Verheyen *et al.*, 2018). All vascular plant species were recorded with an estimate of cover/abundance in each plot. Zlatník scale (Zlatník, 1953) was used for this estimation in the baseline survey and a similar Braun-Blanquet scale (Westhoff & van der Maarel, 1978) was used in the resurvey. Stand age was not recorded; therefore, a systematic change in stand age between the sampling periods cannot be ruled out.

Data analyses

Samples of plant communities from the historical survey and the resurvey were assigned to predefined vegetation types. In the first step, an automated algorithm developed for the Czech national vegetation survey was used (Chytrý & Tichý, 2018; Chytrý *et al.*, 2020a). All samples were classified into basic-level vegetation types, called associations (Chytrý, 2013). The classification is defined by the combination of diagnostic species groups, and sometimes by the dominance of a single species. Species groups include three or more species that are diagnostic for a particular vegetation association (see example in Methods S1). The proportion of directly classified samples that met the predefined criteria was similar in both the baseline and resurvey, totalling 609 (26.2%) and 571 (24.9%) samples, respectively. In the second step, all unclassified samples were assigned to vegetation types by calculating their compositional similarity to the already classified samples using the Frequency-Positive Fidelity Index (Tichý, 2005; Chytrý *et al.*, 2020a).

The classification yielded 45 vegetation associations. Due to the hierarchical nature of the classification system, the next highest category, vegetation alliance, was used (Table 1). The resulting 15 alliances are directly compatible with the European EUNIS Habitat Classification (Chytrý *et al.*, 2020b). Alliances with <60 samples and nonforest vegetation were merged into a single group (Table S1). Three thermophilous oak forest alliances were also merged into one group. The final dataset includes eight groups, representing the main forest habitat types in the region (Table 1). All analyses were performed using JUICE software, v.7.1 (Tichý, 2002).

To assess the nature of habitat change, we used six complementary approaches:

(1) The number of samples classified to individual habitats was compared between the baseline and resurvey to evaluate the changes in the representation of habitat types. Habitat stability was estimated based on the proportion of samples with unchanged classification. Increase or decrease was calculated separately for each habitat type as the proportion of samples classified as a different habitat in the resurvey compared with its counterpart in the baseline survey and tested for significance by McNemar's chi-squared test.

(2) To visualise changes in plot classification over time, a chord diagram was constructed using the R `CHORDDIAG` package (Flor, 2019). Only actual transitions were considered, and the proportions of transitions for each habitat were standardised to account for differences in their frequency.

(3) To evaluate the change in the habitat distinctiveness, we used the list of diagnostic species for each corresponding vegetation alliance from Chytrý & Tichý (2003). For thermophilous oak forests, we selected diagnostic species from all three corresponding alliances. For each sample, we recorded the presence of all diagnostic species associated with each habitat type, regardless of

sample classification. We then calculated the proportion of diagnostic species relative to all species in each sample and compared them between the two surveys using a two-sample Wilcoxon test with Bonferroni adjustment.

(4) Habitat similarities in species composition and individual temporal changes were illustrated by nonmetric multidimensional scaling (NMDS). A matrix of Bray–Curtis dissimilarities was used, with cover data square-root transformed and standardised using Wisconsin double standardisation. To maximise variance along the first ordination axis, principal component analysis was used to centre and rotate the two-dimensional configuration with the lowest stress after 100 random starts. To assess whether the change in NMDS scores along the first and second NMDS axes was significant, we compared plot positions in the baseline and resurvey using the paired Approximative two-sample Fisher–Pitman permutation test with 99 999 permutations. The calculations were done using the `metaMDS` function from the `VEGAN` package (Oksanen *et al.*, 2020) and the `oneway_test` function from the `COIN` package (Hothorn *et al.*, 2006) in R, v.4.3.0 (R Core Team, 2023).

(5) To explore whether there was a shift from nutrient-poor and open habitats to fertile and shady habitats, ecological gradients of light availability and soil nutrients were approximated using Ellenberg indicator values (EIVs; Ellenberg & Leuschner, 2010). Unweighted means calculated for samples from species values were passively fitted to ordination space as a smooth surface through the `ordisurf` function from the `VEGAN` package. We used the EIVs only to facilitate ecological interpretations, as changes in EIVs are not suitable to be used as predictors of compositional changes.

(6) To assess the role of overstorey in the changes, we calculated differences in relative plot cover of 11 tree taxa dominant in the particular habitats between the resurvey and baseline pairs

Table 1 Forest habitat types used to assess long-term shifts in the biodiversity of forest plant communities.

Forest habitat type	No. of samples		Short description
	Baseline	Resurvey	
Acidophilous pine forests	100	74	Lowland open-canopy forests on extremely nutrient-poor, acidic soils of sandy and rocky substrates; dominated by <i>Pinus sylvestris</i> .
Acidophilous oak forests	358	251	Lowland open-canopy forests on acidic, nutrient-poor soils; dominated by <i>Quercus</i> spp.
Thermophilous oak forests	118	76	Lowland open-canopy forests on various types of well-drained substrates; dominated by <i>Quercus</i> spp.
Oak–hornbeam forests	447	326	Lowland semi-open to closed-canopy forests on mesic soils; dominated by <i>Carpinus betulus</i> and <i>Quercus</i> spp.
Ash–alder alluvial forests	102	168	Lowland to mountain semi-open to closed-canopy forests on moist to wet, nutrient-rich soils; dominated by <i>Alnus</i> spp., <i>Fraxinus</i> spp. and <i>Quercus</i> spp.
Ravine forests	100	130	Usually on steep slopes, most commonly in deep river valleys; dominated by <i>Acer</i> spp., <i>Fraxinus</i> spp., <i>Tilia</i> spp. and <i>Ulmus glabra</i> .
Eutrophic beech forests	271	355	Upland to mountain closed-canopy forests on well-drained, relatively nutrient-rich soils; dominated by <i>Fagus sylvatica</i> .
Acidophilous beech forests	549	633	Upland to mountain closed-canopy forests on acidic, well-drained, nutrient-poor soils; dominated by <i>Fagus sylvatica</i> .
Other vegetation types	247	279	Mixed category with different types of communities including spruce forests and nonforest vegetation.

The number of samples assigned to each habitat in the baseline and resurvey is given, totalling 2292 plots.

considering cover estimates (%). Plot pairs where a particular taxon was absent were excluded. The same statistical testing and visualisation as for the diagnostic species were used.

Results

The habitat type has changed in 42% of the plots, with large variation between the habitats (Fig. 1). The greatest loss was in the two habitats of Oak–hornbeam and Acidophilous oak forests, where only 21% and 24% of the plots, respectively, retained their original classification. By contrast, the most stable habitats were Ash–alder alluvial forest and the Ravine forest, where 89% and 71% of plots, respectively, remained in the same group. A complementary pattern was found in the proportion of plots gained by the habitats. Expressed as the number of plots gained in relation to the number of plots in the baseline survey, the largest gains were recorded in Ash–alder alluvial forests (75%) and Eutrophic beech forests (74%), while the opposite was true for Thermophilous oak forests (26%) and Acidophilous pine forests (42%). As a result, the highest net relative gain was observed for Ash–alder alluvial forests (+65%) followed by Acidophilous beech forests (+31%) and Ravine forests (+30%). The largest net relative declines were observed for Thermophilous oak forests (−36%), Acidophilous oak forests (−30%) and Oak–hornbeam forests (−27%). All the changes were statistically significant ($P < 0.05$), except for the mixed group (Other).

An analysis of individual-sample transitions between the forest habitats is presented in Fig. 2. Note that the order of habitats in the diagram follows a clockwise gradient of environmental conditions – to be described later. The analysis revealed a general

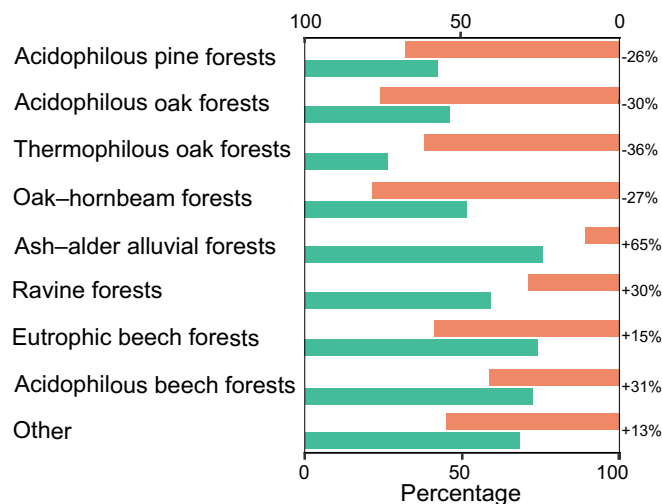


Fig. 1 Stability and change in forest habitats expressed as changes in plot classification between the two surveys. The red bars represent the proportion of plots classified in a different class in the resurvey, while the green bars represent the proportion of plots newly classified in that habitat type compared with the baseline survey. Percentages on the right indicate the net loss/gain of plots in particular habitats. Open-canopy forest habitats (four top ones) show lower stability and gains, while closed-canopy forest habitats (the next four) show higher stability and gains.

pattern of shift from open-canopy oak and pine forests (left, warm colours) towards shady forests dominated by beech and other broadleaved species (right, cold colours).

The decline in the proportion of diagnostic species indicates a decrease in the compositional distinctiveness of the four open-canopy forest habitats (Fig. 3). By contrast, the proportion of diagnostic species of the closed-canopy habitats remained relatively stable or even increased.

The NMDS ordination shows the position of the eight habitats along two main environmental gradients (Fig. 4). As indicated by the EIV for light and nutrients, the primary gradient reflects soil nutrients, while the second gradient corresponds to light availability, which can be interpreted as canopy openness. The four semi-open to closed-canopy habitats are situated in the upper part of the diagram, whereas the three open-canopy habitats are in the lower half of the diagram, with the oak–hornbeam habitats in an intermediate position. The soil nutrient gradient runs partially across the light availability gradient, with acidophilous forest communities of nutrient-poor substrates at the right end gradually transitioning to nutrient-demanding communities often on relatively base-rich soils at the left end.

While the shift along the first NMDS axis was not significant ($Z = -1.575$, $P = 0.115$), there was a significant shift along the second axis ($Z = 9.0407$, $P < 0.001$). The results indicate a clear change in species composition towards communities with more nutrient-demanding and shade-tolerant species (Fig. 4). This trend is not equally strong across the habitats. It is most pronounced in habitats characterised by open-canopy and low soil nutrients, that is Thermophilous and Acidophilous oak forests, and Acidophilous pine forests. By contrast, closed-canopy forests, including Ash–alder alluvial forests, Ravine forests and Eutrophic and Acidophilous beech forests, are relatively stable in terms of change along these gradients.

Changes in the relative plot cover of the main tree species (Fig. 5) corroborate the patterns identified by the analysis of habitat shifts. Trees that are dominant in declining habitats have decreased in cover (*Pinus sylvestris* and *Quercus* spp.). Instead, there was an increase in the cover of trees found in habitats that are increasing (*Fraxinus* spp., *Acer* spp., *Tilia* spp. and *Fagus sylvatica*). A decrease in two common conifer species (*Abies alba* and *Picea abies*) indicates other processes in addition to the main successional shift.

Discussion

Dark or open forests?

We found that the long-term directional changes in the biodiversity of temperate forest communities in Europe can be observed at the level of habitat types. Using over 2000 resurveyed forest plots, we observed a strong decline in oligotrophic open-canopy habitats and an increase in nutrient-rich closed-canopy forest habitats. This pattern paints a consistent picture of a successional shift among the eight broadly defined forest habitat types. However, the succession towards darker and more fertile forests was



Fig. 2 Chord diagram shows shifts of 961 individual plots between the baseline survey and the resurvey based on the classification into forest habitat. Plots that remained unchanged in classification are not shown. To standardise changes across the habitats, the width of each compartment was set to the same size, irrespective of the number of plots.

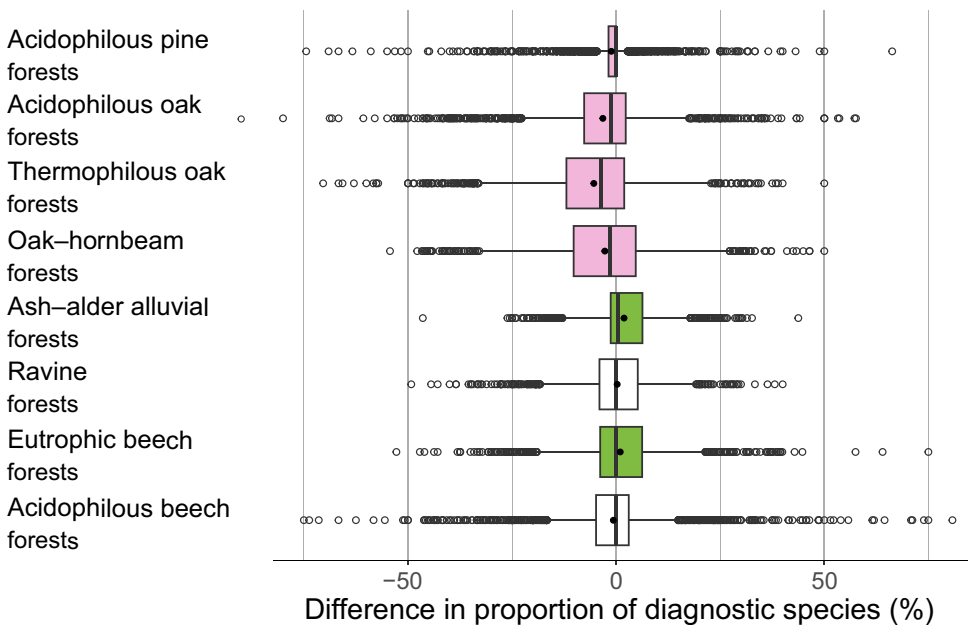


Fig. 3 Shift in floristic distinctiveness of eight forest habitats, measured as change in the proportion of diagnostic species between baseline and resurvey samples. Fills indicate significant ($P < 0.05$; two-sample Wilcoxon test with Bonferroni adjustment) increases (green) or decreases (pink). Boxplots show medians as thick lines and mean as points, 25–75% percentiles, 1.5 interquartile ranges and outliers.

remarkably more pronounced in habitats with low soil fertility and open canopies. The ecological succession and associated decline of communities with light-demanding and oligotrophic

plant species are in line with conclusions from other large-scale studies across various ecosystems (Tape *et al.*, 2006; Verheyen *et al.*, 2012; Dengler *et al.*, 2014; Wang *et al.*, 2015).

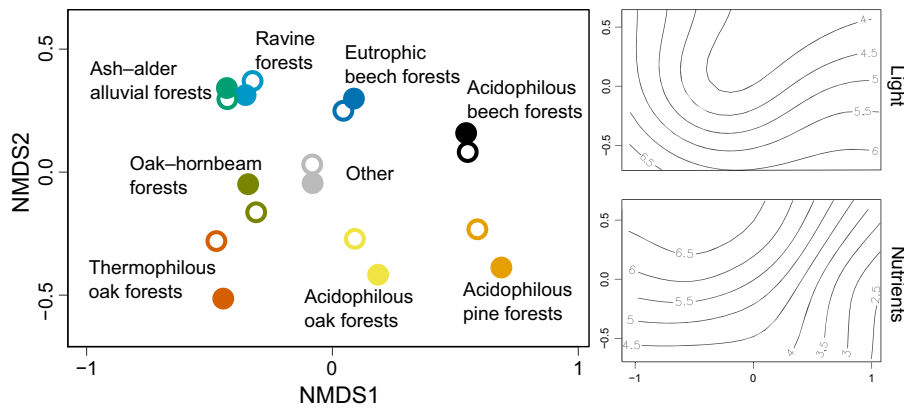


Fig. 4 Nonmetric multidimensional scaling (NMDS) diagram showing temporal shifts in different habitat types due to changes in species composition. Points show centroid positions from the baseline (solid circles) and resurvey (open circles) samples grouped by their baseline habitat type. The largest shifts were observed in open-canopy habitats dominated by oak and pine, where species composition shifted markedly towards more shade-tolerant and nutrient-demanding species. By contrast, closed-canopy beech forest or alluvial forest habitats experienced relatively little change. The main environmental gradients of soil nutrients and light availability, as indicated by plant community composition, are outlined in the two side diagrams, which show the projected isolines of mean Ellenberg indicator values (EIVs). The nutrient gradient runs along the first axis in acidophilous habitats and along the second axis in other habitats, from nutrient-poor soils (EIV for nutrients 2–4) to relatively nutrient-rich soils (> 6). The light gradient, with an opposite pattern along the axes to the nutrient gradient, ranges from shady (EIV for light < 4) to open-canopy forests (> 6).

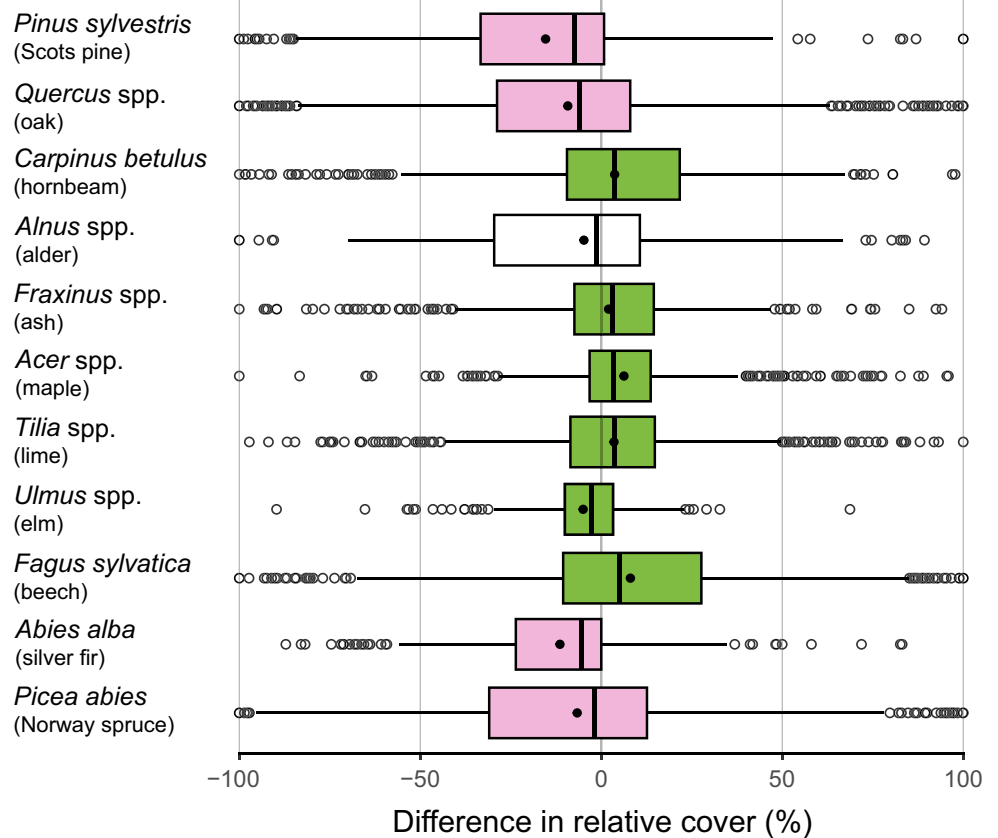


Fig. 5 Change in relative plot cover of the main tree taxa between baseline and resurvey plots. Shading indicates significant ($P < 0.05$; two-sample Wilcoxon test with Bonferroni adjustment) increases (green) or decreases (pink). Boxplots show medians as thick lines and means as points, 25–75% percentiles, 1.5 interquartile ranges and outliers.

Furthermore, the interpretation presented here provides an alternative perspective to the widely accepted ‘forest microclimate buffering’ hypothesis claiming that shady forests are the key to protecting forest plant biodiversity (De Frenne *et al.*, 2013;

Zellweger *et al.*, 2020). Our results point to an adverse aspect of increasing shade levels, namely a decline in biodiversity in formerly widespread open forest habitats. Our comparison across a wide range of forest habitats and a long gradient of

environmental conditions shows that shady forests are not the desired solution for biodiversity conservation, at least for plant communities. These habitats may be more resilient to climate change than the open-canopy forests, but the no less important value of open forests is their biodiversity, consisting of a wide range of species, including those from nonforest habitats (Roleček *et al.*, 2017).

In central Europe, beech forests are generally considered to be at low risk, while most pine- and oak-dominated forest types in the region are red-listed (Chytrý *et al.*, 2019). Our results are in line with these findings and existing scientific consensus that oligotrophic open forest habitats are among the most threatened ecosystems in Europe and are rapidly declining globally (Chudomelová *et al.*, 2017; Knott *et al.*, 2019; Alexander *et al.*, 2021). The decline is due to management changes and sometimes drought-induced shifts in dominant tree species (Rigling *et al.*, 2013; Pederson *et al.*, 2014). We argue that while protecting dark forest environment may be valuable in some cases, maintaining an open-canopy environment should be a priority in other habitats where biodiversity is of concern. The main challenge for biodiversity management is therefore to find ways of maintaining forests with open canopies and rich understories in the face of a changing environment. To do this, we need to understand the complex relationships between species richness and the availability of light and nutrients in a changing environment.

The puzzle of interacting factors

While we have clearly shown that open and nutrient-poor forest habitats and their understories are changing more rapidly in response to changing conditions compared with closed and nutrient-rich forests, the distinction between the two is far from straightforward. Previous studies in broadleaved forests have shown that sites with higher levels of light availability tend to experience more pronounced species turnover and a decrease in species richness over time (Verheyen *et al.*, 2012; Bernhardt-Römermann *et al.*, 2015). This observation can be explained by the gradual closure of the forest canopy, resulting in the displacement of light-demanding species. Instead, this is not as strong in areas with already closed canopies. This process has also been observed in eastern North America, where fire suppression has led to the replacement of oak and pine forests with maple forests (Rogers *et al.*, 2008; Nowacki & Abrams, 2015). In European studies, forests with light-demanding species experienced an increase in shade-tolerant species, and vice versa, leading to a process of biotic homogenisation (Kopecký *et al.*, 2013; Chudomelová *et al.*, 2017; Prach & Kopecký, 2018; Perring *et al.*, 2018a). Our study corroborates the above findings by showing that the formerly open-canopy oak and pine forest habitats and their light-demanding understorey communities have largely shifted towards closed-canopy forest types and have undergone a process of compositional homogenisation.

In addition to light conditions, site fertility is another key factor driving transitions between forest habitats. Previous research by Perring *et al.* (2018b) showed that across much of the nitrogen

deposition gradient in Europe, species composition shifted in favour of light-demanding species on sites with nutrient-poor soils, while the opposite trend occurred on sites with nutrient-rich soils. Our results appear to contradict this pattern, as declining oak and pine habitats generally occur on relatively poor soils. Perring *et al.* (2018b) observed that this pattern can be reversed on sites with lower levels of nitrogen deposition, but this does not explain the pattern observed in our study, as the sites are more in the middle of the European nitrogen deposition spectrum. It appears that initial light conditions were more important than soil fertility in determining the changes in our open-canopy habitats characterised by both light-demanding and oligotrophic species. This may be because the above study had a higher representation of lowland forests with shade-tolerant flora, which are more common in oceanic regions of Europe.

The impact of soil fertility on understorey changes related to nutrient requirements was also investigated in a large-scale study of over 100 000 forest vegetation plots in Europe (Ewald *et al.*, 2013). This study found that stands with initially low levels of nutrients, such as those dominated by pine and oak, experienced a relatively greater increase in nitrogen than initially more fertile stands, including those dominated by beech and alder. These findings are consistent with our results and several smaller-scale long-term studies (Heinrichs & Schmidt, 2016; Dittmann *et al.*, 2018; Prausová *et al.*, 2020; Roth *et al.*, 2022). Ewald *et al.* (2013) suggested that one of the main reasons for the contrasting patterns in soils with different trophic levels may be the recovery from long-term traditional management practices such as litter raking, grazing and coppicing.

Management and conservation implications

Other studies have shown that the transition from coppice to high forest management is a major factor in the changes observed in forest understories (Brunet *et al.*, 1996; Van Calster *et al.*, 2007; Hédli *et al.*, 2010). This is because resprouting capacity, and hence coppice potential, is highly variable between tree species: oak, lime and hornbeam are better at resprouting than beech or conifers (Buckley & Mills, 2015). In forests managed as coppice-with-standards, the coppiced underwood was historically composed of oak, hornbeam, lime, birch or poplar, whereas the standards of oak, beech and conifers formed the overstorey (Szabó *et al.*, 2021).

Other common traditional management types include animal grazing and litter raking (Bürgi *et al.*, 2013). These practices involved the removal of large amounts of biomass and frequent canopy disturbance, leading to nutrient uptake from soils and the creation of relatively open-canopy forests (Glatzel, 1991).

Paleoecological studies suggest that open forests, such as oak and pine forests, only persisted throughout the Holocene in central Europe due to human influence (Jamrichová *et al.*, 2013; Kuneš *et al.*, 2015). Therefore, the decline of plant species in open oligotrophic oakwoods may be exacerbated by succession from historically relatively intensively managed forests to modern long-rotation forests (Ewald *et al.*, 2013; Chudomelová *et al.*, 2017). Human impact at higher elevations (> 500 m asl)

has historically been lower in Europe (Fuller *et al.*, 1998; Kolář *et al.*, 2018), but in terms of vegetation change over the last century, the picture is generally similar to that of lowland forests (Prach & Kopecký, 2018).

Management changes may have led not only to the decrease in light-demanding species but also to the increase in nutrient-demanding species (Máliš *et al.*, 2021). Verheyen *et al.* (2012) found a negative correlation between changes in the frequency of nutrient-demanding and light-demanding species. This suggests that canopy closure and related factors, rather than nitrogen deposition itself, may be the major driver of long-term changes common to temperate understories.

Contrasting environmental and historical factors are clearly responsible for the distinct responses of different forest habitats. As a result, each habitat type faces specific threats resulting in shifts from one habitat to another. This has important implications for conservation and restoration management. Our study helped to identify changes in different forest habitats, which can help to select appropriate conservation measures. Therefore, the conservation of open and nutrient-poor forests should include appropriate forms of active management, such as coppicing, litter raking or grazing, to ensure their long-term survival (Kirby & Watkins, 2015).

Focus on habitat types and conclusions

We have shown that the classification of plant communities into habitat types provides valuable insights into long-term biodiversity changes. In contrast to the prevailing focus on species richness in biodiversity change assessment, our approach has the advantage that it does not explicitly use the number of species. This effectively overcomes the ‘biodiversity conservation paradox’, or the average net zero change in species diversity (Vellend, 2017; Jandt *et al.*, 2022). As recently shown by Valdez *et al.* (2023), repeated local-scale community records based on species richness are likely to be burdened with uncontrollable errors when attempting to detect biodiversity trends at larger spatial and temporal scales. Here, we present a qualitatively different approach that is independent of species richness. It considers a high level of biodiversity organisation, the community and habitat types, that has been almost completely neglected in global change research. Moreover, this approach has an important link to nature conservation policy at the European Union level, as the conceptually and factually identical way of defining habitat types forms the basis for the protection of natural habitat types under the Habitats Directive 92/43/EEC (Natura 2000).

A distinctive feature of forest plant communities is vertical layering. In European temperate forests, the canopy tends to be species-poor, often dominated by a single species. The understory can consist of hundreds of different species of herbs. The basic feature of our classification method is that it considers both the tree overstorey and the herbaceous understory. A key element is groups of co-occurring diagnostic herb species and their specific combinations that define individual communities (Chytrý *et al.*, 2020a). In our classification method, both understory and overstorey were used together and we did not

determine the separate contributions of each layer to the classification. Although changes in the overstorey may be the result of forest management decisions, we are not aware of significant management transitions in most of our study sites, so tree composition has remained largely similar over time.

Future research could build on this approach to explore the role of different driving factors in shaping forest biodiversity in different forest habitat types. Understanding these drivers is crucial to inform effective conservation strategies that can mitigate the negative impacts of anthropogenic pressures on forest ecosystems. Therefore, this study provides valuable insight into the variability of vegetation responses by showing that the general shift from nutrient-poor open forests to fertile and shady forests over the past five decades has not been uniform across all forest types. Nutrient-poor and open habitats showed marked changes, while shady and nutrient-rich forests have been more stable. The study’s approach can be applied to other habitat types and different spatio-temporal scales to better understand the impact of anthropogenic pressures on ecosystems.

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Competing interests

None declared.

Author contributions

RH, OV and MC planned and designed the research. OV and MM analysed the data. OV, RH and MC drafted the manuscript. OV, MC, MM, MK, JP, PP, PH, MJ, MS, JŠ, MV and RH conducted fieldwork and revised and edited the manuscript.

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Data availability

The data that support the findings of this study are available at [10.5281/zenodo.10575571](https://doi.org/10.5281/zenodo.10575571).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Histograms of the distribution of plots for plot sizes, elevation, sampling years and year ranges between baseline and resurvey.

Methods S1 Example of the classification system: formal definition of the *Quercetum pubescenti-roboris* association.

Table S1 Characteristics of habitat types.

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