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Vegetation dynamics and biodiversity conservation in floodplain forests of regulated rivers

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Vegetation dynamics and biodiversity conservation in floodplain forests of regulated rivers

Dissertation Thesis

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I hereby declare that the dissertation thesis entitled **Vegetation dynamics and biodiversity conservation in floodplain forests of regulated rivers** submitted for the degree Doctor of Philosophy in study programme Ecology, field of study Ecology is my original work guided by my supervisor. All sources of information, text, illustration, tables and images have been specifically cited.

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Anežka Holeštová

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Abstract

The thesis provides a complex insight into ongoing processes in Central European floodplain forests, one of the most threatened terrestrial ecosystems in the temperate zone. Floodplain forests are hotspots of biodiversity and provide many climate-related services of global importance. For these reasons, they have been identified as essential for climate change mitigation and key to human survival. The studies presented examine floodplain forests from a variety of perspectives, including investigating species dispersal patterns, describing long-term changes in plant community structure and identifying the driving factors behind them, and most importantly, suggesting an effective management strategy that would prevent the degradation of floodplain forests and restore their original biodiversity. A set of environmental factors other than climate change appeared to be more severe for floodplain forests, confirming their resistance to climate change. In particular, eutrophication and forest ageing were found to significantly affect both phenological guilds, i.e. spring and summer species, but in opposite directions. While summer species show negative effects of eutrophication and forest ageing, leading to their gradual decline, spring species show positive effects of these factors, manifested mainly in increasing abundance. A patchwork of different age classes, including old-growth forest stands, was found to ensure the conservation of both phenological guilds, however, in terms of site environmental conditions, which may dictate the use of other management measures, including traditional forest management practices and river revitalisation.

Abstrakt

Tato disertační práce poskytuje komplexní pohled na probíhající procesy v lužních lesích střední Evropy, jednoho z nejohroženějších terestrických ekosystémů v mírném pásu. Lužní lesy jsou považovány za hotspoty biodiverzity, přičemž zároveň poskytují mnoho s klimatem spojených služeb, a to globálního významu. Z těchto důvodů byly lužní lesy identifikovány jako ekosystémy zmírňující dopady klimatické změny, a proto klíčové pro přežití lidstva. Předložené studie zkoumají lužní lesy z různých perspektiv, zahrnující vzorce šíření rostlinných druhů podél vodních toků, popis dlouhodobých změn ve struktuře rostlinných společenstvech a identifikaci faktorů, které za těmito změnami stojí, a především návrh efektivní managementu, který by zabránil další degradaci lužních lesů a obnovil jejich původní biodiverzitu. Vliv environmentálních faktorů, jiných než klimatická změna, se ukázal být pro lužní lesy mnohem závažnější, což také potvrzuje rezistenci lužních lesů v tomto směru. Zejména eutrofizace a stárnutí lesů měly významný vliv na obě fenologické gildy, tedy jarní a letní druhy, ale v opačných směrech působení. Zatímco letní druhy vykazují negativní účinky eutrofizace a stárnutí lesů, což vede k jejich postupnému úbytku, jarní druhy vykazují pozitivní vliv těchto faktorů, projevující se hlavně v narůstající abundanci. Mozaika různých věkových tříd, zahrnující taktéž dlouhověké lesní porosty, byla shledána jako dostatečná pro zajištění ochrany obou fenologických gild, nicméně s ohledem na environmentální podmínky stanoviště, které mohou určovat použití dalších opatření.

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Part I

Introduction and Theory

Chapter 1

Thesis Preface

1.1 Research motivation

Personally, I consider floodplain forests one of the most beautiful forest habitats in the temperate zone. In spring, the colourfulness of the understorey vegetation is truly captivating. Therefore, it was disappointing to discover that in summer this colourfulness disappears and the whole area is covered by a single shade of green from a few plant species. Especially when you hear that these forests were originally so colourful in summer too. This phenomenon occurs in other forest habitats, such as oak or oak-hornbeam forests, where nature conservationists have already tried to introduce the appropriate intervention management measures to restore biodiversity. In the case of floodplain forests, however, nature conservationists seemed to have missed the boat.

Looking more closely, there were only a few studies that investigated specifically the temperate floodplain forests, focusing more on processes in natural floodplain forests and neglecting those affected by river regulation, the most widespread and probably most important cause of why the floodplain forests look the way they do today. I concluded that there is simply a lack of knowledge about what factors are behind the degradation of floodplain forests and what management approach should be chosen for their restoration, as non-intervention management typically applied in nature reserves is obviously not the way forward.

There are, of course, other reasons for restoring and protecting floodplain forests, as evidenced by their inclusion in *Nature Restoration Law*, a key element of the EU Biodiversity Strategy. This strategy sets binding targets to restore degraded ecosystems, in particular those with the most potential to capture and store carbon and to prevent and reduce the impact of natural disasters. Floodplain forests fulfil all these conditions. In fact, because of the climate-related services they provide, such as carbon storage or rainfall and temperature control, they have been identified as habitats that mitigate the effects of climate change and are therefore crucial to human survival.

It is for these reasons that I have decided to focus my attention on floodplain forests and their in-depth study. I sincerely hope that this thesis will help to prevent further degradation of these precious habitats.

1.2 Thesis structure

The thesis is divided into two parts and 10 chapters. **Part I** provides a theoretical background on floodplain forest characteristics and related processes. **Part II** consists of three published studies and one manuscript and discusses their interrelationship and contribution to conservation management strategies of floodplain forests in a temperate zone. The studies are listed in the following order:

- **Study I:** *Plant species over-occupancy indicates river valleys are natural corridors for migration*
- **Study II:** *Contrasting responses of forest phenological guilds to complex floodplain change*
- **Study III:** *Age heterogeneity in floodplain forest fragments promotes understorey plant diversity (manuscript)*
- **Study IV:** *Historical sampling error: A neglected factor in long-term biodiversity change research*

Chapter 2

Theoretical Background

2.1 Importance of floodplain forests

Although floodplain forests cover only a small percentage of the Earth´s total forest area, they provide many ecosystem services of global importance. Specifically, at the global scale, these include climate-related services such as carbon storage, atmospheric moisture production, rainfall and temperature control, and water purification (Prámová et al., 2012; Ellison et al., 2017; Potapov et al., 2017, Havrdová et al. 2023). These services then interact with other ecosystem services at regional and local scales, such as moderation of water temperature and regulation of nutrient supply, sedimentation and flooding (Creed and Van Noordwijk, 2018). Floodplain forests also represent hotspots of biodiversity as they are created by a patchwork of different habitats due to river-floodplain dynamics (Gregory et al., 1991; Naiman and Rogers, 1997). In addition, floodplain forests provide aesthetic and recreational functions that enhance human well-being (Klimo and Hager, 2001).

For these reasons, floodplain forests have been identified as essential for climate change mitigation and key to human survival (Creed and Van Noordwijk, 2018; Selwood and Zimmer, 2020). Unfortunately, more than 50% of floodplain forests areas have been lost globally in recent decades, with even greater losses in Europe and North America (Davidson and Finlayson, 2018). As a result, efforts to conserve these forests and prevent further loss have increased, leading to their inclusion in *The Agenda 2030* (United Nations, 2015).

2.2 Natural temperate floodplain forests

In natural floodplain forests, flood inundation is a key factor influencing plant species composition and diversity through a number of interrelated mechanisms. First, periodic flooding mechanically disturbs the understorey vegetation, providing space for seed germination from a seed bank and allowing the establishment of new species migrating from adjacent microhabitats (Lite et al., 2005).

Second, large differences in the frequency, duration and magnitude of floods create a varied microtopography that allows a wide range of species with different flood tolerances to coexist (Barnes, 1978; Menges & Waller, 1983; Ferreira & Stohlgren, 1999). Flood characteristics also influence the composition of the overstorey at different altitudes (Douda, 2008). For example, alder and willow require higher groundwater levels and tolerate long-term flooding, so they tend to occur at lower elevations along a channel. Conversely, oak, elm or ash are more flood intolerant and therefore thrive at higher elevations with less frequent and shorter duration floods (Douda, 2009).

Third, flood events increase sediment deposition, which alters local elevation. Hodges (1997) discussed a model of floodplain forest succession based on floodplain systems in the southeastern United States. At a given site,

Alder and willow stands in floodplains along a river channel during spring floods (Libický luh national nature reserve)

sediment deposition increases until an elevation is high enough to remove the site from most of the hydrological influence of the floodplain, resulting in succession to flood-intolerant tree species such as oak or hickory. In temperate Europe, this succession could lead to an increased dominance of maple, linden or hornbeam (Janik et al., 2008). In addition, different deposition rates across the floodplain also influence the species composition of the understorey. Taking together, these mechanisms increase environmental heterogeneity leading to high species diversity in floodplain forests supported by a high nutrient supply from a flood water (Johnson et al., 2016).

Apart from this, there is another factor that affects floodplain forest vegetation to a similar extent - light. Light is the main limiting resource for understorey growth (e.g., Axmanová et al., 2012), and its availability is completely controlled by the overstorey. During the growing season, the phenology of the overstorey determines the beginning and end of the shade phase for the understorey plant species, resulting in their temporal niche separation (Augspurger & Salk, 2017). Vernal or spring ephemerals, emerge and flower in early spring before canopy closure. They usually exhibit a relatively short growth period and rapid phenological transitions due to the decrease in light intensity caused by tree leaf emergence (Meier et al., 1995; Augspurger & Salk, 2017). Conversely, summer species begin their initial phenological events after the forest floor is completely shaded, as they are adapted to low light availability (Bierzychudek, 1982). Nevertheless, the presence of different phenological guilds due to seasonally changing light conditions only contributes to the high plant diversity of floodplain forests.

More debatable is other factor that allegedly contributes to the high plant diversity of floodplain forests. In general, rivers and river valleys are considered to be natural corridors for species migration. Therefore, species dispersal along a river can significantly affect the patterns of species diversity and composition in floodplain areas. However, there is a little evidence that

Spring phenological guild in floodplain forests with Galanthus nivalis, Leucojum vernum, Corydalis cava and Allium ursinum riverine habitats are saturated by plant species from different parts of the watercourse, usually based on population-genetics studies. For example, Pilger et al. (2017) showed that a higher genetic relatedness between populations within a river than between different rivers indicates that riverine populations are connected by water dispersal. Nevertheless, more evidence based on different approaches is needed to prove that river channels actually serve for natural species dispersal.

2.3 River regulations

Over the last few centuries, river regulation in the form of channelling, bank stabilisation, lowering of groundwater levels, draining of floodplains, building of dikes and large dams has led to a sharp decline in natural floodplain forests worldwide (Tockner and Stanford; 2002). These alterations of natural hydrological regimes threaten a delicate balance of fluctuating high and low water levels that create a shifting patchwork of habitat patches at different successional stages and prevent long-term anoxia and death in dry-out periods (Dynesius & Nilsson, 1994; Battaglia et al., 2002; Whited et al., 2007). In addition, river regulations tend to result in less frequent and shorter duration floods that trigger desiccation of floodplains and allow flood-intolerant species to spread to lower elevations (Hale et al., 2008). The composition of understorey vegetation then shifts towards mesophilic species capable of surviving in a wide range of environmental conditions, which may temporally increase the local diversity of floodplain forests but contribute to biotic homogenization in different elevation levels (Johnson et al., 2014).

2.4 Traditional use of floodplain forests

Forests have been extensively used as a source of wood and other raw materials since prehistory, regardless of geography or forest habitat type (Hédl, 2004; Taverna et al., 2005; von Oheimb & Brunet, 2007; Naaf & Wulf, 2011; Oakes et al., 2014; Reinecke et al., 2014; Kirby et al., 2016). Over the centuries, several traditional forms of management have developed including forestry use in the form of coppicing or coppicing-with-standards and non-forestry uses such as litter raking, haymaking or grazing. The combination of these was quite common (with the exception of grazing in coppices, which would prevent the rejuvenation of shoots) and strongly influenced species composition and diversity (Hédl et al., 2010).

In a coppice-with-standards system, young shoots are cut down in short rotations and new shoots resprout from the cut stumps (coppice). Single-stemmed trees (standards) are retained in a sparse canopy for one or more rotations. Frequent alternation of light and shady phases provides a patchwork of contrasting habitats, allowing a wide range of species to coexist in the understorey (Ash & Barkham, 1976; Buckley, 1992). Grazing has a similar effect on light availability as regular removal of seedlings maintains the tree canopy open (Petřík et al. 2009). Litter raking and haymaking affect the distribution of nutrients in the soil, as the collection of biomass causes a massive loss of nutrients from the forest ecosystem (Gimmi et al., 2013; Vild et al., 2013). The use of these traditional forest management practices, and their combination, has shifted plant communities towards oligotrophic, light-demanding species and increased species diversity (Vild et al., 2013; Douda et al., 2017).

Coppicing-with-standards with hornbeam and linden

European floodplain forests, like other temperate forests, have in the past been converted into coppices-with-standards. Typically, the oaks were retained as single-stemmed trees and other tree species such as alder or willow were felled in short seven-year rotations. This management system contributed to the high species diversity of floodplain forests by increasing the variability of light conditions, which favoured mainly light-demanding species (Douda, 2009). Grazing and haymaking prevented excessive eutrophication and preserved patches of varied soil nutrient availability, therefore allowing the oligotrophic species to survive (Vrška et al., 2006). Although river regulation during 19th century and first half of 20th century ended periodic flooding, the biodiversity of the floodplain forests was probably maintained by these traditional forms of forest management.

Conversion to high forest management over the last century is likely to result in shifts in species composition and diversity as trend similar to other forest communities such as oak or beech forests. Janik et al. (2008) observed compositional changes in the overstorey of floodplain forests towards mesophilic tree species such as *Acer campestre*, *Tilia cordata*, *Carpinus betulus*, and a significant decrease in the abundance of *Quercus robur* as a result of the abandonment of coppice-with-standards system and subsequent shading of the forest floor. Strubelt et al. (2017) investigated the effects of changes in forest management on the understorey vegetation of floodplain forests. They documented an overall increase in species richness, mainly due to an increase in true forest species and woody species. The proportion of species typical of open habitats decreased slightly. The authors suggested that these vegetation changes were driven by a decrease in light availability caused by less intensive management.

The results of several studies conducted in European temperate forests either show no significant change in species diversity patterns or confirm that the abandonment of traditional forest management practices has a similar effect on plant species composition, in the form of an increase in the abundance of shade-tolerant species and a decrease in the abundance of open woodland herbs, regardless of forest habitat type (Hédl et al., 2004; Kopecký et al., 2013; Becker et al., 2017; Reczyńska and Świerkosz, 2017; Vojík and Boublík, 2018, Vild et al., 2024). On the other hand, at least in the case of lowland forests, these studies focused mainly on summer species, neglecting the presence of vernal species and spring ephemerals at the beginning of the growing season, when the canopy is still open. It is therefore likely that vernal species and spring geophytes are not as affected as summer species by the increased shading of the forest floor or other factors that usually have negative impacts on species diversity. However, there is no evidence of this yet.

Likewise, these studies suggest that high between-stand variation associated with the variation in the forest management intensity, could increase species diversity within forest fragments. Coppice-with-standards system favours light-demanding species at the expense of shade-tolerant ones (Buckley, 1992). On the other hand, the opposite pattern can be observed in the application of high forest management (Kopecký et al., 2013, Müllerová et al., 2015). It follows that neither of these approaches supports the highest possible species diversity. However, this assumption needs to be tested, as only a few studies have focused at least partially on similar questions (Schall et al., 2017).

2.5 Eutrophication

Eutrophication generally has negative effects on diversity of plant communities because an accumulation of nutrients in the soil increases soil acidification, which progressively determines abundance loss up to the complete extirpation of species adapted to nutrient-poor conditions (Bobbink et al., 2010). In addition, higher nutrient availability increases ecosystem productivity accompanied by an increase in abundances of nutrient-demanding species that cause huge plant diversity losses through enhanced light competition (Hautier et al., 2009).

Natural floodplain forests are considered to be the most productive habitats among temperate forests (Mitsch, 1991; Schnitzler, 2005). The accumulated dead biomass floating from the upper course is decomposed and mineralised, resulting in high nutrient contents in the lower course (Humborg et al. 2004; Ounissi and Bouchareb 2013). Consequently, periodic flood events enrich floodplain soils with large amounts of nitrogen and phosphorus, thus increasing its nutrient availability (Strubelt et al. 2017). Floodplain forests therefore provide a suitable habitat for seed establishment and germination (Johnson et al. 2016). At the same time, the disturbance caused by flooding creates gaps in the understorey vegetation and prevents competitive nutrient-demanding species from becoming dominant (Lite et al. 2005). As disturbances caused by flood events have ceased after the river regulations, and the traditional forest management practices have been abandoned, the abundance of nutrient-demanding species has become to increase, supported by rising nutrient availability due to massive application of NPK fertilisers in agriculture and the deposition of atmospheric nitrogen.

High nutrient availability, coupled with lower groundwater levels and the abandonment of traditional forest management practices across the floodplain, has likely resulted in environmental homogenisation, allowing mesophilic species to expand while rare oligotrophic species have declined. For example, Lameire et al. (2000) observed such a decline in floodplain forest biodiversity caused by high nitrogen deposition and lowering of the water table. However, the consequences of eutrophication, desiccation and abandonment of traditional forest management practices in European floodplain forests are not yet fully understood.

Nutrient-oversaturated floodplains with dominant Urtica dioica (Úpor - Černínovsko nature reserve)

2.6 Climate change

Climate change has been reported as a major driver of ecosystem alterations on a global scale (Rackham, 2008). Higher mean temperatures and less precipitations cause long periods of heats and droughts which in turn negatively affect plant communities (Feeley et al., 2020). For example, with rising temperatures at a given site, the presence or abundance of species adapted to higher temperatures increase, whereas species adapted to lower temperatures decline and eventually become excluded (i.e., “thermophilization”). This process changes the composition of plant communities in favour of warm-adapted species and causes distributional shifts toward higher latitudes and elevations (Lenoir et al., 2010; Gottfried et al., 2012; Savage & Vellend, 2015). Lower water availability and subsequent desiccation, on the other hand, enable the spreading of common mesophilic species at the expense of water specialists (Kopeć et al., 2014; Garssen et al., 2014). Thus, cold-adapted and water-demanding species retreat from plant communities which result in plant diversity losses (Feeley et al., 2020).

These negative effects of climate change, however, seems not to be completely valid in forest ecosystems where the microclimate heterogeneity has been observed to have more significant impact on vegetation than macroclimate itself (De Frenne et al., 2013; Zellweger et al., 2020; De Frenne et al., 2021). Microclimate in forest is given by three-dimensional canopy structure that drives shading, air mixing, and evapotranspirative cooling (Atkinson, 2003; Zellweger et al., 2019) i.e., the tree canopy buffers forest floor against extreme heat and drought, and this buffering capacity constantly changes with tree species, growth, and mortality, leading to highly dynamic microclimates across space and over time (Jucker et al., 2018; De Frenne et al., 2019).

As floodplain forests naturally occur along large rivers, i.e. in areas with high groundwater levels, these habitats could be, at least temporarily, resistant to the effects of climate change (Riis et al., 2020). On the other hand, long periods of drought and heat cause increased evaporation, which is not compensated by sufficient supply of precipitation and flood water, so even these habitats may suffer from desiccation accelerated at sites affected by river regulation (Havrdová et al., 2023).

2.7 Historical sampling error

Long-term time series are needed to assess changes in plant community biodiversity and to identify the main factors driving them, as these changes are certainly observable after several decades. This includes vegetation plot resurveys, a historical ecology method that is now an established line of research and was therefore used for the purposes of this thesis (Vellend et al., 2013; Hédl et al., 2017; Kapfer et al., 2017; Verheyen et al., 2017). However, there are several potential errors associated with plot sampling: relocation error, observer error and seasonal bias (Morrison, 2021).

To date, these errors and their impact on the conclusiveness of the results have rarely been investigated, although it is generally known that they can lead to so-called pseudo-turnover, i.e. false turnover in species composition and subsequent misinterpretations in terms of biodiversity and environmental dynamics (Fischer and Stöcklin, 1997; Kapfer et al., 2017). In the case of relocation errors, the most commonly used quasi-permanent plots (referring to the approximate relocation of historical plots) proved to be the most reliable source for the assessment of long-term vegetation changes (Chytrý et al., 2014). The impact of using different historical datasets to describe and interpret vegetation change over time is, however, still unknown. Therefore, this thesis also compares changes observed in floodplain forests using two historical datasets of vegetation plots.

Chapter 3

Objectives of the Thesis

The aim of this thesis is to contribute to a better understanding of the ongoing processes in floodplain forests of Central Europe that are leading to significant negative changes in plant species composition and diversity, and to propose efficient management strategies that would prevent further loss and degradation of floodplain forests.

Specifically, papers reported here: 1) investigate the importance of natural species dispersal along rivers in contributing to the high biodiversity of riverine communities, including floodplain forests; 2) describe long-term vegetation changes in floodplain forests in relation to the effects of environmental factors, and compare these effects between different phenological guilds; 3) assess how variation in forest age structure between forest stands affect species diversity patterns; 4) highlight the role of historical observer error in floodplain forests resurveys.

Part II

Research

Chapter 4

Study I: Plant species over-occupancy indicates river valleys are natural corridors for migration

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Plant species over-occupancy indicates river valleys are natural corridors for migration

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Abstract River valleys are considered natural corridors for migration of plant species; however, there is a lack of studies confirming higher colonisation rates of plant species in these areas. We compare plant species richness between ancient and recent forests (developed during and after the nineteenth century) and those located in a river valley with those located outside the river valley. We hypothesise that, close to a river, higher plant species richness will be associated with recent forests, thus indicating a higher colonisation rate. The study area includes parts of the Elbe River Valley and a landscape outside the river valley in the Czech Republic. We sampled an equal number of recent and ancient forests (20/20), but lying at different distances from the river. We used generalised linear models to test the effect of distance from the river in dependence upon forest continuity (recent/ancient forest) on two plant species richness categories, i.e. richness of forest species and overall species richness. Outside the river valley, higher richness of forest species was associated with ancient forests, whereas overall species richness was comparable. In the river valley, richness of forest species as well as overall species richness was higher in the recent forests. Recent forests in the river valley were more saturated by plant species than those outside the river valley, indicating that in the river valley, the colonisation rate of plant species is higher. These results confirm the importance of river valleys as natural corridors for migration of plant species.

Keywords Ancient forests · Colonisation rate · Dispersal limitation · River phenomenon · River valley · Species richness

Introduction

It is well known that the plant species diversity is markedly different in and outside a river valley (Blažková 1964; Naiman et al. 1993; Renöfält et al. 2005; Zelený and Chytrý 2007; Nobis et al. 2016). Hence, river valleys are frequently identified as regional hotspots of biodiversity and are also regarded as natural corridors for plant species migration (Jeník and Slavíková 1964; Tockner and Ward 1999; Ward et al. 2001; Saarela et al. 2017; Mollashahi et al. 2020). However, we lack studies which estimate whether the colonisation rate of plant species (i.e. the speed at

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which species colonise habitats) is actually higher in a river valley than outside it.

River valleys may favour species migration for a number of reasons. Among these are the increased fine-scale habitat heterogeneity in such a variable topography, both the mesoclimate and the geological conditions. This is especially true in deep valleys such as the middle part of the Elbe river, where the topography is characterised by steep slopes with exposed rocky outcrops and variable landform shapes on the one side and flat alluvial areas on the other side (Jeník and Slavíková 1964). Also, frequent temperature inversions result from the valley shape, and these increase the contrast between a cold and wet valley bottom and a dry, more continental upper valley edge (Chytrý and Tichý 1998). Similarly, north facing and south facing slopes represent suitable habitats for shade-demanding and light-demanding species and so enabling the close coexistence of these species within a river valley (Blažková 1964; Chytrý and Tichý 1998; Zelený and Chytrý 2007). All these abiotic variables create a set of suitable environmental conditions, which may host a large spectrum of species with quite different habitat requirements. This fine-scale heterogeneity may enhance the connectivity of a river valley for multiple species, rather than presenting a barrier to their migration.

The linear connectivity of a river valley allows plant species to migrate in both downstream and upstream directions and also along interconnecting gullies and so colonise suitable habitats (Gallé et al. 1995; Ward et al. 2002; Czochański and Wiśniewski 2018; Czortek and Pielech 2020). Here, the colonisation rate decreases as the target habitats become more distant from the riverbank which serves as a source of diaspores. Correspondingly, the decrease in habitat connectivity outside of a river valley has a negative effect on colonisation rate (Yao et al. 1999; Renöfält et al. 2005; Vellend 2016; Nobis et al. 2016, 2017). For example, the oak-hornbeam forests of central Europe offer highly connected habitats along the slopes of river valleys, whereas outside of these a patchy agricultural landscape dominates (Chytrý 2013). Therefore, outside of a river valley, compared to colonisation, both the distance from the riverbank and also habitat fragmentation increases the importance of local community processes including competition and ecological drift. The ecological drift and competition at any particular site increase the chances of species extinction. Thus, the balance between the rate of colonisation and that of extinction determines the composition and species richness of a local plant community (Vellend 2016).

Whether or not a plant species reaches a remote habitat depends on its colonisation ability. For example, both anemochorous and zoochorous species produce many seeds which can move over large distances; however, colonisation success is also affected by the seedling establishment conditions. Since prehistory in Europe, forest cover has gradually decreased accompanied by a corresponding increase in cropland cover (Bellemare et al. 2002; Pongratz et al. 2008). Since the intensification of farming practices in the twentieth century, many croplands formerly established on forest soils have been abandoned and the land has returned to forest (Mather et al. 1999). Therefore, two types of forests can be found in European landscapes that differ in respect to their times of origin. Ancient forests are associated with land that has enjoyed continuous forest land use, at least since the second half of the nineteenth century, while recent forests are mostly those that have originated in the second half of the twentieth century after the intensification of agriculture. These are land areas that have suffered temporarily used as pasture, for arable cropping, or for horticulture (Koerner et al. 1997; Webb 1998).

River valleys have been less exposed to these human-induced changes in parts with more rugged topography, although evidence of some traditional farming practices can still be seen in the more accessible locations (Douda 2010). A good number of studies have shown that higher plant species richness is associated with ancient forests due to their long and continuous history (Peterken and Game 1984; Dzwonko and Gawronsky 1994; Hermy et al. 1999; Wulf 2003; Sciama et al. 2009; Matuszkiewicz et al. 2013). Furthermore, particular groups of species are related to ancient forests, namely ancient forest species that have been found to serve well as indicators of forest communities and these are characterised by high diversity (Hermy et al. 1999; Douda 2010; Stefańska-Krzaczek et al. 2016). The recent forests are dependent on diaspore input from ancient forests, i.e. colonisation rate increases in proximity to an ancient forest, and recent forests continuous with ancient forests may also be colonised by herbaceous species

(Dzwonko 1993; Wulf and Heinken 2008; Orczewska 2010; Orczewska and Fernes 2011).

Disentangling the importance of the processes that drive the plant species richness of riverine communities requires information on plant species colonisation. In previous studies, a number of authors have described the patterns of plant species richness along a gradient starting in a river valley and continuing outside the river valley (i.e. a riverine gradient, Blažková 1964; Ložek 1974; Chytrý and Tichý 1998; Renöfält et al. 2005; Zelený and Chytrý 2007; Nobis et al. 2016). Here we seek to provide an additional step in understanding how well plant species richness copes with the riverine phenomenon by recording the species saturation of forest communities along a riverine gradient.

We compare plant species richness between ancient and recent forests. This method allows us to estimate how successfully recent forests can be colonised at different distances from the river and to associate the riverine gradient with the importance of the colonisation processes. The ancient forests provide us information on plant species richness determined by the long-term balance between colonisation, extinction and environmental conditions. Recent forests inform us as to whether the plant species richness here has reached, or even over-reached, a value close to the natural state in an ancient forest (i.e. saturation) due to the rapid spread of plant species or whether the dispersal of plant species is more limited, so that the recent forests are less saturated than the ancient forests. Under these conditions, the proportion of plant species in recent forests compared with that in ancient forests becomes a measure of colonisation rate. In the river valley, a higher saturation of recent forests would then suggest plant species over-occupancy of the river valley, thus indicating river valleys as migration corridors. Use of Ellenberg indicator values (EIVs) helps us to understand patterns of plant species composition with respect to changing environmental conditions along the riverine gradient. Assessing the distribution of plant dispersal vectors in forests located in, and outside, the river valley further contributes to a better explanation of the colonisation processes.

Specifically, we ask how do plant species richness and the prevailing dispersal mode differ between ancient and recent forests, with respect to the distance from a river? We would expect that if a recent forest is located close to a river, its plant species richness will be similar to that in an ancient forest (possibly even higher). This being due to its connectivity with the river corridor that increases plant species colonisation rate. Due to the higher connectivity between a recent and an ancient forest in a river valley, we would also expect higher proportions of species with various dispersal modes in a recent forest. This would include those with limited dispersal, such as myrmecochorous forest species. Such a pattern would also suggest higher colonisation rates for plant species in a river valley. Conversely, we would expect a recent forest far from a river, to be less saturated with plant species, compared with an ancient forest, due to a more limited dispersal. Therefore, if present, forest species will be represented dominantly by anemochorous species.

Methods

Study area

The study was conducted about halfway along the course of Elbe River located in the northern part of the Czech Republic (14° 09′ 25″–14° 09′ 47″ E, 50° 41′ 53″–50°42′ 29″ N). The Elbe River Valley is considered one of the most important natural corridors for species migration in Europe. The study area covers ca. 10 km^2 and includes the western slope of the river valley and the part of a landscape outside the river valley (Fig. 1). The river valley is characterised by steep slopes without developed alluvial flat areas; thus, the river course has never been regulated. The altitude ranges from 153 to 340 m above mean sea level. The climate is subcontinental with annual mean temperature ca. 9 °C. The mean annual precipitation ranges from 450 to 800 mm (Bína and Demek 2012). The geology basement is created by two main geological formations: clay sediments and volcanic rocks (Kachlík 2003). Forest vegetation in the river valley corresponds to more nutrient-poor oak and beech forests dominated by *Quercus petraea* and *Fagus sylvatica*, while more nutrient-rich forests frequently occur outside the river valley, often dominated by *Fraxinus excelsior*. The whole area is a part of a protected landscape České středohoří (IUCN category V) and comprises many primary, but also secondary ecosystems including ancient and recent forests. It, therefore, represents a suitable model system for

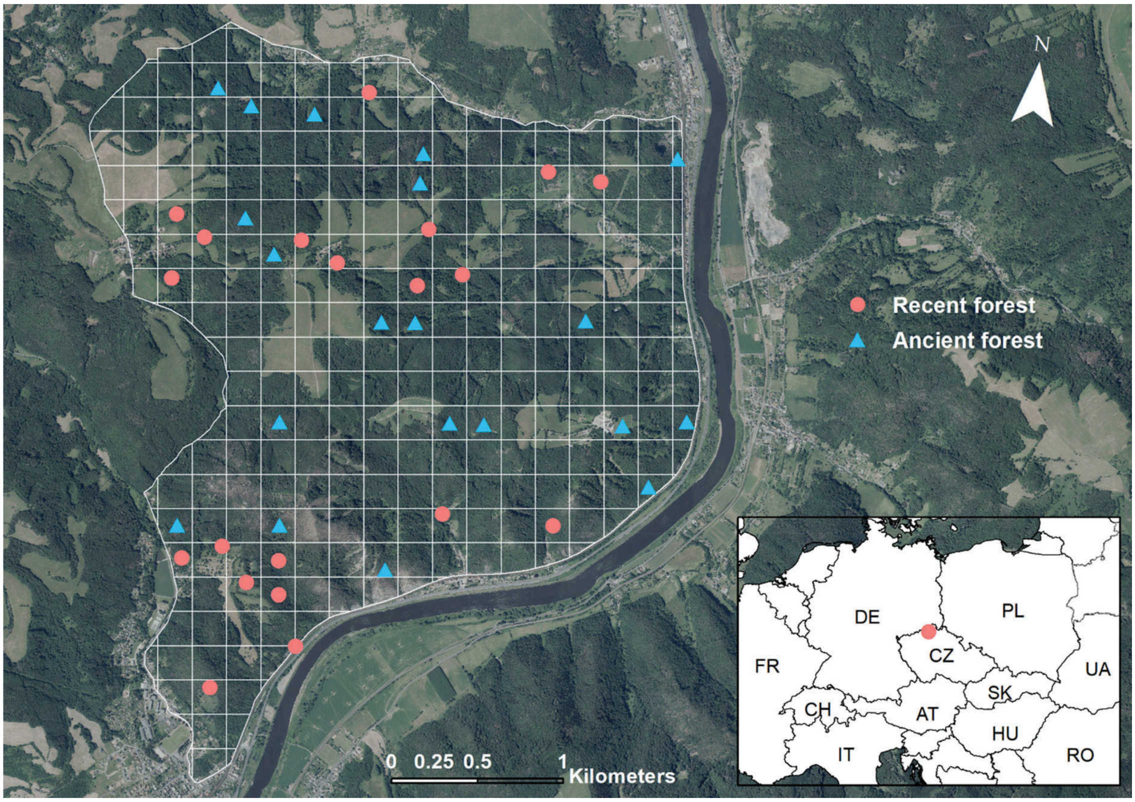

Fig. 1 Study area with 40 vegetation plots distinguished as being either recent or ancient forest. The map was created in ArcMap 10.7 (http://www.esri.com)

studying patterns of plant species richness in forests along a riverine gradient.

Sampling

To select the vegetation plots for random stratified sampling, the study area was overlaid with a square grid with cells of 200 × 200 m. For each cell, forest continuity (ancient/recent forest) was determined based on a comparison of current with historical maps, specifically the third military mapping of Austria-Hungary from 1877 to 1880 on a scale of 1:75,000 (http://oldmaps.geolab.cz/). Random-stratified sampling was carried out as follows: The grid cells were grouped into five 600-m-wide strips, corresponding to their different distances from the river. In each strip, the cells of ancient/recent forest were numbered. Four of these cells were then selected at random and vegetation plots were established at their centres. In cases where ancient/recent forest was absent in a cell centre, the vegetation plot was established in the nearest location in which the forest occurred (Fig. 1). In this way, eight vegetation plots (four ancient forest plots and four recent forest plots) were established in each 600 m strip (Taherdoost 2016). Data were collected in July 2016. A list of vascular plants with species cover was recorded for each plot using the nine-step ordinal Braun-Blanquet scale (Braun-Blanquet 1964; Podani 1984). The standard plot size used for sampling was 400 m^2.

Delimitation of variables

Forest species were selected from the overall dataset based on a study by Chytrý and Tichý (2003), which categorised the affinity of plant species to forest habitats. The number of species belonging to the forest species category (richness of forest species) and the number of all species (overall species richness) were calculated for each vegetation plot. The full list of species recorded, with forest species highlighted, is provided in Supplement Table 1. The nomenclature follows Kaplan et al. (2019).

The shortest distance from each plot centre to the river was calculated using *Measure* tools in ArcMap 10.7 by intersecting a line perpendicular to the river (http://www.esri.com). This distance ranged from a minimum of 56 m (for a plot lying adjacent to the river) to a maximum of 2840 m (for the most distant plot).

For each species, dispersal mode was assigned according to the LEDA database (Kleyer et al. 2008) and the number of species within each mode (autochory, anemochory, endozoochory, epizoochory, myrmecochory) was then calculated for each vegetation plot. For each vegetation plot, the mean EIVs for nutrients, soil reaction, moisture, and light were also calculated and weighted on species cover (Ellenberg et al. 1992).

It is generally well known that the plant species richness of a recent forest is affected by proximity to ancient forest. Specifically, the closer a recent forest is to an ancient forest, the higher is the number of plant species present (Dzwonko 1993). Therefore, it is likely that the plant species richness of a recent forest will be affected not only by distance from a river but also by distance from the nearest ancient forest. To control this effect, the distance from each recent forest plot to the nearest ancient forest plot was calculated (distances ranged from a minimum of 179 m to a maximum of 968 m) and its effect on plant species richness in the recent forest was also assessed.

Statistical analyses

To estimate how successfully recent forests are colonised at different distances from the river, the effect of distance from the river in dependence upon forest continuity (recent/ancient forest) on richness of forest species/overall species richness was tested using generalised linear models with Poisson response distributions (R package *stats*; Hastie and Pregibon 1992).

Several additional analyses were carried out to explain the observed patterns: First, to relate the colonisation rate to the dispersal traits of recorded species, the effect of distance from the river in dependence upon forest continuity and on richness of autochorous, anemochorous, endozoochorous, epizoochorous, and myrmecochorous species was tested using generalised linear models with Poisson response distributions.

Second, to assess the change in environmental conditions along the riverine gradient, the effect of distance from the river in dependence upon forest continuity on distributions of the EIVs for nutrients, soil reaction, moisture and light were tested using liner models with Gaussian response distribution, as the original EIVs were converted on weighted means.

Third, to assess whether the proximity to an ancient forest contributes to higher plant species richness of recent forests, the effect of the interaction between the distance from the river and the distance from an ancient forest (and the separate effects) on richness of forest species/overall species richness in recent forests were tested using generalised linear models with Poisson response distributions. Similar analyses were also used to test the effects of the putative interactions of the richness of autochorous, anemochorous, endozoochorous, epizoochorous and myrmecochorous species in recent forests.

Fourth, detrended correspondence analysis (DCA) was used to assess the overall pattern of variation in species composition. The analyses were carried out using the *decorana* function in the R package *vegan* (Oksanen et al. 2020). To interpret the DCA results in terms of environmental gradients, the significant Ellenberg indicator values were then plotted onto a DCA ordination diagram as supplementary variables using the *envfit* function from the same R package. *Envfit* provides a vector for each variable that maximises correlation between that variable and the projections of ordination points onto that vector. Significance was assessed using 999 permutations of variables. All statistical analyses were carried out in the statistical program R (R Development Core Team 2019).

Results

In general, significant positive correlations were found between distance from the river and each species richness category (i.e. overall and forest species richness). Higher numbers of species were associated with plots located far from the river (outside the river valley; from about 1.06 km), whereas lower number of species persisted on plots located closer to the river (in the river valley; up to about 1.06 km) (Table 1; Fig. 2). Both species richness categories differed significantly for ancient and recent forests (i.e. forest continuity) (Table 1; Fig. 2).

Higher richness of forest species was associated with recent forests in the river valley, whereas outside of the river valley higher richness of forest species was associated with ancient forests. Specifically, the number of species in recent forests located closer to the river (0.056–1.06 km) was 1.6 times higher compared with ancient forests at the same distances. On the other hand, the number of species in recent forests located far from the river (1.07–2.84 km) was 1.14 times lower (Fig. 2a).

In contrast, higher overall species richness was associated with recent forests in the river valley as well as those outside the river valley; however, the difference in the numbers of species between ancient and recent forest decreased gradually as distances increased. Specifically, the numbers of species in recent forests located close to the river (0.056–1.06 km) were 1.8-times higher compared with in ancient forests at the same distance, whereas the numbers of species in recent forests located far from the river were comparable with the numbers of species in ancient forests (Fig. 2b).

A significant positive correlation was found between distance from the river and the dispersal mode. However, we recorded significantly higher numbers of autochorous, endozoochorous and myrmecochorous species associated with recent forests along the entire length of the riverine gradient. In cases of endozoochory and myrmecochory, the numbers of species were higher in plots located close to the river (Table 1; Fig. 3).

Significant positive correlations with distance from the river were found only for the EIVs for nutrients. However, these EIVs did not differ significantly between ancient and recent forests (Table 1; Fig. 4). This result was also supported by the DCA ordination, indicating that the riverine gradient is correlated with the EIV for nutrients, which explains the most important part of the variability in the species composition data (Table 2; Fig. 5).

In recent forests, the effect of interaction between the distance from the river and the distance from the ancient forest was not significant, either for richness of forest species or for overall species richness. Similar results were also found for the richness of

Table 1 The effects of forest continuity, distance from the river and their interaction on plant species richness, dispersal, and Ellenberg indicator values are shown by generalised linear models

	Forest continuity (Forest)		Distance from river (Dist)		Forest*Dist	
	Estimates	*P*	Estimates	*P*	Estimates	*P*
Plant species richness						
Richness of forest species	0.3389	0.043*	0.00039	< 0.001***	− 0.00022	0.0342*
Overall species richness	0.456	0.00158**	0.00043	< 0.001***	− 0.00019	0.02487*
Dispersal mode						
Autochory	0.32	0.0279*	0.00036	< 0.001***	− 0.00009	ns
Anemochory	0.27954	ns	0.00025	0.0291 *	− 0.00027	ns
Endozoochory	0.59366	0.0244*	0.00026	0.0380*	− 0.00022	ns
Epizoochory	0.69185	ns	0.00065	0.0365*	0.00065	ns
Myrmecochory	0.93479	0.0537	0.00082	< 0.001 ***	− 0.00041	ns
Ellenberg indicator values						
Nutrients	0.41628	ns	0.00046	0.0256*	− 0.00025	ns
Soil reaction	0.36884	ns	0.00018	ns	− 0.00017	ns
Moisture	− 0.0039	ns	0.00012	ns	− 0.00009	ns
Light	− 0.23669	ns	− 0.00019	ns	0.00029	ns

ns non-significant

***$P < 0.001$, **$P < 0.01$, *$P< 0.05$

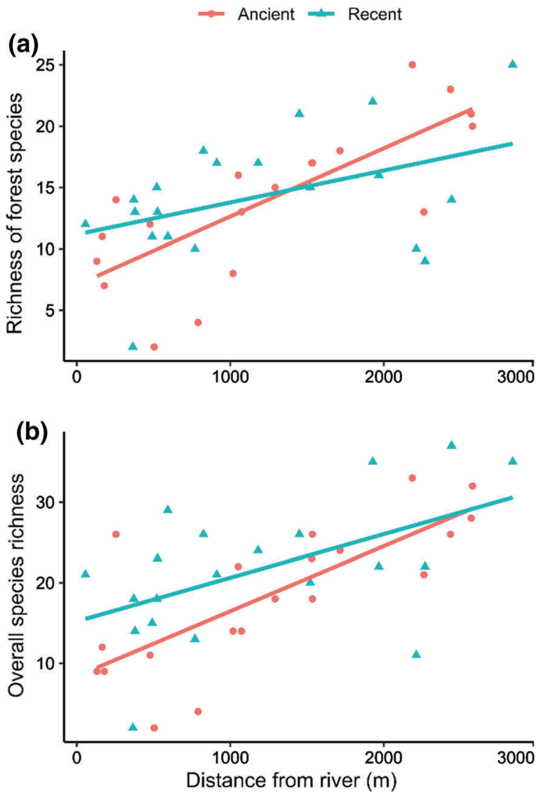

Fig. 2 The effect of distance from the river on **a** richness of forest species, **b** overall species richness distinguished as being either recent or ancient forest

autochorous, anemochorous, endozoochorous, epizoochorous, and myrmecochorous species in recent forests (see Supplement Table 2).

Discussion

Our results support the view that colonisation patterns of plant species strongly reflect the riverine gradient (Renöfält et al. 2005; Zelený and Chytrý 2007; Nobis et al. 2016). The higher plant species richness of recent forests, than of ancient forests situated in the river valley, suggests a higher colonisation rate. This is consistent with our prediction that a recent forest in a river valley is exposed to higher migration. Otherwise, the number of plant species in an ancient forest would be higher than in a recent forest, as can be observed outside the river valley. Such results indicate that migration processes are more important in river valleys than away from them, confirming the view that river valleys serve as migration corridors.

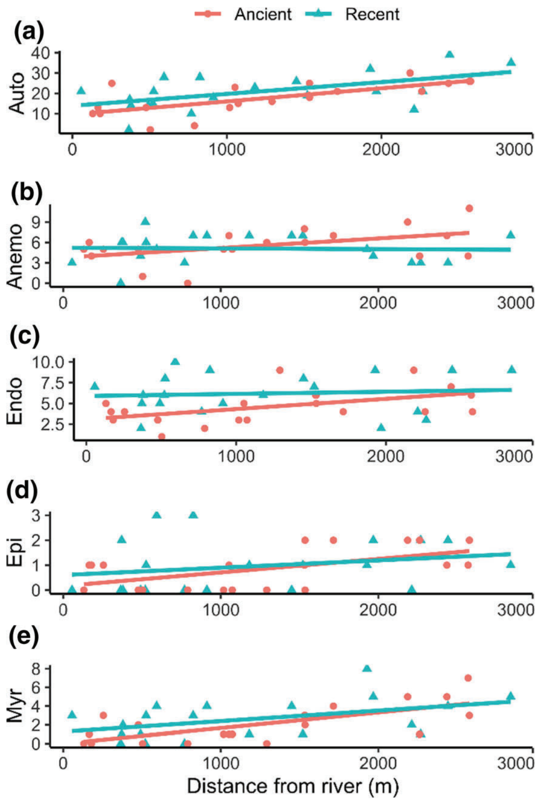

Fig. 3 The effect of distance from the river on richness of **a** autochorous, **b** anemochorous, **c** endozoochorous, **d** epizoochorous and **e** myrmecochorous species distinguished as being either recent or ancient forest

The lower richness of forest species found at greater distances from the river valley, is consistent with other studies which found evidence for low saturation in recent forests (Peterken and Game 1984; Dzwonko and Gawronsky 1994; Hermy et al. 1999; Wulf 2003; Sciama et al. 2009; Matuszkiewicz et al. 2013). In most of these studies, the dearth of forest species is interpreted as being a consequence of limited dispersal or of unsuitable recruitment conditions (Ehrlén and Eriksson 2000; Ehrlén et al. 2006).

According to the dispersal limitation hypothesis (1), forest species that are unable to rapidly colonise recently developed forests, are primarily associated with ancient forests (Hermy et al. 1999; Stefańska-Krzaczek et al. 2016). The reason for this is that these species are adapted to small scale disturbance regimes

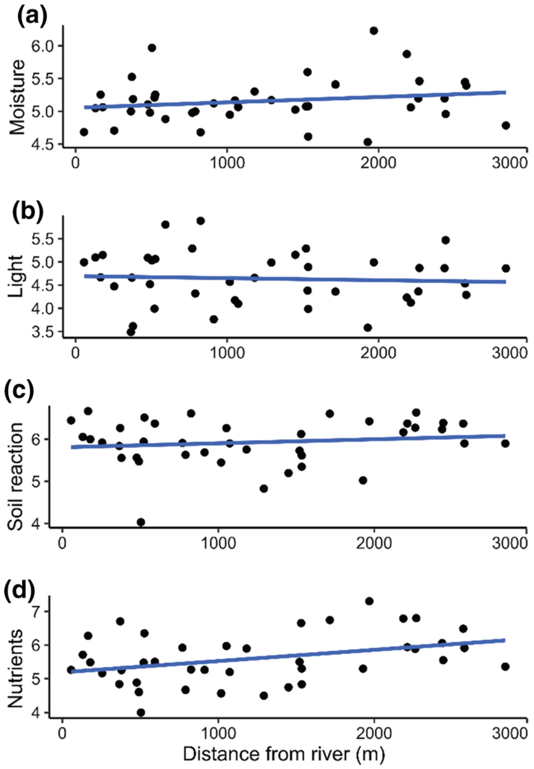

Fig. 4 The effect of distance from the river on Ellenberg indicator values for **a** moisture, **b** light, **c** soil reaction and **d** nutrients

in temperate forests, where species usually spread only over quite short distances as they colonise canopy gaps (Hermy et al. 1999; Bellemare et al. 2002). For example, many forest species are dispersed locally by ants, some species of which are very sensitive to habitat fragmentation and rarely travel through treeless areas (Hermy et al. 1999; Mitchell et al. 2002; Douda 2010). The observed pattern in richness of myrmecochorous species only partly supports this view, as the values between ancient and recent forest differ slightly only in the river valley, where the myrmecochorous species were more frequent in recent forests (Fig. 3e).

Meanwhile, the recruitment limitation hypothesis (2) states that in a recent forest site, the altered soil characteristics resulting from the former agricultural use are retained. These include, increased pH, base saturation and a greater availability of phosphate and nitrogen (Dzwonko and Loster 1992; Richter et al. 1994; Koerner et al. 1997; Honnay et al. 1999). These altered soil conditions restrict the recruitment and population growth of forest species, even though they are able to colonise the site (Hurtt and Pacala 1995).

The second hypothesis does not seem able to account satisfactorily for the patterns of species saturation we observed. Due to altered soil conditions, we would also expect a poor saturation of recent forests in the river valley if the recruitment limitation applied. Instead, the contrast between the levels of forest species in and outside the river valley suggests that dispersal limitation occurs outside of the river valley, with easier dispersal within the river valley. Contrary to the recruitment limitation hypothesis, we did not find differences in the EIVs, which might indicate the different levels of nutrients, light availability or moisture found between recent and ancient forests.

The patterns of overall species richness also support easier dispersal within the river valley, as higher numbers of species are associated with recent forests in the river valley. However, outside the river valley, the effects of dispersal limitation are not so clear, as the values between ancient and recent forests are

Table 2 The significances of the environmental variables are shown by the *envfit* function from the R package *vegan*

	DCA1	DCA2	r^2	P
Distance from river (Dist)	− 0.0942	− 0.9956	0.217	0.015*
Nutrients	− 0.586	− 0.8103	0.6371	< 0.001***
Moisture	− 0.0611	− 0.9981	0.4346	< 0.001***
Soil Reaction	− 0.984	− 0.1782	0.2737	0.002**
Light	− 0.4595	0.8882	0.524	< 0.001***

ns non-significant

$^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$

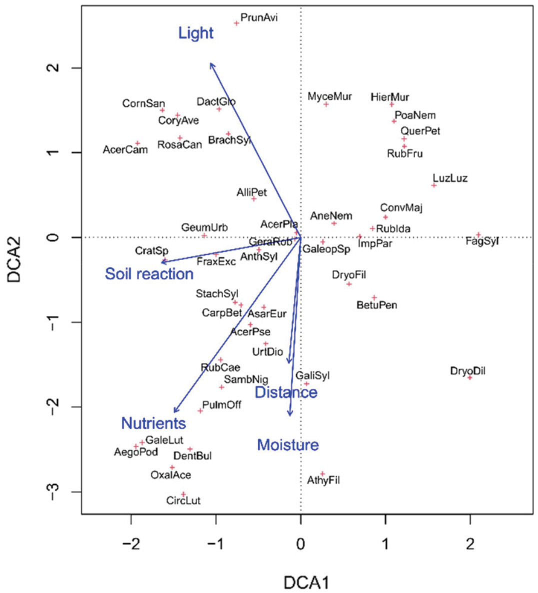

Fig. 5 The variation in species composition with significant environmental variables as detected by DCA and the *envfit* function from the R package *Vegan*. The first and second ordination axes explained 16.2 and 10.4% of the total variation, respectively. *PrunAvi* Prunus avium, *CornSan* Cornus sanguinea, *DactGlo* Dactylis glomerata, *CoryAve* Corylus avellana *AcerCam* Acer campestre *RosaCan* Rosa canina, *BrachSyl* Brachypodium sylvaticum, *AlliPet* Alliaria petiolata, *GeumUrb* Geum urbanum, *AcerPla* Acer platanoides, *MyceMur* Mycelis muralis, *HierMur* Hieracium murorum, *PoaNem* Poa nemoralis, *QuerPet* Quercus petraea, *RubFru* Rubus fruticosus agg., *LuzLuz* Luzula luzuloides, *ConvMaj* Convallaria majalis, *AneNem* Anemone nemorosa, *RubIda* Rubus idaeus, *ImpPar* Impatiens parviflora, *FagSyl* Fagus sylvatica, *GaleopSp Galeopsis* sp., *DryoFil* Dryopteris filix-mas, *BetuPen* Betula pendula, *DryoDil* Dryopteris dilatata, *GaliSyl* Galium sylvaticum, *AthyFil* Athyrium filix-femina, *GeraRob* Geranium robertianum, *CratSp* Crataegus sp., *AnthSyl* Anthriscus sylvestris, *FraxExc* Fraxinus excelsior, *StachSyl* Stachys sylvatica, *CarpBet* Carpinus betulus, *AsarEur* Asarum europaeum, *AcerPse* Acer pseudoplatanus, *UrtDio* Urtica dioica, *RubCae* Rubus caesius, *SambNig* Sambucus nigra, *PulmOff* Pulmonaria officinalis, *GaleLut* Galeobdolon luteum, *AegoPod* Aegopodium podagraria, *DentBul* Dentaria bulbifera, *OxalAce* Oxalis acetosella, *CircLut* Circaea lutetiana

highly comparable. It should be recognised that this analysis included all plant species recorded in the forests, not just the species belonging to the forest species category. In other words, most plant species that occurred in a previously open habitat with the agricultural use could still persist in recent forests.

The reverse species richness patterns were observed in the river valley where more plant species occurred in recent forests than in ancient forests. The over-occupancy of recent forests could be explained by a combination of a fast colonisation rate and a slow extinction rate in the river valley. It is well known that competition among species can be relatively weak early in forest succession during the initial establishment of plant populations, whereas the importance of interspecific competition for light and nutrients grows as a population becomes more established (Slatkin 1974; Goldberg and Barton 1992). At the start of a succession (i.e. in recent forests), a higher colonisation rate leads to an accumulation of species, whereas in later stages of succession (i.e. in ancient forests) the increasing role of competition limits the successful recruitment of new colonisers and leads to elimination of some species from the community. The number of species in ancient forests is determined by the long-term balance between species carrying capacity, the colonisation rate and the extinction rate (Connell and Slatyer 1977; Tilman 1990; Ehrlén and Groenendael 1998; Kneitel and Chase 2004).

We expect low levels of interspecific competition at the start of a succession leading to a rapid recruitment of plant species in recent forests that outnumber those in ancient forests. That this occurred only in the river valley, indicating that colonisation rate is higher there than outside the river valley. Moreover, a higher colonisation rate in the river valley should also be reflected in a higher proportion of plant species with various dispersal modes in recent forests. This was apparent at least in the cases of the endozoochorous and myrmecochorous species, for which numbers of species in the river valley were slightly higher, but non-significantly so (Table 1; Fig. 3).

In the future, we would expect a gradual decrease in plant species richness in the recent forests as it declines to the level observed in ancient forests. However, population decline in perennial species, and especially in forest species, is a very slow process, so the gradual extinction of many forest species is much delayed (Tilman et al. 1994; Vellend et al. 2006).

Contrary to the expectation based on numerous studies (Blažková 1964; Ložek 1974; Chytrý and Tichý 1998; Renöfält et al. 2005; Zelený and Chytrý 2007; Nobis et al. 2016), we found the distance from the river was positively associated with plant species richness. The likely explanation for this is that environmental conditions are more favourable far from the river, so more plant species can establish successfully. This explanation is supported by the increasing EIVs for nutrients with distance from the river as shown in Fig. 4. Moreover, higher resource availability outside the river valley is also suggested by the DCA ordination in which the nutrient and water availabilities are also highly correlated with distance from the river (Fig. 5).

Higher productivity outside the river valley appears to be associated mainly with geological conditions. The geological base for our whole study area comprised two main geological formations: volcanic rocks (predominant in the river valley) and clay sediments (predominant outside the river valley). These have fundamentally different in water holding properties (see Supplement Fig. 1). Clay sediments retain water in the upper levels of the soil horizon and thus create the appropriate moisture conditions for plant species during the larger part of the growing season. Conversely, highly water-permeable volcanic rocks can lose water earlier in the growing season, and this can lead to severe water stress and to a decline in species richness (Cannon 1971; Lite et al. 2005). In general, forest species are adapted to deep, moist soils rather than to the more extreme habitats of exposed rocky outcrops, where dry grassland species increase their proportion (Chytrý and Tichý 2003; Douda et al. 2017).

Many studies mention river valleys as important migration corridors for plant species (Jeník and Slavíková 1964; Tockner and Ward 1999; Ward et al. 2001; Saarela et al. 2017). However, none of these compare the colonisation rates in river valleys with those outside river valleys. This also includes studies of invasive plant species for which dispersal along rivers is fundamental to their rapid spread outside of their native range (Hood and Naiman 2000; Richardson et al. 2007; Osawa et al. 2013; Aronson et al. 2017; Dyderski et al. 2017). In this study, we used an original approach to compare community saturation by plant species along a riverine gradient. Ancient forests served as a control where species richness is determined by the balance between species carrying capacity, colonisation rate and extinction rate. Under these conditions, the proportion of plant species in recent forests compared with that in ancient forests becomes a measure of colonisation rate.

As predicted, the recent forests in the river valley were saturated with plant species as they had been exposed to a high colonisation rate. This result confirms the strong importance of river valleys as natural corridors for species migration. River valleys may also serve as refuges for endangered plant species, with rapid dispersal among river sites helping prevent their extinction. Unfortunately, recent large constructions for irrigation, hydropower and reservoirs for urban water supply have caused major fragmentation of these river valley habitats (Nilsson et al. 2005). We hope that our results will serve to underpin conservation efforts and for the prioritisation of river valleys in conservation strategies.

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Author contributions JD and AH: conceived of the research; AH collected the data; JD and AH carried out the statistical analyses; AH with contributions from JD wrote the paper.

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Data availability Data available on https://plant-ecology-lab-czu.com/publications/.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

Ethical approval Not applicable.

Consent to participate Not applicable.

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Chapter 5

Study II: Contrasting responses of forest phenological guilds to complex floodplain change

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RESEARCH ARTICLE

Contrasting responses of forest phenological guilds to complex floodplain change

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Abstract

1. Understanding the seasonal dynamics of the forest herb layer and the factors that influence it is essential for predicting how the forest ecosystem, including mutualistic interactions, will respond to global change. However, to date, no research has investigated how understorey phenological guilds respond to major environmental threats and forest interventions.
2. We showed the marked changes in the phenological structure of floodplain forest plant communities over half a century at a multi-regional scale in Central Europe. Unlike previous studies focusing on individual species' responses to climate change, we examined shifts in species richness, frequency and abundance between phenological guilds within the plant community. We examined the effects of temporal variation in climate, hydrology, soil conditions and canopy structure, and assessed the effects of non-intervention and intervention management on phenological guild responses.
3. Our results show a significant loss of local species richness and a decline in species frequency in the forest understorey vegetation, associated with species exhibiting summer phenology. In contrast, an increase in abundance and richness of spring flowering species was observed, attributed to high nutrient loads and reduced flooding, respectively. The abundance of spring species increased only in stands where canopy cover increased over time, probably due to the suppression of summer flowering species, allowing spring flowering species to spread on open, bare ground. The community experienced a shift in maximum flowering plant richness from June to May. Despite management interventions such as clearcutting and tree planting, our data show similar temporal trajectories in intervention and non-intervention forests, indicating that changes in phenological structure are largely independent of recent management activities.
4. *Synthesis*. We propose that a complex interplay of environmental factors, rather than climate change alone, is shaping shifts towards earlier phenological guilds in floodplain forests. This study highlights the importance of considering a comprehensive view of phenological guild dynamics and the impact of environmental factors on forest plant community structure in the face of global change.

KEYWORDS
canopy cover, climate change, flowering, management interventions, phenological structure, phosphorus, spring species, summer species

1 | INTRODUCTION

A forest herbaceous layer plays a critical role in mediating carbon sequestration, energy flow and efficient nutrient recycling (Muller, 2014; Neufeld & Young, 2014; Welch et al., 2007). Although it represents only less than 1% of the plant biomass of temperate forests, it includes more than 90% of a total plant species richness (Gilliam, 2007). The level of light received by herbaceous species in the forest understorey is seasonally controlled by the chronology of leaf initiation of canopy trees. In temperate deciduous forests, this is a crucial factor for establishing adaptive differentiation of plant phenological cohorts, starting with shade-intolerant species in the spring and progressing to shade-tolerant species in the summer (Rathcke & Lacey, 1985). Spring flowering species must start their life cycle before leaf development of canopy trees, because their photosynthetic output is not sufficient under reduced photosynthetic radiation (Kudo et al., 2008). In contrast, summer species, that is species growing and blooming later in the shade of the canopy, have a more efficient photosynthesis at lower light levels (Sparling, 1967).

The temporal environmental changes may cause specific species to increase or decrease their presence depending on the phenological cohort (hereafter referred to as phenological guilds, or PhGs). We define a PhG as a group of species that co-occur over time in a given phenophase. Due to existing pre-adaptations, with respect to the use of seasonally available resources, shifts in seasonally available resources can reshape patterns of PhG co-occurrence within the plant community. This may affect seasonal peaks in diversity and overall abundance in the forest understorey by promoting performance or excluding specific PhGs through environmental filtering. Changes in seasonal environmental filters can also narrow or lengthen the period during which rich and abundant herbaceous vegetation is present (hereafter referred to as seasonal evenness in diversity and abundance of PhGs; Menzel & Fabian, 1999; Oehri et al., 2017). Although these phenology-specific environmental effects remain poorly understood, they have a potentially strong impact on nutrient cycling and the performance of other trophic guilds in forest ecosystems (Beard et al., 2019; Rafferty & Ives, 2012).

There is some evidence that the abundance of spring species, that is species with significant biomass development and onset of flowering in the months before tree leafing, has increased in recent decades (Dierschke, 2013; Heinrichs & Schmidt, 2017). Spring species are particularly sensitive to an earlier onset of the growing season, and with a warmer climate in spring, their growth period may be extended (De Frenne et al., 2010). Increasing winter temperatures may promote their rhizome growth (Philipp & Petersen, 2007), alongside with increasing winter and spring precipitation may even promote their performance and population spread (Dierschke, 2013). These factors may contribute to the increased diversity and abundance of spring species. In contrast, stable (Bernhardt-Römermann et al., 2015; Chase et al., 2019; Dornelas et al., 2014; Vellend et al., 2013) or declining (Chudomelová et al., 2017; Hédl et al., 2010) diversity and abundance have been found in studies that include summer species. For temperate forest ecosystems, atmospheric pollution, increased shading following abandonment of traditional forestry practices and game pressure are the most commonly cited drivers of vegetation composition and diversity change (Bernhardt-Römermann et al., 2015; Chudomelová et al., 2017; Hédl et al., 2010; Keith et al., 2009; Staude et al., 2020). In addition, climate change, manifested by a reduction in summer rainfall followed by subsequent desiccation, is allowing some drought-tolerant species to survive at the expense of more water-demanding summer species (Feeley et al., 2020; Garssen et al., 2014).

The negative effects of climate change may not be as obvious, at least for the summer phenological cohort in forest ecosystems, as the canopy microclimate has been shown to mitigate the detrimental effects of the macroclimate (De Frenne et al., 2013; Zellweger et al., 2020). The microclimate in the forest is determined by the three-dimensional canopy structure, which promotes shading, air mixing and evaporative cooling (Atkinson, 2003), thus buffering against extreme heat and drought (De Frenne et al., 2019). However, today's temperate forests are suffering from more unpredictable weather, characterised by more extreme droughts and heavy rainfall (Anderegg et al., 2013; Gonzalez et al., 2010). This is accompanied by the spread of pathogens such as *Phytophthora alni* and *Hymenoscyphus fraxineus*, resulting in higher tree mortality of alder and ash (Bjelke et al., 2016; Grosdidier et al., 2020), which are among the dominant tree species in floodplain forests. This interaction of the aforementioned factors is still yet unknown in floodplain vegetation (Havrdová et al., 2023).

To enhance forest recovery, silvicultural management involving clearcutting and mechanical soil preparation with the application of herbicides prior to new tree planting is often used, which can have a negative effect on the diversity of spring and summer species (Newmaster et al., 2007; Šebesta et al., 2021). Increased drought and pathogens causing tree mortality and logging of woody biomass open forest canopies and accelerate thermophilisation—the onset of warm-adapted species (Stevens et al., 2015; Zellweger et al., 2020) that include competing tall species with higher biomass or dominance (De Frenne et al., 2015; Govaert et al., 2021). It follows that the effects of climate change on forest plant communities must interact strongly with the forest management practices applied in particular locations. Given the current global trend of natural forest opening due to repeated drought events and the spread of pathogens, the impact of clearcutting interventions on the forest understorey should be clearly assessed compared to no intervention.

In addition, recent eutrophication of forest soils may favour the growth of spring species more than summer species. In the past, European temperate deciduous forests have been overexploited by human practices such as tree coppicing, litter raking and grazing, all of which remove biomass, leading to severe soil nutrient limitation (Glatzel, 1991). However, the cessation of regular nutrient removal from forest ecosystems in the 20th century and the massive use of NPK fertilisers in the countryside led to a replenishment of nutrients. Specifically, floodplain forests located on the banks of large rivers were particularly affected by excessive nutrient inputs (Havrdová et al., 2023). Spring species appear to be quite nutrient demanding due to their rapid growth strategy and high photosynthetic rates that require high nitrogen and phosphorus inputs (Anderson & Eickmeier, 2000; Lapointe & Lerat, 2006; Merryweather & Fitter, 1995). The presence of underground storage organs such as bulbs and rhizomes allows nutrients to be taken up and remobilised from the leaves throughout the year, which can also be essential for spring growth (Fichtner et al., 2018; Rothstein & Zak, 2001; Stolle, 2004). An alleviation of soil nutrient limitation may have increased their abundance and diversity in recent decades. The spring species relocate and store nutrients in below-ground organs before summer species become active (Anderson & Eickmeier, 2000; Lapointe & Lerat, 2006; Nault & Gagnon, 1988). They may therefore have an advantage over summer species in capturing nutrients released by leaf decay and accumulated by early spring flooding (Anderson & Eickmeier, 2000; Muller & Bormann, 1976; Tessier & Raynal, 2003).

In this study, we test the effects of temporal changes in climate, hydrology, soil conditions and canopy structure on PhGs of floodplain forests in terms of herbaceous species richness and abundance under non-intervention management compared to intervention. Floodplain forests are a suitable model system for our study because they contain up to 10% of the spring species of total species richness in their herbaceous layer (Douda et al., 2016; Vymazalová et al., 2016). We monitored changes in vegetation at 117 selected sites established in the 1950s and 1960s in several river basins. We then evaluated the effects of the above environmental factors both without and with clearcutting management. We did this by monitoring the original sites, without intervention, with nearby new plots that had been recently logged. This approach makes it possible to determine the interaction between the effects of environmental changes and the management interventions applied in the forests. We hypothesised that spring and summer PhGs will respond differently to environmental changes represented by forest management and succession, climatic and hydrological changes over about 60 years in floodplain forests. This is due to the lower dependence of spring PhGs on changes in forest understorey light conditions and the potential effects and interactions with other environmental factors such as changes in climate, nutrients and hydrological regime.

2 | MATERIAL AND METHODS

2.1 | Study system

The study sites include floodplain forest vegetation distributed along four large rivers in the Czech Republic, represented by mean discharges of 27.2 m^3/s for the Dyje, 74.89 m^3/s for the Labe, 47.6 m^3/s for the Morava and 37,94 m^3/s for Ohře for the study area (Figure 1). They are composed of species-rich tree assemblages dominated mostly by *Fraxinus excelsior* and *Quercus robur* (the frequency of the other tree species is given in Table S13). Common spring species are *Anemone nemorosa*, *Corydalis cava* and *Gagea lutea*, while common summer species are *Brachypodium sylvaticum*, *Lamium maculatum* and *Urtica dioica*. They belong to phytosociological associations of floodplain hardwood forests (*Ficario vernae-Ulmetum campestris* and *Fraxino pannonicae-Ulmetum glabrae*), nutrient-rich elm-ash forests (*Pruno padi-Fraxinetum excelsioris*) and oxbow swamp forests (*Carici ripariae-Alnetum glutinosae*) (phytosociological nomenclature is according to Douda et al., 2016). The climate is sub-continental, with the mean temperature between 9 and 10.5°C and the mean annual precipitation between 500 and 600 mm. Rivers have been regulated since the 19th and first half of the 20th centuries. The Morava and Dyje rivers preserve, in some parts, their natural water regime with regular spring flooding.

In all study sites, the floodplain forest fragments were once managed as coppice or coppice with standards (i.e. regularly cut in a 30–40 year cycle and re-sprout with multiple stems) for hay production or wood pasture until the turn of the 19th and 20th centuries (Havrdová et al., 2023). These forests were then converted to high forests (harvested and replanted from saplings) in the first half of the 20th century. At the time of the original vegetation sampling, the average age of the stands was 44 ± 24 years (mean ± SD), that is 74% of the sampled forest stands were less than 60 years old. Currently, these forests are managed as high forests, using thinning, selection harvesting or clearcutting with long periods of canopy closure, or non-interventional conservation management is applied.

2.2 | Historical vegetation plot dataset

The reference dataset consists of 192 historical vegetation plots that were sampled by four experienced botanists between the years 1955 and 1970 (published in Bednář, 1964; Horák, 1960; Horák & Dvořák, 1968; Neuhäuslová-Novotná, 1965; Novotná, 1958). The aim of the authors was the classification of phytosociological communities in floodplain lowland forests. The authors sampled vegetation using phytosociological relevés following the Braun–Blanquet approach.

To locate the plots, the original authors indicated the location in forest compartments with an average size of 2.33 ± 4.96 ha (mean ± SD) on historical forest maps (scale 1:10000). The dataset may suffer from a type of relocation error that is rarely quantified in research studies (Douda et al., 2023), although there is some evidence that it tends to be less significant than observer error

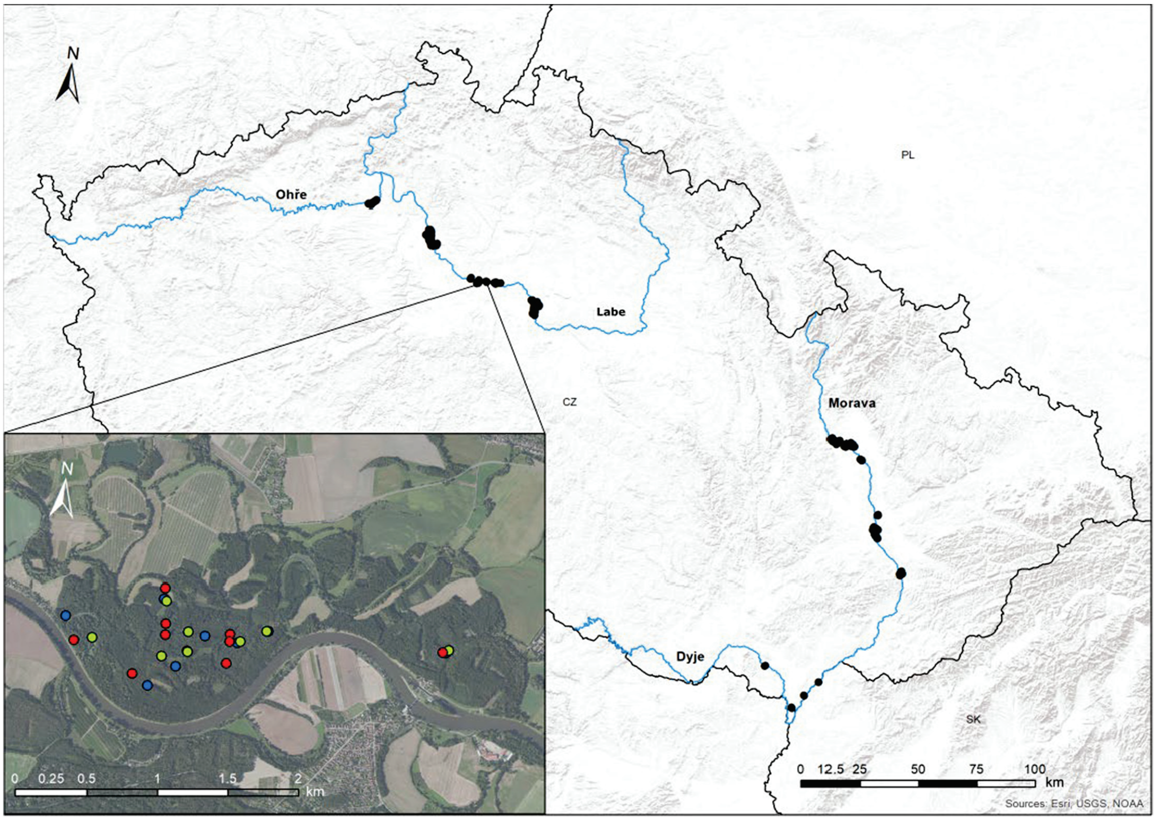

FIGURE 1 Distribution of study sites along four major rivers (Dyje, Labe, Morava and Ohře) in the Czech Republic and an example of their fine-scale distribution in a nature reserve, Mydlovarský luh. Blue dots represent original; red dots represent mature; and green dots represent clear-cut forest stands.

(Verheyen et al., 2018). As the forest compartments were defined by the foresters as homogeneous flat areas with similar growth conditions and tree species structure, the reallocation error is unlikely to have a significant impact on the data.

2.3 | Vegetation resurvey

Coordinates of the centre of forest compartments, taken from historical forest maps, were used to relocate the historical vegetation plots. Two new vegetation plots were sampled at the location of each historical vegetation plot. The first, hereafter referred to as the mature forest, was the forest stand that had not been harvested since the historical sampling, with a corresponding tree layer species composition. In our design, standing mature forest represented forest non-intervention management. For the second vegetation plot, we searched within a radius of 100 m from the original coordinates for the forest stand that had been cut and replanted, hereafter referred to as clear-cut forest. This forest had to be similar in age (±10 years) to the forest stand at the time of historical sampling, that is original forest.

The original vegetation plot was not resampled if the age of the current forest stand, as determined by current forest maps, was younger than would be expected based on natural ageing (i.e. the stand has been cut or thinned out over time). In the end, 117 of the 192 historical vegetation plots were re-surveyed. Plots were sampled within 30 days of the original sampling date in years 2019–2022. Those plots that were originally sampled twice per season for spring and summer aspects were resampled in spring and summer (i.e. 72 of the total 117 plots). The plot size corresponded to the original sampling and was 200–500 m^2. For comparison with the original plots, all vascular plants present were assigned to four vertical layers (i.e. trees: >3 m, shrubs: 1–3 m, seedlings and saplings of woody species: <1 m and herb layer); their cover was estimated using the 7-step version of the Braun–Blanquet scale (categories and their back-transformation into percentage cover: $r = 1\%$, $+ = 2\%$, $1 = 3\%$, $2 = 13\%$, $3 = 38\%$, $4 = 68\%$, $5 = 88\%$) as implemented in the programme TURBOVEG (Hennekens & Schaminée, 2001). Plant nomenclature follows Kaplan et al. (2019). No permission was required for the fieldwork conducted in this study.

2.4 | Climate, hydrology and canopy changes

To assess climatic and hydrological changes between historical and current sampling periods, we analysed data for mean daily temperature, monthly precipitation and mean daily discharge. These data were measured 10 years prior to the year of sampling at the site (Table S1). The data were obtained at the nearest climatic and hydrological stations operated by the Czech Hydrometeorological Institute. We calculated several variables that characterise changes in the spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February) seasons. They included variables that characterise changes in the mean daily temperature and the balance between drought and humidity, calculated using the Standardised Precipitation-Evapotranspiration Index (SPEI). SPEI was calculated from monthly potential evapotranspiration (PE) using the Thornthwaite equation (Thornthwaite, 1948). SPEI expresses the climatic water balance for each month as precipitation minus potential evapotranspiration (Beguería et al., 2014; Vicente-Serrano et al., 2010).

The hydrological regime of the rivers was represented by variables describing changes in river flood regimes characterised by the difference between daily discharge (m^3/s) and flooding reached or exceeded once a year on a long-term average (i.e. *Q1*, according to the Czech Hydrometeorological Institute). We also calculated the relative elevation (m) of each vegetation plot above/below the flood level reached or exceeded once every 5 years, using a digital terrain model (DMR 4G, a total standard error of 0.3 m in elevation) and maps showing areas covered by 5-year floods (using a hydrological map developed by T. G. Masaryk Water Research Institute).

Canopy changes were characterised by changes in canopy tree cover, tree richness, cover of *Quercus robur* and litter quality and community tree species dissimilarity between historical and current vegetation plots. Tree litter quality was estimated using an ordinal scale (1–5), according to Maes et al. (2019), with increasing values indicating higher litter quality. The Bray–Curtis measure was calculated for community tree species dissimilarity using non-transformed species cover values. A detailed description of all variables can be found in the chapter *Description of the environmental variables* in Supporting Information.

2.5 | Soil conditions

To characterise soil conditions, we measured soil reaction, bioavailable nutrients and particle size that were collected only for the current sampling period, except for pH-H_2O, which was also measured during historical sampling. The soil samples of the upper 10 cm of the mineral soil were taken from five locations of each plot (four corner points and one centre). The samples were mixed together, dried and passed through a 2-mm mesh. The soil samples were analysed for pH-H_2O, proportions of exchangeable base cations (Ca^{2+}, Mg^{2+} and K^+) and bioavailable phosphorus concentration. A detailed soil analysis methodology is described in Supporting Information (see chapter *Soil analysis*).

2.6 | Data analyses

To assess the temporal responses of PhGs, we used changes in their total plant cover (TPC) and species richness. Gymnosperms, as well as other tree species, were not included in the analysis of TPC and species richness. On the other hand, we kept ferns and horsetails in the dataset, despite their non-flowering status, as they also have important phenology in spore and biomass production. The TPC and species richness of month (March–October) PhGs were determined based on the species recorded in a given plot that flower in a given month. The flowering time of each species, defined by the months between the start and end of flowering, was taken from Kaplan et al. (2019). TPC was defined as the sum of the back-transformed per cent cover of herbaceous species. Therefore, TPC in a community can exceed 100%. We did not account for species cover overlap (Fischer, 2015; Jennings et al., 2009), which have a fixed upper limit (100%) and may lead to underestimation of dense, structurally diverse vegetation (Axmanová et al., 2012). Seasonal evenness (SE) in species richness and TPC was calculated for each plot using a normalised measure of their distributions across months (Levins, 1968): $SE = \left[\left(1 / \sum_i^M p_i^2\right) - 1\right] / (M - 1)$, where M is equal to eight, and corresponds to 8 months (March to October) and p_i is the proportional species richness and TPC at plot i in each month M, that is $\left(\sum_i^M p_i = 1\right)$. The value of SE ranged from 0 (if species flower exclusively in 1 month) to 1.0 (if species flower in equal proportions in all months). We then expressed the seasonal maximum (SM) as the PhG with the highest species number (richness maximum) or abundance (TPC maximum) in each vegetation plot.

We built linear mixed-effect models (LMMs) to test how the TPC and species richness of PhGs differed among original, clear-cut and mature forest plots (further referred to as treatments). We tested whether the response of TPC or species richness of specific PhGs differed among treatments using the interaction term. For the PhGs, we used the quadratic function with the months of the growing season coded as an ordinal variable (March–October). As a random factor, we used the PhGs to remove pseudoreplication given by species flowering in several months. This variable was nested within the plot ID as all PhGs shared the same plot. LMMs were constructed to test the effects of treatments on the SE and SM. Site ID, which always included three plots with different treatments, was included as a random effect. The LMMs were implemented using the lme4 package.

We constructed piecewise structural equation models (SEMs) to determine the direct and indirect effects of soil conditions and changes in climate, hydrology and canopy on TPC and the species richness of PhGs. In addition, we identified how these effects interact with the treatment. We separately constructed SEM for each PhG to assess differences in the importance of influencing factors.

In total, eight SEMs (March–October) were built. The SEMs allow the fitting of mixed-effect models with site ID as a random factor. For the SEMs, we always selected a maximum of three biologically relevant variables within the category of environmental factors (i.e. climate, hydrology, soil conditions and canopy) in order to keep the models as simple as possible, but to include explanatory variables with the most important effect (Table S1, see chapter *Rationale and selection procedure for variables* in Supporting Information). In the end, we selected a total of 12 explanatory variables (Table 1): bioavailable phosphorus, calcium, proportion of coarse sand soil fraction, changes in spring and summer humidity, change in winter temperature, changes in spring and summer flooding, relative site elevation to 5-year flood, change in tree canopy cover, change in tree species richness and change in mean leaf litter quality. We considered species richness, TPCs and environmental changes calculated as differences between current (i.e. mature, clear-cut forest) and historical (original forest) sampling (Δ, Table 1). To remove the effects of differences in species richness, TPC and environmental predictors between plots of the historical survey, and to consider only the implicit rate of change of these variables over the study period, we used in all models the Δ of all these variables, but also the values of the same factors estimated at the time of the first survey as covariates. Prior to model fitting, we log-transformed the dependent variable where necessary to achieve normality of the model residuals.

The SEMs were evaluated using Fisher's C statistic, with a model accepted if the associated $p > 0.05$ and has the lowest Akaike's information criterion (AIC; Shipley, 2009). After fitting our initial models (Table S3), we started the backward stepwise selection procedure (Grace, 2006). First, we removed all non-significant interactions. Then, at each step of backward selection, the non-significant path with the highest p-value was dropped. This was done until the best-fitting model was identified. Standardised path coefficients were used to assess the effects of predictors for best-fit models (Grace & Bollen, 2005). For all dependent variables, we calculated the explained variability as the marginal R^2m value (fixed effect) following Nakagawa et al. (2017). The summaries of the best models are given in Table S4. Piecewise SEMs were calculated using the piecewise SEM package (Lefcheck, 2016). All analyses were performed in R (R Core Team, 2022).

To describe changes in the species composition of PhGs among original, clear-cut and mature forest plots, we calculated non-metric multidimensional scaling (NMDS) analysis using the vegan package (Oksanen et al., 2020). The Bray–Curtis index was used as a measure of dissimilarity on log-transformed species cover data.

3 | RESULTS

3.1 | Temporal changes in plant phenological guilds

Total plant cover and species richness showed different temporal changes between spring and summer flowering species, as indicated by significant interactions between treatment and PhG (Table 2).

The total cover of spring flowering species (PhG: March–May) increased on average by 24 ± 51.84% (mean ± SD) compared to the original forest plots with 47.6 ± 45.51%. On the contrary, summer PhGs (July–August) decreased by 20.11 ± 56.34% compared to the original plots with 86.35 ± 38.91% (Figure 2A). Species richness decreased between original and mature forest plots (Figure 3A), with an average decrease of 6.85 ± 5.74 compared to original plots with 16.37 ± 6.67 for May–September PhGs. Species richness did not change for March and April PhGs.

The phenological structure of the community also changed over the study period, with a shift from a June maximum in flowering plant richness to the current May maximum in flowering plant richness (Figure 3B). The TPC of some PhGs also changed, with May flowering species increasing cover and July flowering species decreasing cover (Figure 2B). These changes resulted in higher seasonal evenness in diversity and abundance of PhGs throughout the growing season (Figures 2C and 3C).

These trends are also reflected in frequency changes of species site occupancy and community composition. Species frequency data showed that 50% of the summer flowering species (June–August) were present on at least 5% of the historical vegetation plots, whereas at most half of the species (25%) are currently present on the same number of vegetation plots (Figures S1–S3). Almost 50% of the summer flowering species have been lost, as indicated by their zero frequency in mature forest stands. Many common summer flowering species, such as *Campanula trachelium*, *Fragaria moschata* and *Deschampsia cespitosa*, have almost completely disappeared (Table 3). On the contrary, several originally low or moderately frequent spring flowering species, such as *Anemone ranunculoides* and *Corydalis cava*, doubled in frequency. Consistent with this, the main trends in species composition change between the original and current plots detected by NMDS analysis corresponded to an increase in spring flowering species and a few resource-acquisitive summer species (e.g. *Galium aparine* and *Urtica dioica*), and a decrease in most summer flowering species (Figure S4).

3.2 | Environmental factors affecting plant phenological guilds

The SEMs showed that the interaction effect between bioavailable P and tree cover was the most important in explaining changes in total spring PhG cover (Figure 4a). Spring PhG cover increased with increasing tree cover, but only at sites with higher P levels (Figure S5). Maintenance of regional humidity and reduced spring flooding also contributed to the increase in PhG cover of spring flowering species (Figure 4a). The negative direct effect of tree cover was found for summer PhG cover (Figure 4b), but the most important predictors were bioavailable nutrients (P and Ca), which were positively correlated with increases in summer flowering species cover. The species richness of the spring PhGs was negatively correlated with the maintenance of the spring flooding (Figure 4c). Contrary to its positive effect on total summer species cover, bioavailable P was negatively

TABLE 1 Average values and changes (Δ) of environmental factors considered as explanatory variables for species richness and total plant cover (TPC) of PhGs during the resurvey period.

Category	Variable	Description	Mean ± SD	Δ ± SD
Canopy	LitterQuality	Tree species litter quality[a]	3.26 ± 1.16	0.41 ± 0.97
	TreeCover	Total tree species cover (%)	76.22 ± 26.0	−8.91 ± 31.83
	TreeRichness	Number of tree species	3.58 ± 1.71	−0.29 ± 2.07
Climate	HumiditySpring	Spring months SPEI[b] average	−0.08 ± 0.38	−0.66 ± 0.34
	HumiditySummer	Summer months SPEI average	−0.01 ± 0.41	−0.63 ± 0.41
	TempWinter	Winter months average temperature (°C)	−0.27 ± 0.42	1.53 ± 0.28
Hydrology	FloodElevation	Relative elevation of vegetation plot to Q5 flood (m)	−0.39 ± 1.64	—
	FloodingSpring	Discharge in spring months relative to Q1 flood (m^3/s)	−437.93 ± 123.88	−15.71 ± 6.28
	FloodingSummer	Discharge in summer months relative to Q1 flood (m^3/s)	−471.41 ± 133.80	−2.84 ± 6.17
Management	Management	Mature forest/clear-cut forest	—	—
Soil	Coarse sand	Soil texture; grain size 0.25–2 mm (%)	7.15 ± 10.53	NA
	Ca	Bioavailable calcium (mg/kg)	3412.92 ± 1885.67	NA
	P	Bioavailable phosphorus (mg/kg)	36.59 ± 32.72	NA

Note: NA data not available.

[a] Tree species litter quality is estimated on an ordinal scale (1–5), with increasing values indicating higher litter quality (Maes et al., 2019).

[b] Standardised Precipitation-Evapotranspiration Index (SPEI); values above 0 indicate average wet conditions and below 0 indicate average dry conditions;

correlated with summer PhG richness in regions that maintained their humidity and summer flooding (Figure 4d).

3.3 | The effects of intervention management

The TPC, species richness, frequency and composition showed no remarkable differences in temporal trends between clear-cut and mature plots (Figures 2 and 3 and Figures S1–S4). However, the species richness of summer PhG species increased on clear-cut sites with a higher proportion of coarse sand particles in the soil (Figure 4d, Figure S6). On the more frequently flooded plots, the management intervention led to a decrease in tree diversity (Figure 4 and Figure S7).

4 | DISCUSSION

Our study describes a marked change in the phenological structure of the forest plant community over half a century in several catchments of Central Europe. In contrast to the often discussed direct effect of climate change on a shift towards earlier flowering of individual plant species (Inouye, 2022; Parmesan & Yohe, 2003), our study focuses on shifts in species richness and abundance between phenological guilds within a plant community. We suggest that a more complex set of environmental factors is important for phenological structure in forest communities that appear to be relatively resistant to climatic stressors (Atkinson, 2003; De Frenne et al., 2013, 2019; Zellweger et al., 2020). Other widespread negative pressures, such as nutrient overloading and forest ageing, appear to be more severe for them (Doudová et al., 2022; Landuyt et al., 2020; Maes et al., 2019; Verheyen et al., 2012).

We confirmed a significant loss of local species richness and a decline in species frequency across forest understorey sites. This is consistent with several other forest resurvey studies that have shown species decline at the spatial scale of the study site (Chudomelová et al., 2017; Hédl et al., 2010) or at the habitat scale (gamma diversity; Staude et al., 2020). In our case, this decline was only related to species with summer phenology. At the same time, we observed an unexpected increase in the abundance of spring flowering species associated with high nutrient loads and increased

TABLE 2 Effects of management intervention (treatment) on the course of total plant cover (TPC) and species richness of PhGs during the growing season (March–October) tested by linear mixed effects models (LMMs). PhGs were coded continuously. LMMs were also constructed to test the effects of treatments on seasonal evenness (SE) and the seasonal maximum (SM) of TPC and species richness. Site ID, which included three plots with different treatments, was a random effect.

Dependent	Independent	SS	NumDF	DenDF	*F*-value	*p*-value
TPC	Treatment	1904	2	343	1.45	0.237
	PhG	958,348	2	343	727.42	<0.001
	Treat × PhG	29,234	4	343	11.1	<0.001
Richness	Treatment	1916	2	345	127.3	<0.001
	PhG	17,801	2	373	1182.7	<0.001
	Treat × PhG	1856	4	373	61.7	<0.001
Seasonal evenness (SE)						
TPC	Treatment	0.231	2	229	9.1	<0.001
Richness	Treatment	0.200	2	228	25.2	<0.001
Seasonal maximum (SM)						
TPC	Treatment	7.438	2	228	10.8	<0.001
Richness	Treatment	8.047	2	231	10.2	<0.001

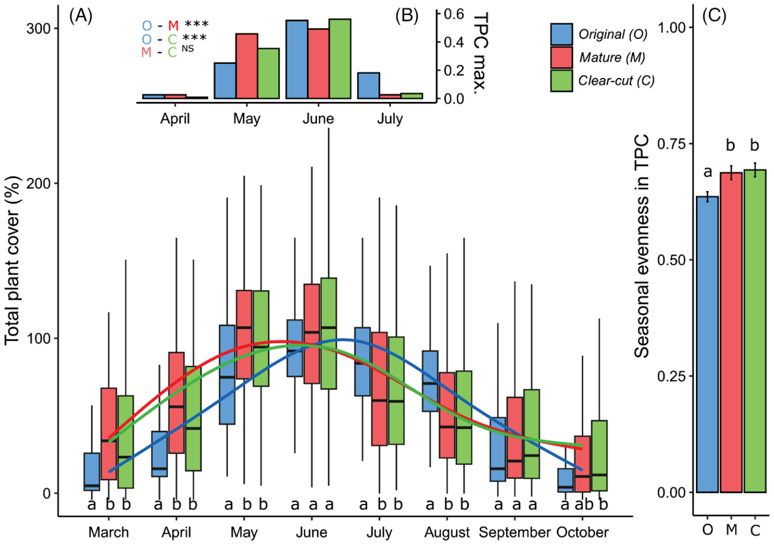

FIGURE 2 Effects of treatment on (A) total plant cover (TPC) of monthly phenological guilds, (B) seasonal maximum (SM) and (C) seasonal evenness in TPC. In panel (A), different letters below box plots (showing median, lower and upper quartiles and 1.5 times the length of the interquartile range) indicate significant differences ($p < 0.05$) between treatments for each phenological guild, with lines smoothed using parameter *k* set to five. In panel (B), the values of TPC max (SM) show the frequency of vegetation plots with the highest abundance of flowering species in individual months; *** indicates differences ($p < 0.001$) between treatments. In panel (C), different letters indicate differences ($p < 0.05$) between treatments (data are means ± standard errors). NS indicates non-significant differences. Differences between treatments were tested using the Tukey post-hoc test.

canopy cover. Below, we discuss in detail specific environmental factors that influence the responses of particular phenological guilds, and highlight the potential consequences of different management actions currently being taken to protect forest communities.

4.1 | Summer species

We found a significant decrease in the number of species with summer phenology, with an average decrease of almost 50% species per vegetation plot. Reduced light perception below the canopy due to successional changes or infrequent management interventions is considered one of the most important causes of forest biodiversity decline (Chudomelová et al., 2017; Douda et al., 2021; Doudová et al., 2022; Hédl et al., 2010). In this study, however, we did not find support for the negative effect of canopy shading on the species richness of the understorey. Instead, there was a strong negative effect of nutrient overload on the richness of species with summer phenology and a positive effect on the abundance of this guild. Bioavailable phosphorus had a significant direct positive effect on total summer species cover, alongside a less significant positive effect of exchangeable soil Ca^{2+} concentrations and a negative effect

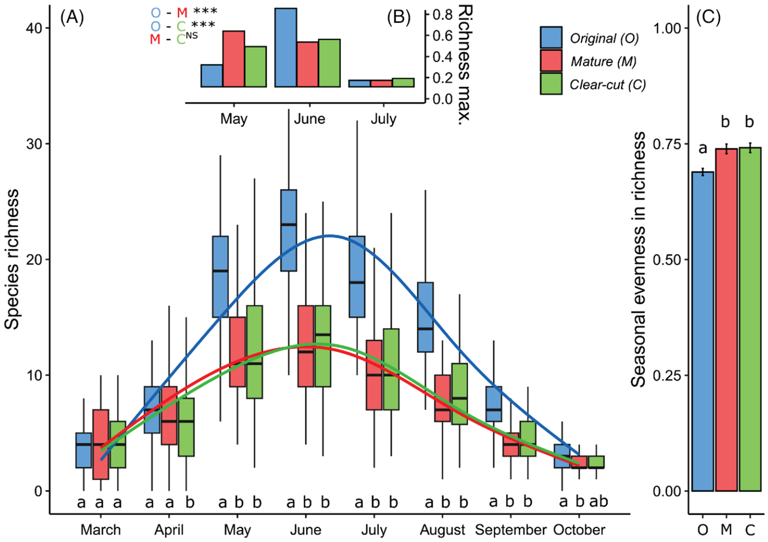

FIGURE 3 Effects of treatment on (A) species richness of monthly phenological guilds, (B) seasonal maximum (SM) and (C) seasonal evenness in species richness. In panel (A), different letters below box plots (showing median, lower and upper quartiles and 1.5 times the length of the interquartile range) indicate significant differences ($p < 0.05$) between treatments for each phenological guild, with lines smoothed using parameter k set to five. In panel (B), the values of richness max (SM) show the frequency of vegetation plots with a predominance of flowering species in individual months; *** indicates differences ($p < 0.001$) between treatments. In panel (C), different letters indicate differences ($p < 0.05$) between treatments (data are means ± standard errors). NS indicates non-significant differences. Differences between treatments were tested using the Tukey post-hoc test.

of canopy shading. The negative effect of soil phosphate content on herb layer diversity has been demonstrated for alluvial hardwood forests (Strubelt et al., 2017). The nutrient-demanding species benefit most from increased phosphorus bioavailability, as they are able to extract and utilise nutrients more efficiently and thus rapidly increase their abundance (Hipps et al., 2005). In our study, this was particularly true in sites with more frequent summer flooding, making phosphorus available to nutrient-demanding plants. This is the case for species such as *Urtica dioica*, *Impatiens parviflora* and *Galium aparine*, which have increased in abundance in floodplain forests over the last half century, with potentially negative effects on the understorey (Figure S4). While the native dominant *Urtica dioica* has been shown to have a strong negative effect on herbaceous species diversity (Hejda et al., 2021), no negative effect on understorey diversity has been observed for the non-native *Impatiens parviflora* (Hejda, 2012).

4.2 | Spring species

As the growth of spring species seems to be supported by increasing temperature and precipitation in winter and spring (De Frenne et al., 2010; Dierschke, 2013; Philipp & Petersen, 2007), we expected their abundance to increase with an earlier onset of the growing season. However, our results showed no correlation between winter temperature and the abundance of spring flowering species. Instead, the factors that contributed to an increase in the abundance of spring species were the maintenance of spring moisture over time. By analysing multiple factors in SEM, we were able to disentangle that the interactive effect of bioavailable phosphorus with increased canopy cover in the forests was likely to be the main driver of their success. Spring species benefit from higher phosphorus bioavailability due to their rapid growth strategy, which requires the accumulation of large amounts of phosphorus to ensure a proper development of above-ground organs (Anderson & Eickmeier, 2000; Lapointe & Lerat, 2006; Nault & Gagnon, 1988). Surprisingly, the increase in abundance of spring flowering species was only associated with the closed canopy forest stands with reduced solar radiation during most of the growing season. SEM shows that the abundance of species with summer phenology decreased with canopy closure. This may provide more space for spring ephemerals to colonise gaps without the abundant biomass of summer species in closed stands. Conversely, in more open stands, the higher amount of dry biomass from the previous year and the early emergence of seedlings from the more abundant summer phenology guild may limit the expansion of spring species. This is well known from grassland communities, where increasing accumulation of litter from competing grass species reduces light availability and accelerates loss of species diversity (Bobbink & Willems, 1987; Ruprecht et al., 2010; Špačková et al., 1998). Some studies have shown that spring geophytes perform best on sites with the lowest dry litter mass of summer species on the ground (Elias et al., 2018).

TABLE 3 List of species most affected by complex floodplain change (species with at least 30% increase or decrease). Data show the number of plots with species present in two different sampling periods, percentage of change (red indicates decrease, blue indicates increase) and first month of flowering. Only species that occur on an average of more than 10 plots between original and mature are included. Non-native species are marked with*.

	Number of occurrence plots ($n = 117$)		Change	
Plant species	**1950s–1960s**	**2018–2021**	**%**	**First month of flowering**
Fragaria moschata	31	0	−100	V
Campanula trachelium	59	4	−93	VII
Veronica chamaedrys agg.	55	5	−91	V
Ajuga reptans	53	5	−91	IV
Hypericum hirsutum	37	4	−89	VI
Paris quadrifolia	31	4	−87	IV
Scrophularia nodosa	53	7	−87	VI
Lysimachia nummularia	68	9	−87	V
Stellaria media agg.	34	5	−85	IV
Lapsana communis	27	4	−85	V
Symphytum officinale agg.	30	5	−83	V
Poa nemoralis	52	9	−83	VI
Deschampsia cespitosa	72	17	−76	VI
Convalaria majalis	42	10	−76	V
Filipendula ulmaria	30	10	−67	VI
Phalaris arundinacea	23	8	−65	VI
Iris pseudacorus	26	10	−62	V
Lathyrus vernus	36	16	−56	IV
Impatiens noli-tangere	33	16	−52	VII
Pulmonaria officinalis agg.	77	38	−51	III
Maianthemum bifolium	20	10	−50	V
Galium odoratum	16	8	−50	V
Silene dioica	21	11	−48	V
Moehringia trinervia	35	20	−43	VI
Aegopodium podagraria	95	63	−34	V
Dactylis polygama	98	67	−32	V
Gagea lutea	36	59	39	III
Anemone nemorosa	17	29	41	III
Ficaria verna	39	69	43	III
Corydalis cava	33	66	50	III
Veronica hederifolia agg.	25	57	56	III
Galeobdolon luteum agg.	15	37	59	IV
*Impatiens parviflora**	25	82	70	VI
Anemone ranunculoides	8	31	74	III

We found a positive effect of reduced spring flooding on spring species. Spring floods provide the wet, bare substrate that spring species need for germination and recruitment (Johnson et al., 2016). They also transport seeds and bulbs and accelerate the colonisation of floodplain forests by new species. Despite this, our results showed that increased flood frequency reduced the abundance and richness of spring species, indicating the negative effect of disturbances on geophyte growth. This could be due to the timing of the floods in the middle or end of their life cycle, which removes the above-ground parts of the plants.

4.3 | Community phenological shifts

Although a shift of the seasonal maximum towards earlier phenological guilds would be expected as an effect of climate change (De Frenne et al., 2010; Dierschke, 2013; Philipp & Petersen, 2007), our results show that non-climatic factors, particularly eutrophication, canopy shading and flooding, are the main drivers of vegetation change in riparian forests. Whereas half a century ago, the June phenological guild was the most diverse and abundant, the herbaceous layer is now dominated by species of May phenology.

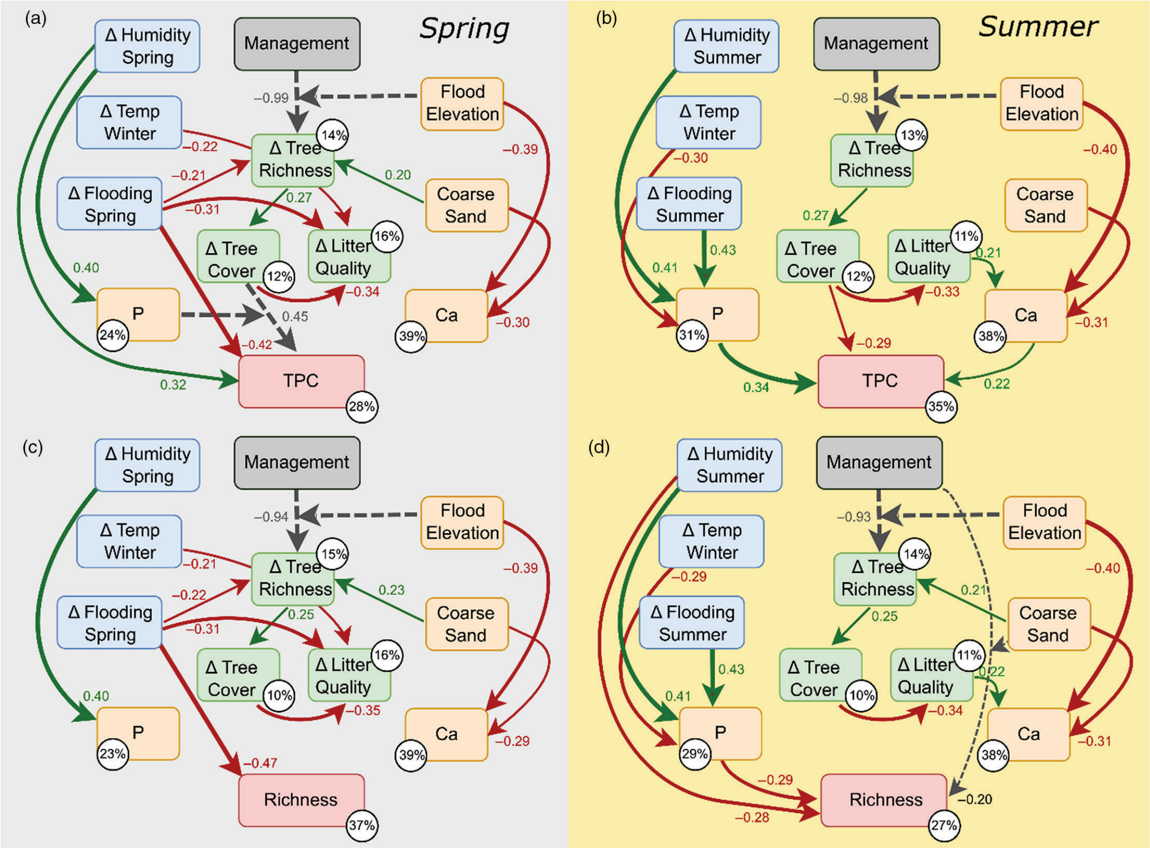

FIGURE 4 Path diagrams representing the best-fitting models for (a) total plant cover (TPC) of spring flowering species (Fisher's $C=68.73$, $df=58$, $p=0.158$), (b) TPC of summer flowering species (respectively 73.41, 62, 0.152), (c) richness of spring flowering species (respectively 68.78, 58, 0.138) and (d) richness of summer flowering species (respectively 65.59, 60, 0.289). The March and July phenological guilds represent spring and summer species. The best path models were obtained using a backward stepwise selection procedure and AICc. Piecewise structural equation models were fitted using linear mixed-effect models, with site ID identified as a random effect. Arrow widths are proportional to the value of the standardised path coefficients. Only relationships with coefficients less than −0.2 and greater than 0.2 are reported (see Table S3 for complete models). Green solid arrows indicate positive relationships; red solid arrows indicate negative relationships; and grey dashed arrows indicate significant interactions. Marginal R^2m values (fixed effect) are shown in a circle for each endogenous variable. Path diagrams for all phenological guilds are presented in the supplementary material (Figures S8–S10).

Wolf et al. (2017) have shown that shifts in community structure and biotic interactions can alter the timing and distribution of flowering events, and that these changes in phenology are similar in magnitude to effects induced by climate change. Consistent with this, our observed shift towards early-flowering guilds appears to interact with decreases in the abundance of summer guilds, and also resulted in increased seasonal evenness in community phenology.

A European meta-analysis of 39 resurvey studies of temperate forests showed no net local loss of diversity, while indicating considerable variation in diversity change between sites, which was attributed to temporal changes in local environmental factors (Bernhardt-Römermann et al., 2015). The strong decline in summer species diversity observed in our study suggests that floodplain forests are among the most threatened vegetation types in terms of biodiversity loss. This is not very surprising considering that these forest types are located at the most nutrient-rich parts of the productivity gradient and are affected by additional external sources of nutrients from the surrounding landscape (Havrdová et al., 2023), which could accelerate ongoing vegetation changes. This species loss occurs despite the extension of the season in which herbaceous vegetation is present (indicated by increased seasonal evenness). This could potentially negatively affect the diversity of mutualistic interactions (Rafferty & Ives, 2012) and nutrient cycling (Beard et al., 2019) in forest ecosystems during the summer. On the other hand, dense populations of spring plant species and their high nectar production make them an attractive food source for spring pollinators (Kudo et al., 2008). They can also potentially accumulate nutrients released from litter decomposition, preventing their loss through leaching into surface waters (Anderson & Eickmeier, 2000; Muller & Bormann, 1976; Tessier & Raynal, 2003). This suggests that the observed temporal shifts in phenological guild structure may also lead to strong changes in forest ecosystem functioning.

Species richness and abundance of phenological guilds (PhGs) were determined based on the species recorded in a given plot that flower in a given month, according to the literature. This approach limits the interpretation of our results in two ways. First, our results do not imply that community flowering has shifted to earlier months, as a species could be present in a plot in a given month but not flower. Therefore, our data should be interpreted as a change in abundance and species richness. Secondly, some herb species may have a relatively short flowering period but may be persistent throughout the year and contribute to the TPC and richness of the community. However, when we analysed changes in species richness and TPC according to other phenological metrics, such as seasonal leaf persistence of species (Figure S12), we found similar trends for leaf seasonality as for flowering, that is richness and TPC of summer species decreased and spring species increased.

4.4 | Management effect

We expected that opening the forest canopy would accelerate thermophilisation, leading to a reduction in the plant diversity of spring and summer species (Stevens et al., 2015). However, our comparison of changes in total cover and species richness showed the same trends for spring and summer phenological guilds between intervention and non-intervention forests (Figures 2 and 3). Thus, despite the expected role of management interventions on trends in species abundance, diversity and composition (Newmaster et al., 2007; Šebesta et al., 2021), our data show very similar temporal trajectories. This suggests that clearcutting and tree planting, followed by succession of the herbaceous layer based on processes of colonisation and plant residence in situ, do not contribute strongly to the process of forest degradation caused by environmental change.

Some positive effect of the forest intervention was observed on soils with a higher proportion of coarse sand particles, as this led to an increase in the alpha diversity of summer flowering species. However, most parsimonious path analyses do not indicate either direct or mediated effects of canopy characteristics such as canopy cover, as would be expected based on the generally known factor positively influencing forest understorey diversity, that is light availability at the forest floor (Bernhardt-Römermann et al., 2015; Chudomelová et al., 2017; Hédl et al., 2010; Keith et al., 2009). Instead, the results of the most parsimonious path analysis showed a negative effect of soils rich in sand particles on the TPC of summer flowering species. Higher TPC, represented by increased dominance of more competitive species, is expected on clay soils due to their greater ability to retain moisture during the summer months, which supports the growth of resource-demanding species (Butterfield et al., 2016). They may prevent the spread of less competitive species post-intervention on soils rich in clay particles, but they are not as prevalent on nutrient-poor soils. In summary, this trend in the data suggests that any intervention in nutrient-rich ecosystems, such as floodplain forests, should be carefully considered in relation to the environmental conditions of a site. While thinning to support summer species may be desirable on nutrient-poor sites, a more conservative approach to supporting the abundance of spring species may be more appropriate in forest stands with soils rich in clay particles.

5 | CONCLUSIONS

Our study suggests that changes in the phenological structure of forest communities were largely driven by non-climatic variables. The complex interplay of environmental factors, rather than climate change alone, is driving shifts towards earlier phenological guilds in floodplain forests. We found that contrasting trends in changes in abundance and diversity among phenological guilds were influenced by changes in competitive interactions modified by nutrient oversaturation of the ecosystem over the half a century. Tracking the fate of different phenological guilds in response to environmental change highlights the importance of such a comprehensive view, as it shows that the depletion of a plant community within a single guild can be compensated by an increase in the population of an overlooked guild of equal importance in the ecosystem food web.

AUTHOR CONTRIBUTIONS

Jan Douda and Jana Doudová designed the study, and all authors contributed to data collection. Jan Douda analysed the data with helpful contributions from Anežka Holeštová, Alena Havrdová and Jana Doudová. Anežka Holeštová, Jan Douda and Jana Doudová wrote the first draft, and all authors contributed to the revision of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1vhhmgr2c (Douda et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Environmental factors considered as explanatory variables for species richness and abundance of PhGs. Variables used in SEMs are indicated by asterisks.

Table S2. The Pearson correlation coefficient between richness or total plant cover (TPC) of PhGs and the variables considered for the theoretical structural equation models (SEMs).

Table S3. Overview of full and most parsimonious models.

Table S4. Overview of model quality of the most parsimonious SEMs using Fisher's *C* statistic.

Table S5. Frequency (%) of canopy tree species (E3) occurring in original, mature and clear-cut plots.

Figure S1. Species rank frequency curves for March, April and May phenological guilds in original, mature and clear-cut forest stands.

Figure S2. Species rank frequency curves for June, July and August phenological guilds in original, mature and clear-cut forest stands.

Figure S3. Species rank frequency curves for September and October phenological guilds in original, mature and clear-cut forest stands.

Figure S4. Non-metric multidimensional scaling (NMDS) showing (a) spider plot of differences in species composition of forest sites between treatments (mean site coordinate shown as centroid) and (b) associated species with colours indicating onset of plant flowering.

Figure S5. Interaction effect of log P and Δ TreeCover on TPC change for March, April, May and June PhGs, calculated using the R package sjPlot.

Figure S6. Interaction effect of treatment and coarse sand on richness change for July and August PhGs, calculated using the R package sjPlot.

Figure S7. Interaction effect of treatment and FloodElevation on tree richness change, calculated using the R package sjPlot.

Figure S8. Path diagrams representing the best-fitting models for total plant cover (TPC) and richness of (a, d) March, (b, e) April and (c, f) May phenological guilds.

Figure S9. Path diagrams representing the best-fitting models for total plant cover (TPC) and richness of (a, d) June, (b, e) July and (c, f) August phenological guilds.

Figure S10. Path diagrams representing the best-fitting models for total plant cover (TPC) and richness of (a, c) September and (b, d) October phenological guilds. Best path models were obtained using a backward stepwise selection procedure and AICc.

Figure S11. The Pearson correlation coefficient matrix of the variables considered for the theoretical structural equation models (SEMs).

Figure S12. Total plant cover (TPC) and species richness of original, mature and clear-cut plots.

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Chapter 6

Study III: Age heterogeneity in floodplain forest fragments promotes understorey plant diversity (*manuscript*)

Age heterogeneity in floodplain forest fragments promotes understorey plant diversity

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Abstract

Although most of floodplain forests in Central Europe are protected as nature reserves, there is ongoing significant biodiversity loss. The current practises leaving these forest ecosystems to natural processes seems inadequate and should be adapted to include active management. The age-class diversity, much like the structural diversity created by traditional forest practices, can be essential for maintaining biodiversity by providing a variety of microhabitats. We assessed the effects of different age-class structures between two time periods, i.e. 60 years ago and present on forest understorey vegetation across four floodplain areas of large rivers in Central Europe. We resampled 117 vegetation plots to find significant differences in species richness and composition between age classes and calculated so-called age-class evenness to compare overall distribution of age classes between historical and current sampling. The age class structures of 60 years ago were associated with much higher species richness than the age class structures of today. We concluded that a patchwork of diverse age classes including old-growth stands promotes the highest possible species richness in floodplain forests as each of those age classes provide different light conditions and thus light-demanding as well as shade-tolerant species can coexist. In addition, the younger forest stands should be used as

coppices or coppices-with-standards. On nutrient-rich soils with high clay content, the coppicing should be accompanied by traditional management practices that regularly remove a significant proportion of the biomass.

1 Introduction

Over the last century, Central European forests have undergone major structural changes due to human intervention, particularly shifts in forest management practices (Szabó, 2005; Müllerová et al., 2014; Kamp, 2022). One of the consequences of these changes is a significant biodiversity loss in temperate forests, leading to ongoing discussions about new forest management and conservation approaches (Buckley, 2020).

Until the first half of the 20th century, the heterogeneous light conditions and low nutrient levels that supported high biodiversity in forest ecosystems were maintained by practices such as coppicing, grazing, and litter raking (Gimmi et al., 2008; Kopecký et al., 2013; Douda, 2017). In a coppice system, young shoots were cut in short rotations (every 7–30 years), with new shoots resprouting from coppice stools or roots. In the coppice-with-standards variant, single-stemmed trees (standards) were retained in a sparse canopy among coppice stools for one or more rotations (Müllerová et al., 2014). However, traditional management practices, including coppicing, have been largely abandoned across most of Europe since the mid-20th century. Coppices were gradually transformed into high forests with prolonged canopy closure, leading to an increased and long-term shading of the forest floor (Savill, 2015). The lack of light led to the replacement of original species with predominantly shade-tolerant ones, causing further biodiversity loss (Beneš et al., 2006; Spitzer et al., 2008; Miklín & Čížek, 2014; Müllerová et al., 2015; Suchomel, 2020; Vild et al., 2024).

Although many valuable floodplain forest fragments in Central Europe are protected, biodiversity loss is still observed even in these areas (Kopecký et al., 2013; Miklín & Čížek, 2014;

Šebek et al., 2015). Current conservation policies often favour non-intervention management in forest habitats, to promote the development of late successional stages, which are valued for their high taxonomic diversity (Schultze, 2014; Havrdová et al., 2023). Late successional stages also provide suitable conditions for so-called true forest species, which are associated with long-term forest presence and are unable to survive in other environments (Hermy et al., 1999). These species are therefore highly valued, and their presence in temperate forests is considered crucial. However, this approach predominantly benefits shade-tolerant species and limits the spread of light-demanding species (Šebek et al., 2015; Becker et al., 2017; Vojík & Boublík, 2018; Vild et al., 2024). In abandoned coppices, non-intervention management has led to overgrowth, resulting in dense, poorly accessible forests that resemble the shading conditions of commercial forests (Kopecký et al., 2013, Müllerová et al., 2015). As a result, both commercial and protected forests are increasingly dominated by old-growth, shady, and homogenous forest stands with reduced biodiversity.

In recent decades, efforts have been made to restore open canopy conditions in experimental plots across various parts of European forests (Plieninger, 2015; Unrau et al., 2018; Johann, 2021; Tinya et al., 2023; Kozdasová et al., 2024). These interventions reflect a growing recognition of the importance of age-class heterogeneity in forest ecosystems. Age-class diversity, much like the structural diversity created by historical coppicing practices, is essential for maintaining biodiversity by providing a variety of microhabitats that support both light-demanding and shade-tolerant species through varied light conditions. A balanced age-class structure is particularly important for the survival of metapopulations, especially dispersal-limited species such as many understorey plant species that rely on myrmecochory or clonal dispersal. As the light intensity reaching to the forest floor varies between age classes, the age classes can be considered as different habitats with unevenly distributed light availability. It follows that an increase in the number of age classes within a given area should lead to an increase in species richness. Overall, this suggests that the highest possible species richness in temperate forests could be achieved by creating a patchwork of different age classes covering variously sized areas, i.e. high age-class heterogeneity. While coppicing historically maintained such diversity through regular cutting cycles, ecologically sustainable strategies can restore these dynamic conditions through targeted forest management practices.

To assess the effects of age-class structure on forest understorey vegetation, we compared species richness and species composition between age classes over the past 60 years in floodplain forests across four floodplain areas of large rivers of Central Europe. Using historical forest inventory maps and recent resampling of vegetation plots (Holeštová et al. 2024), we analysed 117 plots originally established by expert botanists in the 1950s and 1960s. We asked: (a) Has the age-class structure significantly changed over the past half-century? And (b) if such changes have occurred, have they influenced the heterogeneity of the understorey vegetation? We also investigated which age classes were associated with the highest understorey species richness and whether this increase was independent of the time of sampling and thus accompanying environmental change.

2 Material and Methods

2.1 Study area

The study area (Fig. 1) consists of floodplain forest fragments along four major rivers Labe, Morava, Dyje, and Ohře in the Czech Republic. The forest fragments belong to the phytosociological associations of floodplain hardwood forests (*Ficario vernae-Ulmetum campestris* and *Fraxino pannonicae-Ulmetum glabrae*), nutrient-rich elm-ash forests *(Pruno padi-Fraxinetum excelsioris*), and oxbow swamp forests (*Carici ripariae-Alnetum glutinosae*) (phytosociological nomenclature follows Douda et al., 2016). The study area has a temperate climate, with a mean annual temperature ranging from 9 °C to 10.5 °C and average annual precipitation between 500 and 650 mm. The altitude ranges between 150 and 250 metres above sea level. From the Middle Ages until the 19th century, the forest fragments were managed as coppice or coppice-with-standards, however, during the first half of 20th century, they were gradually transformed into high forests with prolonged canopy closure (Müllerová et al., 2014).

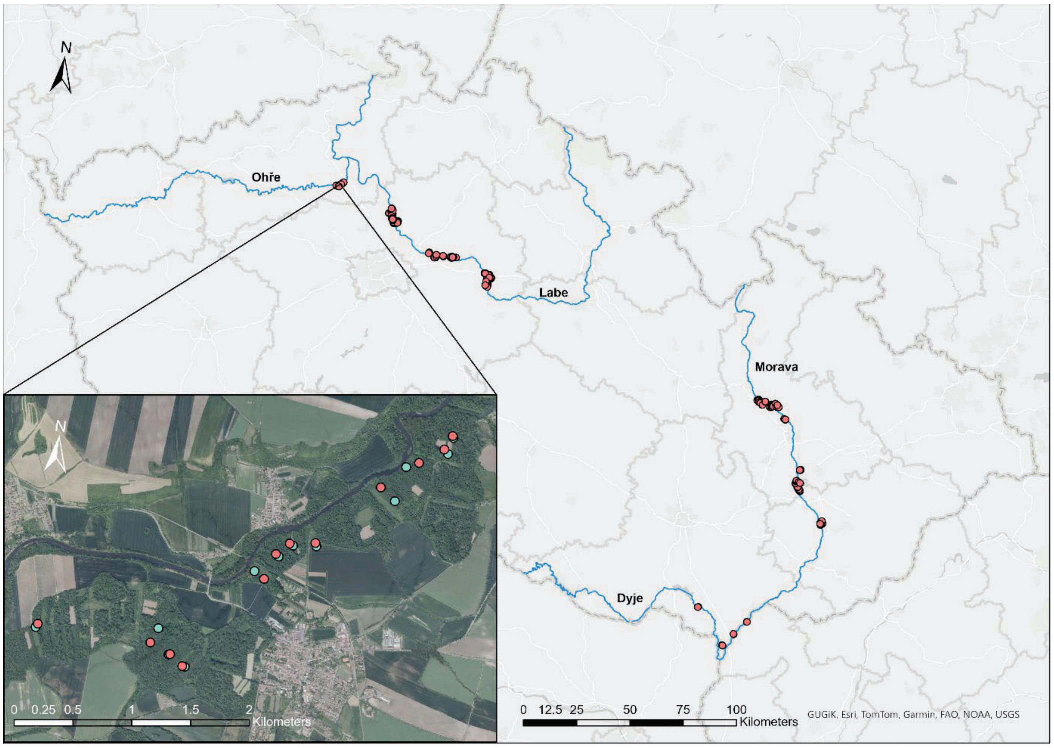

Figure 1 Distribution of vegetation plots along four major rivers (Dyje, Labe, Morava and Ohře) in the Czech Republic and an example of their fine-scale distribution in the Pístecký luh nature reserve. Blue dots represent historical plots and pink dots represent current plots.

2.2 Resurvey

Our dataset consists of historical vegetation plots surveyed in the 1950s and 1960s by four expert botanists (published in Bednář, 1964; Horák, 1960; Horák & Dvořák, 1968; Neuhäuslová-

Novotná, 1965; Novotná, 1958). The re-survey following experienced botanists reduced potential sources of historical observer error and ensured the comparability of historical and current datasets (Douda et al. 2023). They documented the specific forest stands sampled, referencing the IDs from historical forest inventory maps at a 1:10,000 scale. The average size of these forest stands was 2.33 ± 4.96 ha (mean ± SD). To relocate the plots, we used coordinates of the centre of forest stands. If the forest stand was harvested and replanted, the historical vegetation plot was not resampled. In total, 117 historical vegetation plots were resurveyed (for details see Holeštová et al. 2024).

The resurveys took place within 30 days of the original sampling date in years 2019 – 2022. 72 plots that were resampled in the same way as the original plots, twice per season to detect spring and summer species were also resampled twice in spring and summer. The plot size was 200–500 m^2 and corresponded to the historical sampling. All vascular plants present were assigned to four vertical layers (i.e. trees: >3 m, shrubs: 1–3 m, seedlings and saplings of woody species: <1 m and herb layer). Their cover was estimated using the 7-step version of the Braun–Blanquet scale (categories and their back-transformation into percentage cover: r = 1%, + = 2%, 1 = 3%, 2 = 13%, 3 = 38%, 4 = 68%, 5 = 88%) as implemented in the programme TURBOVEG (Hennekens & Schaminée, 2001). Plant nomenclature follows Kaplan et al. (2019).

The data may suffer from relocation error, but there is evidence that the use of qausi-permanent plots (the approximate location of the historical vegetation plots) is robust when the plots are established in homogeneous environments (Chytrý et al., 2014, Verheyen er al., 2018). The original observers established the vegetation plots in forest stands, which are defined by foresters as homogeneous flat areas with similar growing conditions and tree species structure. Therefore, any potential relocation error in the data has a reduced effect.

2.3 Forest inventory maps

For determination of age classes for each historical and current vegetation plot, we used historical forest inventory maps received from archives (the State Regional Archives in Prague, the Moravian Land Archive in Brno, and the State District Archive Olomouc) and current forest inventory maps already available in a digital form as shapefiles. The historical forest inventory maps were scanned and subsequently georeferenced in ArcGIS Pro (3.3.0) using georeferencing tools. The georeferenced maps were than manually transformed in polygon shapefiles using editor toolbar. Age classes were determined based on legend in the historical forest inventory maps for 10 forest fragments (i.e., Libický luh, Káraný-Hrbáčkovy tůně, Vrť, Pístecký les, Budyňský les, Úpor, Litovelské Pomoraví, Soutok, Bulhary, Lužní les u Otrokovic). For each forest fragment surveyed, we created a summary figure showing the age-class structure differences between 1950s – 1960s and 2020s (Fig. S1). For Libický luh national nature reserve, we were also able to receive the forest inventory map from the end of 19th century showing distribution of age classes as well as distribution of high forest stands alongside coppices. Finally, we calculated area percentages for each age class and visualised them using pie charts.

2.4 Delimitation of variables and statistical analysis

To evaluate temporal changes in the age-class structures of all forest fragments surveyed, we calculated so-called age-class evenness, which considers both the number of age classes and their distribution within a given area. Specifically, we modified Simpson's evenness index by replacing the number of species and species abundances with the number of age classes and their areas. The age-class evenness was then calculated for each historical and current vegetation plot at radius 300, 500, 1000, 3000 and 5000 m. To assess temporal changes in species composition, we used Bray-Curtis dissimilarity to compare all pairs within historical and current vegetation plot datasets at distances of 300 m, 500 m, 1000 m, 3000 m, and 5000 m. To assess the impact of specific age classes on species richness, we calculated the number of species for each age class within historical and current plots.

For analysing the changes in species richness between each pair of age classes within historical and current plots, we used the generalised linear models (GLMs) with Poisson distribution. For analysing the changes in Bray-Curtis dissimilarity and age-class evenness between distance categories (300, 500, 1000, 3000 and 5000 m) and between historical and current plots, we used linear models (LMs). We evaluated the effect of age classes on species composition of historical and current plots separately by using non-metric multidimensional scaling (NMDS) and tested by the *envfit* function from the R package vegan. *Envfit* provides a vector for each variable that maximises correlation between that variable and the projections of ordination points onto that vector. Significance was assessed using 999 permutations of variables. All statistical analyses were carried out in R software (R Core Team, 2024).

3 Results

3.1 Age-class structure

The comparison of forest inventory maps revealed significant changes in the age-class structure of all forest fragments surveyed over the last 60 years (Fig. 2, Fig. S1). The age classes up to 80 years were mostly present, and evenly distributed, as shown by the area percentages calculated for each age class. Such structure also allowed the occurrence of different age class at a relatively short distance (Fig. 4b). On the other hand, at present, the age classes of more than 80 years predominate in all forest fragments and cover large areas. These observations were also supported by significantly higher age-class evenness in the past for the 300 m, 500 m and 5000 m distance categories (Table 1, Fig. 4b). In addition, the case of the Libický luh national nature reserve revealed the age-class structure of forest fragments at the end of the

19th century (Fig. 2). The age classes up to 40 years completely predominated in forest fragments coppiced in that time.

	Bray - Curtis dissimilarity	Age class evenness
300 m	1.955 *	-5.946 **
500 m	0.995	-4.112 **
1000 m	0.708	-1.554
3000 m	0.667	0.329
5000 m	1.658	1.929 *

***P < 0.001, **P < 0.01, *P < 0.05

Table 1 Comparison of Bray-Curtis dissimilarity and Age class evenness between historical and current plots for each distance category separately, tested by linear models (LMs). T values are presented with asterisks indicating the level of significance.

3.2 Species composition

The NMDS revealed significant differences between age classes within both, historical and current plots, indicating different species composition of each age class (Table 2). The differences between age classes within historical plots are higher than within current plots, indicating higher beta diversity between age classes in the past (Fig. 3). The Bray-Curtis dissimilarity also supported a significantly higher compositional differences for the 300 m distance category (Table 1, Fig. 4a), i.e. within a distance where a different age class was most likely to be present.

	r^2	*P*
Age class		
Historical plots	0.1219	0.005 **
Current plots	0.0754	0.025 *

***P < 0.001, **P < 0.01, *P < 0.05

Table 2 The effect of age classes on species composition of historical and current plots separately, evaluated by NMDS and tested by the *envfit* function from the R package *vegan*.

3.3 Species richness

Total species richness decreased significantly by an average of 11.35 ± 7.39 (mean ± SD, < 0.001***) over the study period, showing that forest stands were much more species-rich in the past than at present. The significant differences were also found between age classes within historical plots and current plots, indicating that certain age classes host more species than others (Table 3, Fig. 5). Specifically, for species richness in historical plots, the significant differences were found between age class 61 – 80 with 1 – 20, 21 – 40 and 41 – 60. The age class 61 – 80 was associated with the highest species richness. For species richness in current plots, the significant differences were found between age class 21 – 40 with 1 – 20, 41 – 60, 61 – 80 and 81 – 100, and between age class 1 – 20 with 61 – 80 and 81 – 100. The age class 21 – 40 was associated with the lowest species richness, while the age class 1 – 20 was associated with the highest species richness.

Table 3 Comparison of species richness between each pair of age classes, and between historical and current plots separately, tested by generalised linear models (GLMs) with Poisson distribution. Z values are presented with asterisks indicating the level of significance.

Age classes			**Species richness**	
			Historical plots	Current plots
1 - 20	*vs.*	61 - 80	3.128 **	-2.393 *
21 - 40	*vs.*	61 - 80	2.382 *	4.078 ***
41 - 60	*vs.*	61 - 80	1.892 *	-1.343
81 - 100	*vs.*	61 - 80	- 1.291	0.175
1 - 20	*vs.*	21 - 40	1.135	-6.036 ***
1 - 20	*vs.*	41 - 60	1.629	-0.951
1 - 20	*vs.*	81 - 100	1.099	-2.361 *
21 - 40	*vs.*	41 - 60	0.571	5.061 ***
21 - 40	*vs.*	81 - 100	0.329	4.395 ***
41 - 60	*vs.*	81 - 100	- 0.03	-1.252

***P < 0.001, **P < 0.01, *P < 0.05

4 Discussion

Our study confirms that different age-class structures significantly affect plant communities in terms of species composition and species richness. It shows that not only the age class, but also the number of different age classes in proximity, i.e. age-class heterogeneity, determine the plant species diversity of temperate forests. Importantly, our results suggest that the age structure of the floodplain vegetation of the 1960s and that of today have affected species diversity in differing ways.

4.1 The combined effect of nutrient overloading and forest ageing

This study builds on our previous research, which focused on long-term vegetation changes and the identification of driving factors behind them in floodplain forests of Central Europe using the same dataset (Holeštová et al. 2024). Specifically, Holeštová et al. (2024) showed that nutrient overloading significantly outweighs the influence of other factors such as forest ageing or desiccation and causes gradual decline in plant species diversity and extensive homogenisation. Nutrient-demanding species such as *Urtica dioica* or *Galium aparine* frequently dominate in today´s floodplain forest vegetation as they benefit most from increased nutrient availability (Holeštová et al., 2024). They can extract and utilise nutrients more efficiently than other species and thus rapidly increase their abundances and quickly outcompete less competitive species (Bobbink et al., 2010; Verheyen et al., 2012).

The comparison of forest inventory maps between 1950s–1960s and 2020s presented in this study revealed major changes in age-class structure of floodplain forests. At present, the age classes of more than 80 years prevail. It follows that the effect of forest ageing leading to an increased shading of the forest floor do appear in floodplain forests. Among recorded species, whose frequency decreased over the study period, a large proportion is represented by light-demanding species such as *Fragaria moschata*, *Campanula trachelium* or *Hypericum hirsutum* (Table 3 in Holeštová et al., 2024). It seems that insufficient light availability reduces the competitiveness of these species, resulting in their replacement by mesophilic nutrient-demanding species as was also confirmed by other studies (e.g. Lanta et al., 2024).

4.2 Age-class structures and plant diversity

The detailed case of the Libický luh national nature reserve showed how the forests were structured before the change in forest management approaches, i.e. until the first half of the 20th century. The forests consisted mainly of two age classes, 1 - 20 and 21 - 40, with coppices covering most of the total forest fragment area. On the other hand, in the period 60 years ago, the observed age-class structures (Fig. 2, Fig S1) correspond to the initial transition of coppices into high forests with prolonged period of canopy closure. The number of age classes in the forest fragments increased as the forest stands that replaced the coppiced forest at the beginning of the 20th century (Fig. 2) reached the age of 60 or 80 years. At the same time, the younger age classes remained, suggesting that the original coppices have been continuously harvested, and new forest stands were thus established and planted. This has led to the higher fragmentation of forests and the presence of forest stands of different areas and ages. In addition, the age classes were more evenly distributed than in other periods resulting in more heterogenous (diverse) forest fragments.

Such age-class structure appeared to support much higher species richness than the current age-class structures of floodplain forests. Higher plant beta diversity between historical vegetation plots within 300 meters was associated with greater age-class variability. It follows that each age class likely offer different habitat conditions allowing the presence of

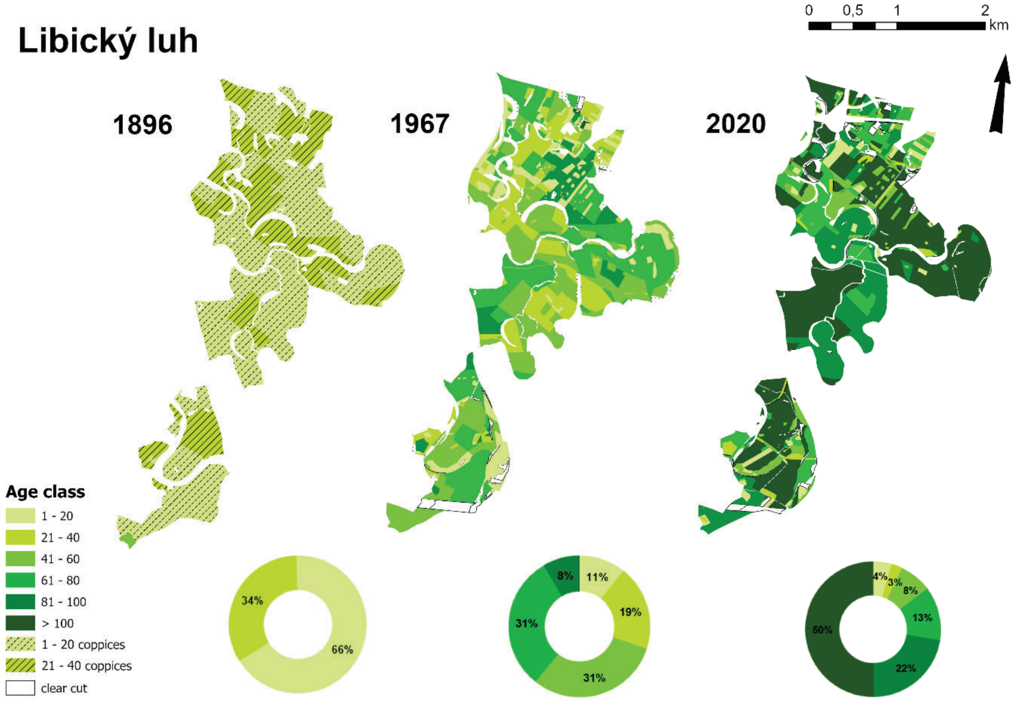

Figure 2 Age class structures of the Libický luh national nature reserve in three different periods, i.e. 1896, 1967 and 2020, supplemented by area percentages of each age class. The darker green, the older forest stand.

species with different ecological requirements. We can assume that light availability as well as the frequency of human intervention are the main drivers. The contrasting age classes create different light conditions supporting species with different light preferences. At the same time, the frequency of human intervention varies between forest stands, allowing species adapted to frequent disturbance to coexist with those that require a more stable environment.

The results indicate that the oldest forest stands (61 – 80 years) in the 1960s played a crucial role in maintaining high alpha and beta diversity in floodplain forests. These stands were the most species-rich (Fig. 5) and compositionally distinct from younger age classes (Fig. 3a). This suggests that the 80 – 100 year old forests are likely to be the last remnants of the historically diverse, traditionally managed forests. In contrast, younger forests have experienced a decline in diversity due to factors such as increased canopy closure, shading and

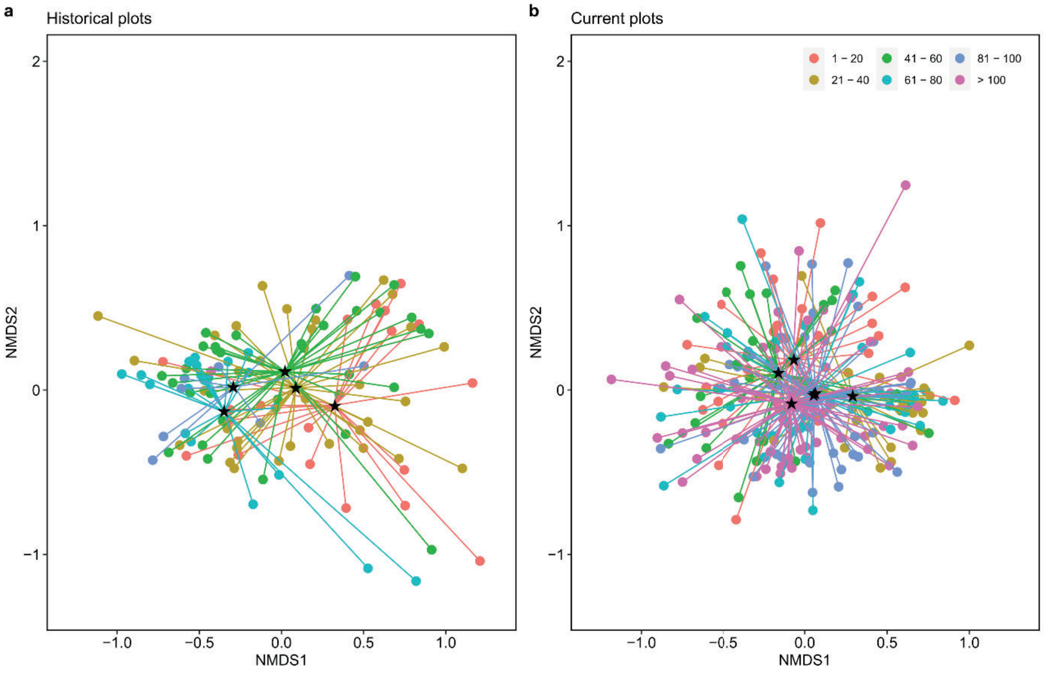

Figure 3 Dissimilarity of species composition between age classes according to NMDS, separately for historical plots (a) and current plots (b).

eutrophication. Today, however, most forests over 80 – 100 years old have lost their unique diversity and are compositionally similar to the younger, less diverse forests of the 1960s (Fig. 3).

4.3 Diversity maintaining management

Coppicing or coppicing-with-standards represents a traditional forest management which has been repeatedly applied in nature reserves recently with positive effects on species richness (Vild et al., 2013; Strubelt et al. 2019; Máliš et al., 2021). Even though, such management strategy is unlikely to achieve the highest possible species richness. The forest inventory map of the Libický luh national nature reserve from the end of the 19th century shows that the forest stands consisted mainly of younger age classes up to 40 years with coppices covering most of the total area. Such age-class structure shows the major application of coppicing as in other former forests in the past (Szabó, 2005; Müllerová et al., 2014, Slach et al., 2021; Kamp, 2022). However, it also suggests the maintenance of a homogeneous environment in terms of high light availability and frequent disturbance. It follows that light-demanding species and species adapted to frequent disturbances were likely to be present at the expense of shade-tolerant species and species requiring stable

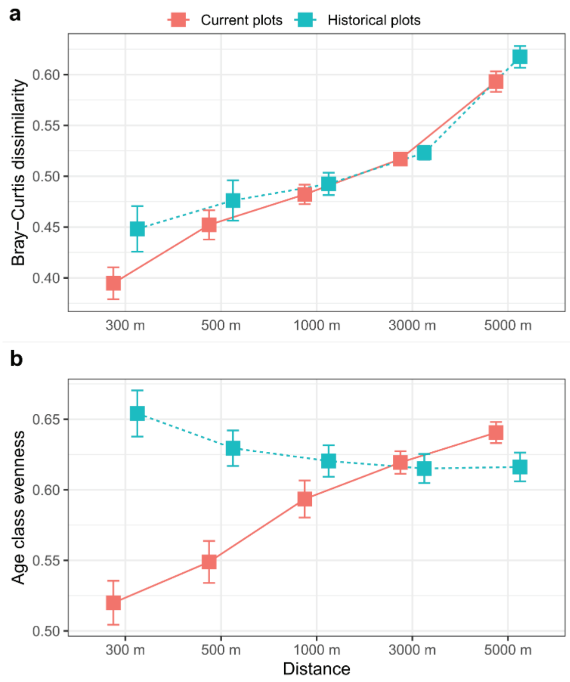

Figure 4 Comparison of Bray-Curtis dissimilarity (a) and Age class evenness (b) between historical and current plots, and between distance categories.

environment. Therefore, reintroduction of coppicing cannot be considered as sufficiently effective as the occurrence of later-successional species, especially true forest species, is also desirable. Instead, a patchwork of different age classes with forest stands of different sizes seems like an appropriate management strategy to ensure the highest possible species richness in temperate forests (Boch et al., 2013; Šebek et al., 2015; Schall et al., 2018; Hilmers et al., 2018).

The patchwork management should be suggested in relation to the environmental conditions, particularly the soil conditions. On nutrient-poor soils, the introduction of forest management with more frequent intervention usually leads to an increase in plant species diversity (Vild et al., 2013; Šebek et al., 2015; Douda et al., 2017; Strubelt et al., 2019). On nutrient-rich soils, however, the establishment of younger age classes could lead to a shift towards light-demanding species with the same nutrient requirements as the original species. These species would quickly become dominant and prevent the spread of less competitive (mainly oligotrophic) light-demanding species. Such trend was observed in Holeštová et al. (2024) when comparing intervention and non-intervention floodplain forests. On sites with a

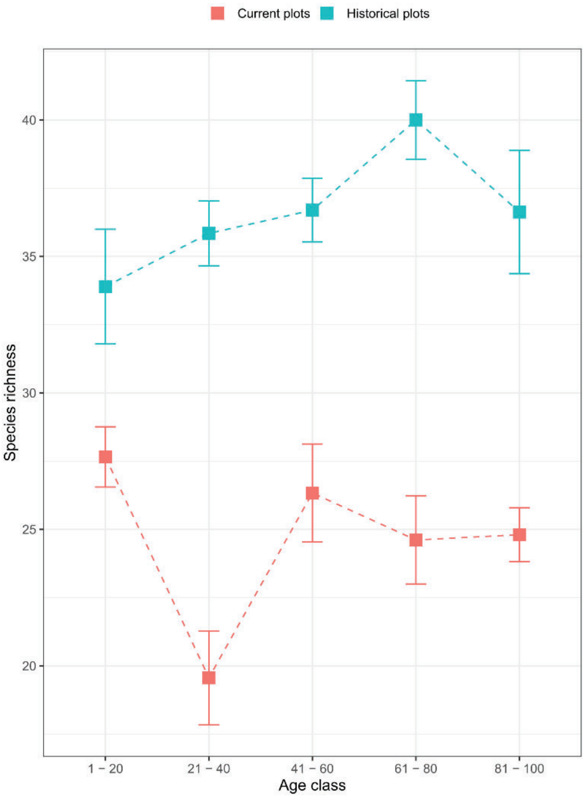

Figure 5 Comparison of species richness between age classes and between historical and current plots.

higher proportion of coarse sand particles, tree cutting may have a positive effect on species richness. More rapid desiccation leads to less favourable moisture conditions, which in turn limits species growth and dispersal. Tree cutting and canopy opening accelerate this process, so less competitive, drought-tolerant species may persist on these sites, leading to an increase in species richness. On sites with a higher proportion of clay particles, the soil retains water for longer time, allowing species without moisture constraints to thrive. Resource-demanding species can then rapidly become dominant, with a consequent decline in species richness.

As floodplain forests 60 years ago were likely significantly less eutrophic, the patchwork management introducing the variability of forest age classes could be accompanied by other management practices that can decrease eutrophication by the regular biomass removal from ecosystems such as extensive grazing or litter raking (Doudová et al. 2023). If it is possible, at least some parts of the river channel should be revitalized. The restoration of flood regime in case of regulated rivers is crucial as regular flooding mechanically disturbs the understorey vegetation, providing space for seed germination from a seed bank and allowing the establishment of new species migrating from adjacent microhabitats. At the same time, regular flooding prevents nutrient-demanding species from becoming dominant and outcompeting less competitive species from a site. This mechanism maintains the high plant species diversity of natural floodplain forests (Lite et al., 2005).

5 Conclusion

Our study showed that greater spatial heterogeneity in forest age structure was associated with higher plant species diversity in floodplain forests. This heterogeneity, characterised by a patchwork of age classes up to 100 years, developed as these forests transitioned from traditional coppices to high forest stands during the first half of the 20th century. In particular, the oldest forests in the 1960s aged 60 – 80 years exhibited exceptional species diversity and made a significant contribution to the beta-diversity of floodplain ecosystems. However, this diversity was lost in the second half of the 20th century, mainly due to eutrophication and increased canopy shading. In the light of current discussions on effective management of lowland forests, we suggest that the reintroduction of both coppices-with-standards and old-growth forests may be the most effective strategies for restoring forest biodiversity. In addition, coppicing regimes aimed at creating younger age classes should be adapted to the soil conditions of each site. On nutrient-rich soils with high clay content, traditional management practices that regularly remove a significant proportion of the biomass should be used.

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Author contributions

Jan Douda and Jana Doudová designed the study, and all authors contributed to data collection. Anežka Holeštová analysed the data with helpful contributions from Jan Douda. Anežka Holeštová and Marie Černá wrote the first draft, and all authors contributed to the revision of the manuscript.

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Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

Supporting information

Figure S1. Age class structures of forest fragments surveyed in 1950s – 1960s and 2020s, supplemented by area percentages of each age class. The darker green, the older forest stand.

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Chapter 7

Study IV: Historical sampling error: A neglected factor in long-term biodiversity change research

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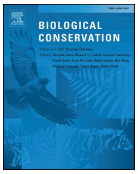

Historical sampling error: A neglected factor in long-term biodiversity change research

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ABSTRACT

Long-term time series are increasingly used to assess the effects of global change on plant community diversity and to guide management of target plant communities. However, historical biodiversity data may contain neglected sources of error that can have a significant impact on the results and their interpretation. In our study, we focus on historical sampling error, a source of potential bias in long-term biodiversity assessments that has not been systematically addressed. We resampled two historical datasets of a different origin in the floodplain forests of the Czech Republic, with 534 vegetation plots originally sampled in the 1950s and 1960s. We compared temporal trends in alpha diversity and Ellenberg indicator values (EIVs) between the two parallel surveys. To assess compositional differences, we compared temporal changes in species frequencies. Alpha diversity increased by 9.3 % in one resurvey, but decreased by an average of 30.8 % in the second resurvey. The distribution of EIVs for plots also differed, indicating that each resurvey covered a different part of the environmental gradient. We conclude that preferential historical sampling of the vegetation-environment continuum and species omission may have contributed to the differences in biodiversity and environmental change between the datasets. Our study shows that historical sampling error can have a significant impact on assessments of long-term biodiversity trends. We recommend that historical reference datasets should be critically assessed for potential sources of error in assessments of environmental change and management objectives.

1. Introduction

Long-term time series are an invaluable source for assessing the impact of global change on plant community biodiversity (Leach and Givnish, 1996; Damschen et al., 2010; De Frenne et al., 2013; Vellend et al., 2013a; Zhumanova et al., 2021; Jandt et al., 2022). This includes vegetation plot resurveys, an approach based on comparing the local composition of plant communities over several decades, thus bridging the time and knowledge gap between classical monitoring and approaches exploring archival or fossil data (Hédl et al., 2017; Kapfer et al., 2017; Verheyen et al., 2017; Waller, 2022). Vegetation plot resurveys are now an established line of research, embedded within a wide range of historical ecology methods (Szabó and Hédl, 2011; Vellend et al., 2013b; Decocq, 2022).

Resurveys of historical vegetation plots have provided information on much debated issues, including long-term trends in anthropogenic loss of species richness (Hédl et al., 2010; Van Calster et al., 2007; Vellend et al., 2013a) and biotic homogenization (Keith et al., 2009; Naaf and Wulf, 2010; Amatangelo et al., 2011; Šebesta et al., 2011; Staude et al., 2022). Vegetation resurveys contributed significantly to our knowledge of land use legacy in community trajectories (Vittoz et al., 2009; Waller et al., 2012; Baeten et al., 2010; Naaf and Kolk, 2016; Perring et al., 2018) and effects of nutrient accumulation, thermophilization, light availability and density of large herbivores (Damschen et al., 2010; Van den Berg et al., 2011; Verheyen et al., 2012; Simkin et al., 2016; Gilliam, 2022; Segar et al., 2022). The focus on vegetation

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resurveys indicates a demand for targeted management measures in plant communities that address various drivers of environmental change (Bergamini et al., 2009; Kopecký et al., 2013; Meyer et al., 2013).

Like most approaches in the natural sciences, the vegetation resurvey approach involves methodological shortcomings that may hamper the robustness of results. There are three commonly considered potential errors associated with the plot sampling: relocation error, observer error, and seasonal bias (Morrison, 2021). First, relocation error refers to the approximate relocation of historical plots, which are then referred to as semi-permanent or quasi-permanent plots (Fischer and Stöcklin, 1997; Kopecký and Macek, 2015; Kapfer et al., 2017). This source of error is rarely considered or even quantified in research studies. Second, observer error is due to subjectivity in species determination, abundance estimates, and related variables. It is often studied (e.g., Lepš and Hadincová, 1992; Archaux et al., 2006; Vittoz and Guisan, 2007; Milberg et al., 2008; Morrison, 2016; Verheyen et al., 2018), but almost never included in estimates of plant community change. Finally, seasonal error is caused by variability in sampling dates in environments with significant climatic seasonality (Van Calster et al., 2008; Kirby et al., 1986; Brunet and Tyler, 2000; Vymazalová et al., 2012; Cleland et al., 2013; Hédl and Chudomelová, 2020). Although the vegetation scientists are well aware of the potential errors, they only rarely assess their influence in individual vegetation resurveys, which can lead to false turnover in species composition and misinterpretations in terms of biodiversity and environmental dynamics (i.e., pseudo-turnover; Fischer and Stöcklin, 1997, Kapfer et al., 2017).

Observer error appears to be pervasive in vegetation resurvey studies (Morrison, 2021). Assessments in species richness can vary between 10 % and 30 % (Burg et al., 2015; Morrison, 2016; Verheyen et al., 2018). Archaux et al. (2009) found that the omission of a species during the survey when it is actually present (estimated at 19.2 %) can be a more important component of observer error than the determination error, estimated at 5.3 %. Verheyen et al. (2018) found that observer error accounted for 15 % of the variability in species richness changes, while relocation error did not contribute significantly to the observed change.

In our study, we propose for the first time a historical observer error in vegetation resurveys. In addition to observer error caused by current observers, authors of historical datasets may also be responsible for a significant variability in data. We argue that potential errors due to authorship subjectivity in baseline surveys should be considered in long-term biodiversity studies. Individual datasets can vary considerably in terms of sampling design (subjectively determined number and distribution of plots) and personal sampling skills.

It should be noted that the historical observer error may include systematic biases due to individual preferences for certain vegetation types or the overlooking of certain species. Historical vegetation plot datasets were often collected to document and describe pre-defined vegetation types. Plots were placed subjectively or according to some implicit rules that are difficult to identify today (Ewald, 2003; Hédl, 2007). Even within a single vegetation type, the sampling strategies varied among observers as they sampled vegetation according to environmental gradients that the observers considered important (Bruelheide and Chytrý, 2000). An emphasis on vegetation classification led to preferential sampling of species-rich communities (Hédl, 2007; Michalcová et al., 2011), which could potentially significantly bias observed temporal trends in biodiversity and environmental change.

Here we have attempted to estimate the effect of the historical sampling error in long-term vegetation resurveys. We used the example of floodplain forest vegetation because it has been extensively sampled in the past for various research and application purposes. By comparing two resurveys of historical vegetation datasets, we focused on i) variability in the extent and direction of temporal biodiversity and environmental change, and ii) effects of preferential sampling and species omission.

2. Methods

2.1. Historical surveys

Our reference dataset consists of 534 historical vegetation plots surveyed in the 1950s and 1960s. It provides information about the composition and relative species abundance in floodplain lowland forests along two main river systems in the Czech Republic. Two historical datasets differing by origin were selected based on the following criteria: i) sampling in approximately the same period, ii) multiple regions that were included in both datasets (Appendix S1), and iii) location of the historical plots using maps with fine resolution (scale 1:10,000). A main difference between the datasets was the purpose of data collection. The Dataset 1, collected from 1956 to 1969, was historically part of a country-wide forestry monitoring programme (Průša, 2001). Its digitized version is stored in the Database of Czech Forest Typology (Zouhar, 2012). The data used in our study were collected by 14 authors working regionally according to standardized protocols. The Dataset 2, collected from 1955 to 1967, was historically sampled by only four authors (published in Novotná, 1958, Horák, 1960, Bednář, 1964, Neuhäuslová-Novotná, 1965, Horák and Dvořák, 1968). The purpose was to phytosociologically classify communities of floodplain lowland forests. The two datasets selected for our study contain 417 and 117 resurveyed plots, respectively. To localize the plots, the authors of the Dataset 1 marked the locations directly in the map, while the authors of the Dataset 2 only indicated location in forest compartments sized in terms of hectares. The both historical surveys sampled the vegetation by using phytosociological relevés according to the Braun-Blanquet approach (Braun-Blanquet, 1964).

2.2. Resurveys

To relocate the historical vegetation plots, we used plot coordinates derived from the original maps (Dataset 1), or coordinates of the centres of forest compartments taken from contemporary forest management maps (Dataset 2). The latter approach is less precise than the former one, implying Dataset 2 suffers from potentially higher relocation error. To relocate the plots, we navigated to the approximate plot area using a GPS receiver, then looked for a place with the same or similar tree species composition as in the original survey, and subjectively established the sampling plot. The resampling was carried out in the years 2013–2021 in the same period of the growing season as was the historical sampling (within one month of the original sampling date) and with the same plot size (ranging from 200 to 500 m^2). For comparison with historical samples, a) vascular plants were recorded, their cover estimated using the Braun-Blanquet scale and assigned to three vertical layers (Tree: >5 m, Shrub: 1–5 m, and Herb and seedling layer: <1 m). Ten authors contributed to the Datasets 1 and 2, some of them participating in both.

2.3. Data analysis

We asked whether the resurveys of vegetation plots originally sampled for different purposes (i.e., Datasets 1 and 2, see *Historical surveys* above) will lead to different results on temporal changes in vegetation and environmental conditions. For this purpose, we used absolute differences in alpha diversity and Ellenberg indicator values (EIV) among the pairs of time samples – historical survey and recent resurvey. Alpha diversity per sample was estimated as the number of species in plot (hereafter referred to as *species richness*). The site environmental conditions were calculated using community weighted means of Ellenberg indicator values (EIVcwm) for light, temperature, soil moisture, reaction and nutrients (Chytrý et al., 2018). The percent cover of each species after transformation by the natural logarithm was used for mean weighting. We used mid-range percentage values of abundance-cover scale. The extent and direction of temporal biodiversity change was calculated using absolute difference in current species richness minus historical species richness. To evaluate differences in environmental changes between datasets we calculated absolute difference for EIVcwm.

We assessed whether the differences in temporal turnover between the datasets could be due to personal traits of the authors, by analysing rates of species omission. We expected that species achieving low cover (i.e., rare species) would be underestimated compared to high-cover (i.e., easier to detect) species in the data set with higher omission error. Species with >20 occurrences in the entire dataset were divided into four categories of average plant species cover (<3 %, 3–5 %, 5–10 % and >10 %) calculated across all datasets (calculated only from sites where species occur). For each species, we calculated if its frequency change (current frequency minus frequency in original sampling) differed between datasets. The frequency of each species was calculated as the number of occurrences divided by the number of samples in each dataset and time period.

To assess signs of observer preferential sampling for certain parts of environmental gradients, we calculated the probability of sampling on the gradients of Ellenberg indicator values in each dataset. Probability density curves for each dataset were constructed using plot-EIVcwm.

For statistical evaluation of temporal differences between the datasets, we used linear models with absolute difference in species richness and EIVcwm as dependent variables and datasets (Dataset 1 and 2) as explanatory variables. We used a one-way analysis of variance with the differences in species absolute frequency-time changes as the dependent variable and categories of mean plant species cover as explanatory variables. Differences in probability density curves were tested by permutation test. All statistical analyses were performed using R (R Core Team, 2022).

3. Results

The mean overall change in species richness was 0.5 species (0.9 %) and did not significantly differ from null change (Table 1). Analysing the two datasets separately, the extent and direction of change significantly differed. Mean species richness in Dataset 1 increased by 3.4 species (9.3 %), while it decreased in average by 11.2 species (30.8 %) in Dataset 2 (Table 1, Fig. 1). The assessment of environmental change by Ellenberg indicator values (EIVcwm) significantly differed between the datasets (Table 1, Fig. 2). All values increased in Dataset 1, while remained the same for temperature, reaction and nutrients and decreased for light and moisture in Dataset 2 (Fig. 2a to e).

Comparison of species temporal trends showed that significantly more species increased their frequency in Dataset 1 than in Dataset 2 (Fig. 3a). The difference between the datasets can be mainly attributed to low-abundant species (Fig. 3b). The low-abundant species became more frequent in Dataset 1, while they often declined in Dataset 2 (upper left quarter in Fig. 3a). On the contrary, more abundant species had same responses in both datasets (Fig. 3b).

We found differences in gradients of environmental conditions between the datasets (Fig. 4). Dataset 2 showed significantly higher EIVcwm compared to Dataset 1 ($P < 0.001$ for all indicator values).

Table 1
Absolute differences in species richness and Ellenberg indicator values between historical and current sampling and datasets. *Total* indicates differences between historical and current sampling regardless particular dataset. t-value describes differences in temporal changes between datasets. NS, non-significant; ***, $P \leq 0.001$.

	Total	Dataset 1	Dataset 2	t - value
Richness	0.47^{NS}	3.44***	−11.18***	13.02***
Temperature	0.25***	0.32***	$< 0.01^{NS}$	8.18***
Light	$< 0.01^{NS}$	0.08***	−0.31***	8.566***
Moisture	0.11***	0.18***	−0.18***	6.85***
Reaction	0.31***	0.38***	0.03^{NS}	7.064***
Nutrients	0.37***	0.44***	0.07^{NS}	6.028***

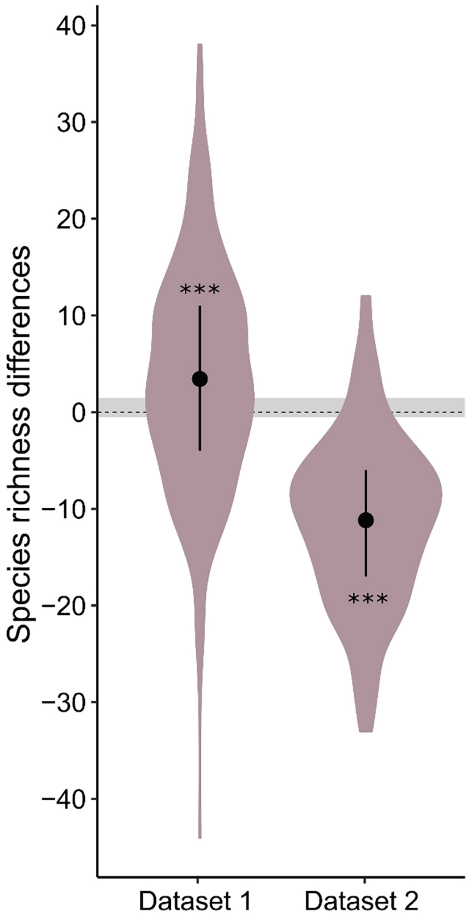

Fig. 1. Species richness at plot level follows opposite trends in the two datasets. While absolute differences in species richness per plot increased over time in Dataset 1 (originally a forest inventory survey), they decreased significantly in Dataset 2 (originally a phytosociological survey). The grey band indicates 95 % confidence interval of the total absolute differences regardless of samplings. Asterisks behind the differences indicate significant non-zero differences. NS, non-significant; ***, $P \leq 0.001$.

4. Discussion

We show that using historical datasets to assess biodiversity and environmental change can lead to misleading results. We argue that authorship subjectivity factors, such as species omission or sampling preferences, may be responsible for the observed bias. Here, we discuss the potential reasons and interpret them in the context of the changes observed using the example of the plant communities of floodplain forests.

The first striking difference between the datasets is the change in species richness. If analysed jointly, our resurvey datasets in floodplain forest plant communities correspond to the no net species richness change hypothesis (Vellend et al., 2013a; Dornelas et al., 2014; Bernhardt-Römermann et al., 2015; Chase et al., 2019). However, when analysed separately, contrasting trends in species richness were observed in the two datasets. One explanation may be differences in the sampling design of the historical surveys. Several studies have shown

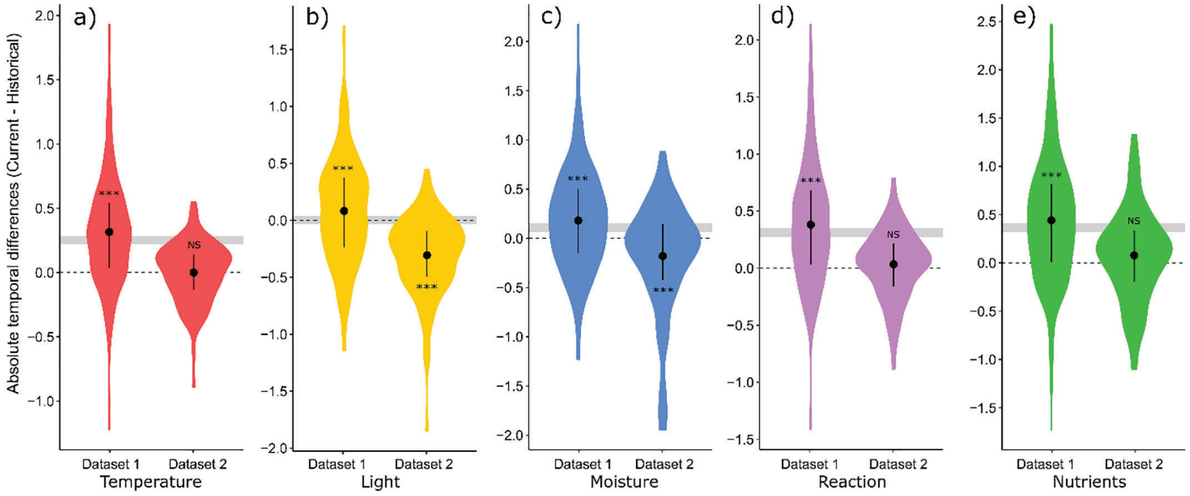

Fig. 2. Marked increase in Ellenberg indicator values (EIVs) over time in Dataset 1 compared to no change or decrease in Dataset 2. The distribution graphs show absolute differences at plot level in EIVs for temperature, light, soil moisture, reaction and nutrients. The grey band indicates the 95 % confidence interval of the total absolute differences regardless of samplings. Asterisks behind the differences indicate significant non-zero differences. NS, non-significant; ***, P ≤ 0.001.

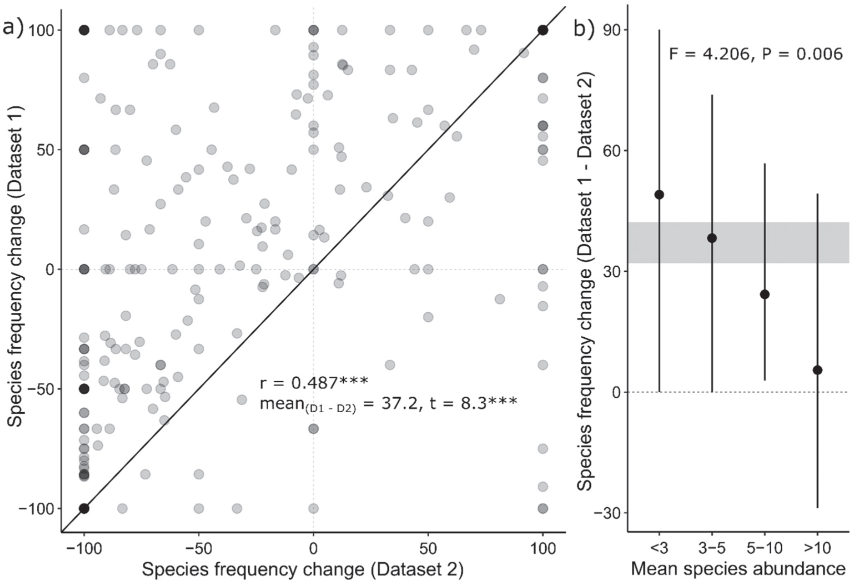

Fig. 3. Increases in species frequency over time that prevail in Dataset 1 are largely driven by low-abundant species. Absolute frequency-time changes of each species compared between the Datasets 1 and 2 (a), and dependence of differences in species absolute frequency-time changes between the datasets on mean species abundance in a plot (b). In (a) the diagonal line marks the same frequency change of a species in both datasets. Species that increased or decreased less in their frequency in Dataset 1 than in Dataset 2 are above the diagonal, whereas the underline species increased more in Dataset 2. Fit between datasets is expressed using Pearson correlation coefficient (r), mean value of differences between datasets (D1 – D2) and one-sample *t*-test testing the deviation from null differences along the diagonal line. Darker dots indicate more species reaching the same value. For b) mean differences (dot) and first and third quartiles (whiskers) are shown with the result of one-way analysis of variance and the grey band indicating 95 % credibility range of random differences between categories (999 permutations).

that the preferential (subjective) sampling, applied typically in phytosociology for vegetation classification purposes, tends to relatively increase species richness (Hédl, 2007; Diekmann et al., 2007; Michalcová et al., 2011; Swacha et al., 2017). The reason is that phytosociologists likely prefer species-rich vegetation with the presence of diagnostic species (Ewald, 2003). This can partly explain the observed decrease in species richness in Dataset 2, which converged from the species-rich to "average" diversity of the sampled plant community.

The differences in sampling design between the historical datasets may not have been solely related to the subjective preferences. Main aspect is the general purpose of sampling. In our comparison, the historical Dataset 1 was a small subset of a country-wide forestry inventory, covering over thirty thousand non-overlapping plots repeatedly sampled from 1950 to the present (Zouhar, 2012). The forestry classification

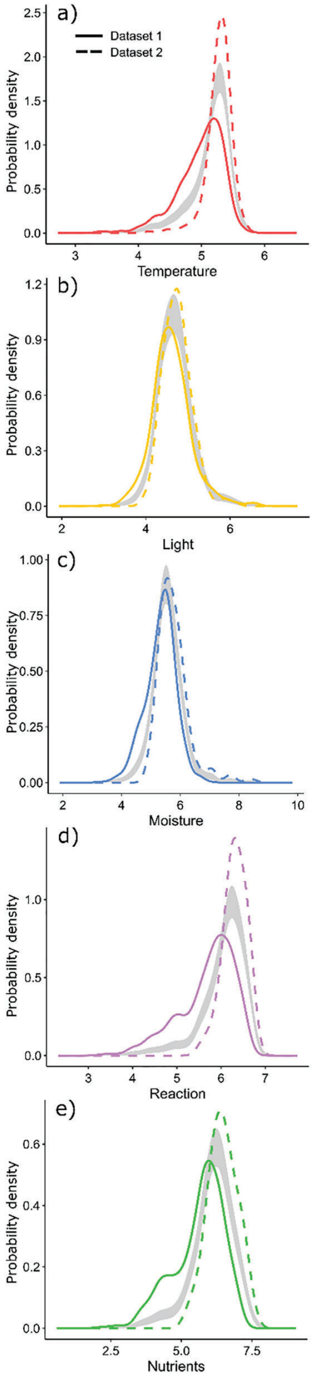

Fig. 4. Phytosociologists (Dataset 2) tended to place their plots towards the upper parts of the environmental gradients, whereas forest typologists (Dataset 1) preferred more average conditions. The solid lines show the probability of sampling along five environmental gradients (Ellenberg indicator values) in Dataset 1 and the dashed lines show the same in Dataset 2. The grey bands indicate 95 % credibility range of random differences between datasets (999 permutations).

system encompasses the full range of environmental conditions and corresponding forest vegetation types in the Czech Republic (Viewegh et al., 2003), including predominant stands managed for timber production. The values of the Ellenberg indicator values in the Dataset 1 display a pronounced peak in the intermediate part of the soil moisture gradient. In contrast to that, both extremes were very poorly captured (Fig. 4), which concerns alder carrs on waterlogged substrates and relatively dry thermophilic habitats. The middle segment of the flood intensity gradient is highly productive and with relatively low disturbance frequency (Slezák et al., 2022), it is therefore suitable for conventional forest management and disproportionally better represented in the forestry inventory. The forest inventory likely considered extreme habitats as peculiarities unsuitable for conventional management. Furthermore, frequent small-scale phenomena probably did not fit into the 1:10,000 forest maps produced for practical use.

The main purpose of the historical Dataset 2 was to obtain material for the phytosociological classification of floodplain forest vegetation in the Czech Republic (Neuhäuslová-Novotná, 1965). Phytosociologists placed the sampling plots based on their expert assessment of the main environmental gradients reflected in the species compositional turnover (Diekmann et al., 2007). We assume that the extreme ends of the environmental gradients were relatively over-sampled, compared to the real abundance of the vegetation types (Michalcová et al., 2011). This is the likely reason for the higher Ellenberg indicator values on average in the Dataset 2, compared to the Dataset 1, as the vegetation of extreme segments of the gradient corresponds to higher Ellenberg indicator values.

As indicated by extensive records from many studies, throughout the 20th century, floodplain forests have been drying out as a result of regulated flooding and their canopy closed due to the abandonment of traditional forest uses such as tree coppicing and wood pasture (Havrdová et al., 2023). These trends appear only in the Dataset 2, where indicators of soil moisture and light level decreased over time. The more extreme areas of the vegetation continuum recorded in this dataset may have experienced greater changes in light conditions because such forest stands were more opened in the past. Periodic flooding in the lower parts of the floodplain and intensive forest use in the dry and unproductive higher parts of the floodplain created open stands (Mezera, 1958) where succession could take place. Floodplain drying might be more evident in the wet areas of the floodplain from which wetland plant species have retreated. On the contrary, the eutrophication of floodplain forests (Havrdová et al., 2023) was only evident in the Dataset 1. This may reflect the fact that nutrient limitation mostly ceased in the middle parts of the moisture gradient or that Dataset 2 was already biased towards plots with high fertility scores.

In addition to signs of preferential sampling, the analysis of species frequency changes over time indicate that species omission error significantly contributed to contrasting trends in species richness between the datasets. The analysis showed that different trends are mainly influenced by less abundant species. Rare species generally tend to decline unless there is some environmental change that makes the site favourable and promotes their expansion (Waller et al., 2018). However, in Dataset 1, the frequency of these species increased between surveys. Such an unexpected turn suggests that rare species had been likely overlooked more often in Dataset 1 than in Dataset 2. The species omission error is related to the time spent at the site by searching for new plant species as well as the experience of the observer (Verheyen et al., 2018). The higher omission rate recorded in Dataset 1 may be due to greater interobserver variability in the sampling effort. Forest inventories were more time consuming considering they focused also on sampling many other environmental characteristics (e.g. soil types) as their purpose was different compared to phytosociological surveys, whose primary purpose was to describe the vegetation.

The resurvey studies are considered a valuable and often the only source for identifying environmental threats to populations of endangered species and for targeted conservation management (Bergamini et al., 2009; Kopecký et al., 2013; Meyer et al., 2013). Unfortunately, preferences of historical observers for different parts of environmental gradients can lead to incorrect interpretations of vegetation changes and, consequently, inappropriate management decisions. In our study, sampling of more extreme parts of environmental gradients (Dataset 2) showed strong environmental change accompanied by a decrease in species diversity. These extreme habitats, represented in floodplains by river oxbows or riverine sand dunes which are fundamentally important for nature conservation, were only marginally recorded in the Dataset 1. Therefore, if the Dataset 1 was used to assess vegetation changes, the management proposal would likely be to continue the existing management focused on timber production, as the results would not indicate any major changes. However, a resurvey of the Dataset 2 showed that main cause leading to the population decline of moisture- and temperature-demanding species are disrupted water regime and canopy shading. Since Dataset 2 covers such habitats, the restoration of the water regime in floodplains and stand canopy opening with suitable forms of forest management should be proposed in order to protect these species.

We conclude that the source data for the assessment of long-term changes in biodiversity (i.e. historical datasets) are not all the same. Historical sampling error, which has so far been neglected, can be a serious source of misinterpretation in vegetation resurvey studies. Historical reference datasets should be critically evaluated for potential sources of error in environmental change analyses and management objectives. They should be carefully checked with respect to the original purpose of their collection, the topic of the target study and the spatial scale of their results. It should be kept in mind that vegetation and environmental trends may differ depending on the part of the vegetation continuum being analysed. The data stratification that would capture the entire vegetation spectrum in a balanced way, should be therefore used for analyses of metadata composed by multiple historical datasets. Systematic preferences or omission of historical observers for some habitat types or species can be assessed prior to vegetation trend analysis. As an example, we plotted the distribution of site ecological indicator values and tested if some species guilds are over/underrepresented in studied datasets. We showed that omission of rare species appears to be critical for detecting trends in species diversity. Therefore, the conclusions about the long-term diversity changes should always be made with caution. The data should be inspected for suspicious trends in rare species. If such trends exist, the influence of rare species should be downweighted. Furthermore, only analyses that are less sensitive to rare species should be applied. In serious cases, the affected datasets shall not be used at all.

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CRediT authorship contribution statement

JanD and JanaD conceived the idea. JanD, JanaD, NP, AnH, MČ, MS, PP, JV, JŠ, KB and AlH collected vegetation data of the resurvey. AnH and MC prepared data for analyses. JanD and RH coordinated the study. JanD analysed the data and wrote the text. JanaD, RH, MC, OV and AlH contributed to writing. All authors commented the final draft of the manuscript.

Declaration of competing interest

The authors declare that there is no conflict of interest associated with this manuscript. Jan Douda, Jana Doudová, Anežka Holeštová, Markéta Chudomelová, Ondřej Vild, Karel Boublík, Marie Černá, Alena Havrdová, Petr Petřík, Nikola Pychová, Marie Smyčková, Jan Šebesta, Jiří Vaníček and Radim Hédl.

Data availability statement

Vegetation samples are available upon request from their authors.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110317.

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Chapter 8

Discussion and Summary

8.1 Species dispersal patterns in floodplains

Floodplain forests are among the species-richer habitats in the temperate zone (Mitsch, 1991; Schnitzler et al., 2005; Ward et al., 2002; Douda, 2010). Periodic flooding creates a heterogeneous environment that is highly suitable for the coexistence of a wide range of species, supported by high resource availability, i.e. sufficiently moist, nutrient and light conditions (Gregory et al., 1991; Naiman and Rogers, 1997). The changing light conditions during the growing season even increase the species diversity of floodplain forests by separating the phenological guilds, resulting in completely different species compositions in the understorey at the beginning and later in the growing season (Augspurger & Salk, 2017). However, this thesis reveals another mechanism that contributes significantly to the high species diversity of riverine communities in general.

The river valleys are considered as natural corridors for species dispersal. So far, there is a little evidence that this assumption is true. Most of the studies dealing with this topic are based on the population-genetics analyses and only a few of them focus on plant communities. For example, Pilger et al. (2017) found that fish populations within a river, rather than between different rivers had higher genetic relatedness. Other studies showed that a substantial proportion of plant species growing in or near water have propagules able to disperse by water, either floating, submerged in flowing water, or with the help of floating vessels. Therefore, due to these unidirectional dispersal modes, downstream populations may receive more immigrants than upstream ones (Honnay et al., 2010; Nilsson et al., 2010). However, neither of these studies provide evidence that in river valleys the colonisation rate of plant species is higher, thus confirming river valleys as migration corridors. In addition, these studies only focus on water dispersal, i.e. in a river, and neglect other dispersal modes which can be more pronounced along a river. **Study I** is therefore unique in using an approach that examines the plant species dispersal along a river, and thus contributes greatly to the understanding of species dispersal patterns in plant communities adjacent to the river, such as floodplain forests.

The findings of **Study I** confirm that migration processes are accelerated along the river from the reasons detailed described in **Study I** introduction and discussion. As floodplain forests occur along the down streams of large rivers, it can be assumed that a higher colonisation rate of plant species contributes significantly to the high species diversity of these habitats. In addition, it is likely that these processes are even more accelerated in floodplains. As mentioned above, periodic flooding mechanically disturbs the understorey vegetation and creates gaps of bare soil. These gaps are much easier for migrating plant species from different parts of riverbank to reach, and thus can be colonise more quickly. The high resource availability of floodplains additionally supports the establishment of propagules. In summary, the characteristics of floodplains allow for an even faster colonisation rate of plant species compared to other habitats typically occurred in river valleys.

However, such a process is only to be observed in natural floodplain forests where the river-floodplain dynamics are unaffected. In the case of floodplain forests along regulated rivers, where floods are less frequent or absent, species dispersal may be much more difficult, despite the presence of floodplain forests in river valleys, i.e. migration corridors. Frequent flooding disrupts understorey vegetation, preventing competitive species from becoming dominant and occupying all available space. Otherwise, migrating species are not able to establish in a completely covered area and, if they do, they are outcompeted. Unfortunately, the findings of **Study II** suggest exactly this trend.

8.2 The effects of environmental factors on floodplain forest vegetation in the context of establishing appropriate management strategies

Floodplain forests are often stressed as habitats resistant to climate change. There are two reasons for this assumption: 1) the occurrence of floodplain forests is determined by high groundwater levels and periodic flooding, usually associated with the presence of large rivers, 2) the tree canopy buffers the forest floor from extreme heat and drought. The findings of **Study II** confirm this assumption as a complex set of environmental factors other than climate change appeared to be more severe for changes in plant community structure. In fact, eutrophication and forest ageing proved to be the main drivers of changes in species richness and total plant cover of both phenological guilds commonly found in floodplain forests, i.e. spring and summer species.

The spring phenological guild is often neglected in long-term vegetation surveys, so the effects of environmental factors, which are well studied in the case of summer species, are unknown. The **Study II** clarifies this and brings surprising results. As expected, eutrophication and forest ageing exhibited significant negative effects on the summer phenological guild. However, spring phenological guild was found to be positively affected by these factors. In addition, the positive effect of less frequent spring flooding on spring species was found as well. From a conservation point of view, this should be taken into account when designing appropriate management strategies.

Old-growth floodplain forests in early spring (Cahnov – Soutok national nature reserve)

The **Study II** additionally highlights the importance of assessing the soil conditions at a given site. It appeared that the proportion of sand/clay particles in a soil can make a difference in the response of the summer phenological guild to the application of intervention management. On sites with higher proportion of coarse sand particles, tree cutting may even have positive effect on species richness. These sites dry out much faster, resulting in a less suitable moisture conditions that further limit the species growth and colonisation. Tree cutting and subsequent canopy opening accelerate this process, therefore, rather less competitive, drought-tolerant species could persist on these sites, leading to an increase in species diversity. On the other hand, sites with a higher proportion of clay particles retain moisture in the soil for a long time, allowing species to thrive without environmental constraints and shifting the species composition towards resource-demanding species that occupy all available space.

In summary, the findings of **Study II** suggest that different management strategies should be applied in floodplain forests depending on the environmental conditions of a particular site and the target phenological guild. This is consistent with the findings of **Study III**, which focused more on the effects of intervention management, which varies in its intensity. Specifically, **Study III** shows that a patchwork of different age classes, including old-growth forest stands, with different forest stand sizes, is highly suitable for restoring and maintaining the highest species diversity in forests, as each provides different light conditions and thus allows the presence of species that occupy contrasting light niches.

However, this type of forest management as applied by foresters today (also known as even-aged management) doesn't provide the same light conditions in certain age classes as in the past. The age class of 21 – 40 years can serve as an example (**Study III**). Whereas in the past this age class provided high light availability as these forest stands were likely much sparser (Müllerová et al., 2014), at present it is represented by a high number of young trees standing very close together resulting in young but dense forests with a completely shaded forest floor.

Young dense forest stands during late spring in Libický luh national nature reserve

Therefore, the "younger" age classes (up to 40 years) should be established by using forest stands as coppices or coppices-with-standards. In a coppice system, young shoots are cut in short rotations (every 7–30 years), with new shoots resprouting from coppice stools or roots. In the coppice-with-standards variant, single-stemmed trees (standards) were retained in a sparse canopy among coppice stools for one or more rotations (Müllerová et al., 2014). This traditional forest management increases species richness by frequent alteration of light and shady phases enabling the coexistence of a wide range of species in the understorey (Ash & Barkham, 1976; Buckley, 1992).

Middle-aged floodplain forests in 1950´s with light conditions allowing development of plant species-rich community in the understorey (J. Zikmund, taken from Mezera 1958)

On sites where the "younger" age classes would be established it should be accompanied by other management practices, which are necessary to achieve the restoration of the original species diversity in floodplain forests. Reintroduction of forest management with more frequent human interventions usually leads to higher light availability for understorey species and shift species composition backwords to less competitive light-demanding species. However, in nutrient-saturated floodplains, this would only result in a replacement by higher competitive light-demanding species with the same nutrient requirements as original species, and species richness patterns would remain unchanged (as observed in intervention forests – **Study II**). Therefore, to support a colonisation of floodplain forests by less competitive light-demanding species and their long-term survival is crucial to restore flood regime of regulated rivers. Frequent flooding mechanically disrupts the understorey vegetation, creating gaps of bare soil that are more accessible to migrating species (**Study I**), and reducing the abundance of competitive, resource-demanding species, which allow less competitive species to establish and persist. However, the process of restoration of flood regimes is time-consuming, financially and technically demanding, and thus only some parts of the regulated rivers can be restored.

Other management approaches must therefore be adopted for the remaining parts of the river, taking into account local environmental conditions, in particular soil conditions. For example, on sites with a higher proportion of clay particles, the establishment of “younger” age classes must be accompanied by traditional management practices such as litter raking and grazing, which continuously remove large proportion of the biomass from a site and thus reduce nutrient availability. On sites with a higher proportion of coarse sand particles, the establishment of middle age classes, i.e. 41 – 60 and 61 – 80 years, could be sufficient to restore the original species diversity, as these sites provide less moisture than others that limit the spread and persistence of competitive resource demanding species (detailed explanation above). On the other hand, these forest stands should be managed as so-called open forests with continuous selective cutting of younger trees and leaving older trees, for example oaks (which were typically retained as standards in the past), to maintain sparse canopy providing semi-shaded conditions. Finally, the maintaining the older age classes, i.e. more than 80 years in floodplain forest seems crucial for preserving of spring phenological guild as shaded conditions appeared to indirectly promotes its total cover. In addition, true forest species which are tied to the long-term presence of forests and therefore highly valued and desirable, could also thrive in such forest stands.

Old-growth floodplain forest in late summer with completely shaded forest floor (Ranšpurk national nature reserve)

8.3 Resampling errors

Two different sources of historical data were used in the research related to this thesis: the vegetation plots originally established by experienced botanists, and the vegetation plots originally established by foresters for the purpose of determining forest typology. However, when these sources were analysed separately, the results showed opposite trends in vegetation change, which in turn led to a more detailed investigation of the impact of historical observer error (**Study IV**). For the purposes of the **Studies II** and **III**, the data originally established by foresters were excluded, as **Study IV** clearly showed that these data were unreliable and led to incorrect results due to species omission.

As we were only able to identify the approximate location of the historical vegetation plots (quasi-permanent plots), **Studies II** and **III** may suffer from relocation error, but there is evidence that the use of qausi-permanent plots is robust when the plots are established in homogeneous environments (Chytrý et al., 2014, Verheyen er al., 2018). The original observers (experienced botanists) established the vegetation plots in forest stands, which are defined by foresters as homogeneous flat areas with similar growing conditions and tree species structure. Therefore, the occurrence of relocation error in the data is unlikely. Furthermore, Kopecký and Macek (2015), for example, concluded that the use of quasi-permanent plots is robust even in heterogeneous environments.

Seasonal bias is another potential error associated with the method of resampling the historical vegetation plots. However, the original observers left the sampling date information, so we were able to resample the plots at a similar time of the growing season. The effect of seasonal bias should therefore be negligible.

8.4 Future research

The thesis provides new insights into the development and conservation of temperate floodplain forests. However, the research has so far been carried out in a limited geographical area, i.e. Central Europe. It is therefore desirable to extend the research to other parts of Europe, especially the Mediterranean area. There is some evidence that Mediterranean floodplain forests are suffering more from climate change than temperate floodplain forests, with increased heat and prolonged drought. We cooperate with plant ecologists in Portugal and Poland and have had the opportunity to participate in re-surveys of vegetation plots, for example in the Doñana National Park. So far, initial results indicate a significant decline in species richness after a decade of drought. Although climatic conditions have stabilised since then, the original species richness has not recovered, indicating the low resilience and resistance of Mediterranean floodplain forests.

In the future, we would like to re-sample the vegetation plots we established in floodplain forests across Europe between 2011 and 2013. This time we will focus on the combined effects of climate extremes and atmospheric deposition (nitrogen and sulphur). During the last decade, we have increasingly experienced climatic extremes, such as heat waves or prolonged droughts, which are likely to exacerbate the effects of past and present atmospheric deposition and thus contribute significantly to the current changes in forest ecosystems. We aim to predict changes in the diversity and composition of the vegetation of floodplain forests in Europe based on scenarios of different climate development and landscape use, assess the resilience of European riparian vegetation to climate extremes and atmospheric deposition, and assess their role as possible future refugia for selected forest species in mitigating the effects of ongoing climate change. Hopefully, this research will be conducted.

8.5 Conclusion

The thesis showed that changes in floodplain forest vegetation are driven by a complex set of environmental factors, in particular eutrophication and forest ageing, rather than climatic variables. Eutrophication and forest ageing significantly affect both phenological guilds commonly found in floodplain forests, i.e. spring and summer species, however, with opposite trends in their community structure. While summer species show a drastic decrease in richness and an increase in the abundance of competitive mesophilic species, leading to biotic homogenisation later in the growing season, spring species show positive responses in both abundance and richness.

It follows that the non-intervention management typically applied in nature reserves tends to contribute to the ongoing degradation of floodplain forests and should be adapted. We propose an intervention management including an establishing of a patchwork of different age classes, including old-growth forest stands, complemented by traditional forest management practices that increase heterogeneity in light availability and decrease eutrophication. In forest stands of “younger” age classes the coppicing or coppicing-with-standards should be reintroduced. On sites with higher clay content, the low forest management should be accompanied by practices that regularly remove biomass from a site such as grazing or litter raking. On sites with a higher proportion of sand particles, the “middle” age classes can be established but with the efforts to maintain sparse canopy by selective tree cutting and leaving older trees. Litter raking and grazing are not necessary on these sites as more rapid desiccation limits the spread of resource-demanding species, allowing less competitive species to persist and thus increasing species diversity. Finally, the “older” age classes can remain as strong shaded conditions support spring phenological guild. In addition, longer presence of forests also supports so-called true forest species, which are highly valued in nature conservation. If it is possible, at least some parts of the river channel should be revitalized.

Chapter 9

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Chapter 10

Curriculum Vitae and List of Publications

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Education

2019 – present Ph.D. degree at the Faculty of Environmental Sciences, Czech university of live sciences in Prague

Field of study: Ecology

Ph.D. thesis: Vegetation changes and biodiversity conservation of floodplain forests

2017 – 2019 Master's degree at the Faculty of Environmental Sciences, Czech university of live sciences in Prague

Field of study: Nature conservation

Diploma thesis: How does strict protection of old-growth wetland forest benefit threatened species?

2014 – 2017 Bachelor's degree at the Faculty of Environmental Sciences, Czech university of live sciences in Prague

Field of study: Applied ecology

Bachelor thesis: Do plant species colonize recent forest more quickly in river valleys: test of the river migration phenomenon.

List of Projects

GAČR (23-07716S, team member, 2023): Linking performance trade-off with modern coexistence theory and functional trait approach

IGA (2020B0035, main solver, 2020 – 2022): Vegetation changes and biodiversity conservation of floodplain forests; the Faculty of Environmental Sciences, Czech university of live sciences in Prague

INTERCOST (LTC18045, team member, 2018 – 2021): The understanding of long-term sustainability of ecosystem services of European floodplain forests; the Ministry of Education, Youth and Sports of the Czech Republic

List of Publications

Holeštová, A., Doudová, J., Havrdová, A., Černá, M., Boublík, K., & Douda, J. (2024). Contrasting responses of forest phenological guilds to complex floodplain change. *Journal of Ecology*, *112*(6), 1397-1412.

Douda, J., Doudová, J., Holeštová, A., Chudomelová, M., Vild, O., Boublík, K., ... & Hédl, R. (2023). Historical sampling error: A neglected factor in long-term biodiversity change research. *Biological Conservation*, *286*, 110317.

Holeštová, A., & Douda, J. (2022). Plant species over-occupancy indicates river valleys are natural corridors for migration. *Plant Ecology, 223*(1), 71-83.

Douda, J., Doudová, J., Holeštová, A., Boublík, K., Havrdová, A., & Slezák, M. (2021). Interplay of above-and belowground resource limitations: a competition–facilitation shift maintains species coexistence. *Oikos, 130* (12), 2122-2135.