

Czech University of Life Sciences Prague

Faculty of Environmental Sciences



**Vegetation dynamics and biodiversity conservation in
floodplain forests of regulated rivers**

Anežka Holešťová

This dissertation thesis is submitted for the degree *Doctor of Philosophy* at
the Department of Ecology

Prague

2024

**Vegetation dynamics and biodiversity conservation in floodplain forests of
regulated rivers**

Dissertation Thesis

Author: **Anežka Holešťová**

Supervisor: **doc. Ing. Jan Douda, Ph.D.**

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.

.....

Anežka Holešťová

Acknowledgements

First and foremost, I would like to thank the entire team of the Plant Ecology Lab for helping me every step of the way to complete this thesis, starting with data collection and ending with the final reading of the manuscripts. Many thanks to my supervisor doc. Ing. Jan Douda, Ph.D. and his wife Ing. Jana Doudová, Ph.D. for their guidance, patience and great advice since the beginning of my studies. I am also very grateful to my friend Marie Černá for her big help in the field as well as in the office and her energetic, cheerful nature, which made every task more pleasant. I would also like to thank my family, who have supported and encouraged me since my childhood, and whose belief in me has brought me to this point in my life.

The scientific papers included in this thesis was funded by the following research projects:

2020B0035

Internal Grant Agency of the Faculty of Environmental Sciences, Czech University of Life Sciences Prague

LTC18045

The understanding of long-term sustainability of ecosystem services of European floodplain forests of the Ministry of Education, Youth and Sports of the Czech Republic

23-07716S

Czech Science Foundation

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.

Contents

Thesis Preface	11
1.1 Research motivation.....	11
1.2 Thesis structure	13
Theoretical Background.....	14
2.1 Importance of floodplain forests	14
2.2 Natural temperate floodplain forests.....	15
2.3 River regulations	19
2.4 Traditional use of floodplain forests.....	20
2.5 Eutrophication.....	23
2.6 Climate change.....	25
2.7 Historical sampling error	27
Objectives of the Thesis	29
Study I: Plant species over-occupancy indicates river valleys are natural corridors for migration	31
Study II: Contrasting responses of forest phenological guilds to complex floodplain change.....	32
Study III: Age heterogeneity in floodplain forest fragments promotes understorey plant diversity (<i>manuscript</i>)	33
Study IV: Historical sampling error: A neglected factor in long-term biodiversity change research.....	34
Discussion and Summary.....	35
8.1 Species dispersal patterns in floodplains.....	35
8.2 The effects of environmental factors on floodplain forest vegetation in the context of establishing appropriate management strategies.....	37

8.3 Resampling errors	44
8.4 Future research.....	45
8.5 Conclusion.....	46
References	48
Curriculum Vitae and List of Publications	61

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 understory 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 (Hédli 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

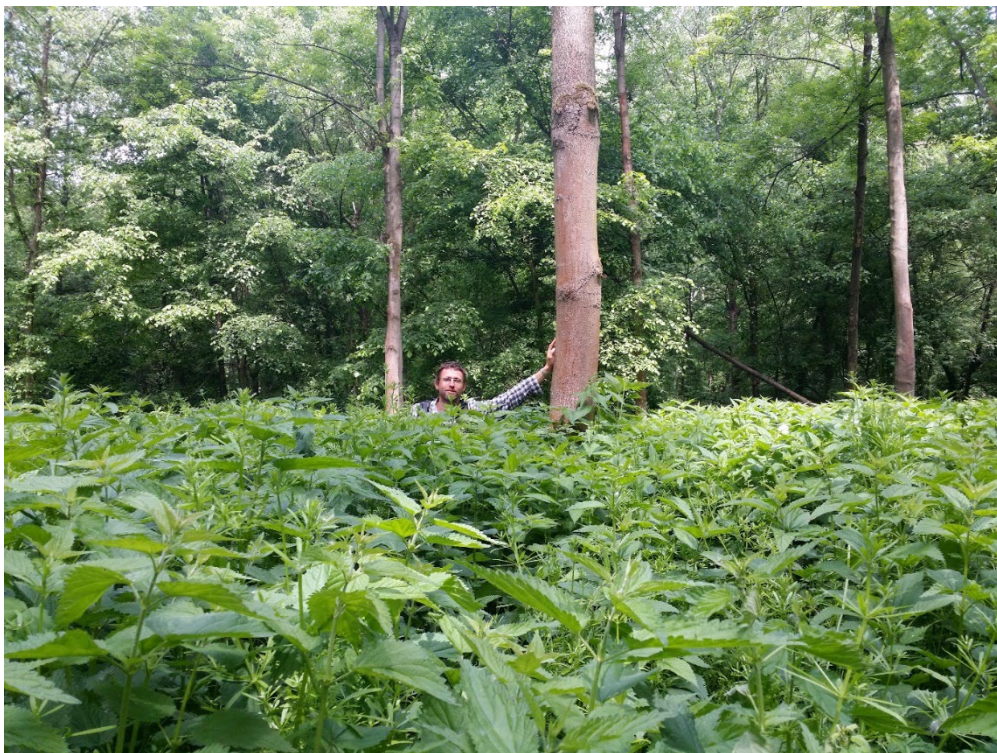
Eutrophication generally has negative effects on diversity of plant communities because an accumulation of nutrients in the soil increases soil acidification, which progressively determines abundance loss up to the complete extirpation of species adapted to nutrient-poor conditions (Bobbink et al., 2010). 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; Hédli 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

Chapter 5

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

Chapter 6

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

Chapter 7

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

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; Doua, 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 (Augsburger & 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 understory 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 backwards 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 quasi-permanent plots is robust when the plots are established in homogeneous environments (Chytrý et al., 2014, Verheyen et 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

References

- Ash, J. E., & Barkham, J. P. (1976). Changes and variability in the field layer of a coppiced woodland in Norfolk, England. *The Journal of Ecology*, 697-712. <https://doi.org/10.2307/2258779>
- Atkinson, B. W. (2003). *The climate near the ground*, R. Geiger, RH Aron and P. Todhunter, Rowman and Littlefield Publishers, Lanham, MD, USA, 2003. No. of pages xviii+ 584. ISBN 0-7425-1857-4. <https://doi.org/10.1002/joc.967>
- Augsburger, C. K., & Salk, C. F. (2017). Constraints of cold and shade on the phenology of spring ephemeral herb species. *Journal of Ecology*, 105(1), 246-254. <https://doi.org/10.1111/1365-2745.12651>
- Axmanová, I., Chytrý, M., Zelený, D., Li, C. F., Vymazalová, M., Danihelka, J., ... & Diekmann, M. (2012). The species richness–productivity relationship in the herb layer of European deciduous forests. *Global Ecology and Biogeography*, 21(6), 657-667. <https://doi.org/10.1111/j.1466-8238.2011.00707.x>
- Barnes, W. J. 1978. The distribution of floodplain herbs as influenced by annual flood elevation. *Wisconsin Acad. Science, Arts and Letters* 66, 254–266.
- Battaglia, L. L., Minchin, P. R., & Pritchett, D. W. (2002). Sixteen years of old-field succession and reestablishment of a bottomland hardwood forest in the Lower Mississippi Alluvial Valley. *Wetlands*, 22(1), 1-17. [https://doi.org/10.1672/0277-5212\(2002\)022\[0001:SYOOF5\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0001:SYOOF5]2.0.CO;2)

- Becker, T., Spanka, J., Schröder, L., & Leuschner, C. (2017). Forty years of vegetation change in former coppice-with-standards woodlands as a result of management change and N deposition. *Applied Vegetation Science*, 20(2), 304-313. <https://doi.org/10.1111/avsc.12282>
- Bierzychudek, P. (1982). Life histories and demography of shade-tolerant temperate forest herbs: a review. *New phytologist*, 90(4), 757-776. <https://doi.org/10.1111/j.1469-8137.1982.tb03285.x>
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., ... & De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological applications*, 20(1), 30-59. <https://doi.org/10.1890/08-1140.1>
- Buckley, G.P. (1992). *Ecology and Management of Coppice Woodlands*. Chapman & Hall, London.
- Chytrý, M., Tichý, L., Hennekens, S. M., & Schaminée, J. H. (2014). Assessing vegetation change using vegetation-plot databases: a risky business. *Applied Vegetation Science*, 17(1), 32-41. <https://doi.org/10.1111/avsc.12050>
- Creed, I.F., Van Noordwijk, M., 2018. Forest and water on a changing planet: Vulnerability, adaptation and governance opportunities. A Global Assessment Report. IUFRO Worlds Series, Vienna.
- Davidson, N. C., & Finlayson, C. M. (2018). Extent, regional distribution and changes in area of different classes of wetland. *Marine and Freshwater Research*, 69(10), 1525-1533. <https://doi.org/10.1071/MF17377>
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ... & Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46), 18561-18565. <https://doi.org/10.1073/pnas.1311190110>

- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744-749. <https://doi.org/10.1038/s41559-019-0842-1>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., ... & Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279-2297. <https://doi.org/10.1111/gcb.15569>
- Douda, J. (2008). Formalized classification of the vegetation of alder carr and floodplain forests in the Czech Republic.
- Douda, J. (2009). O vegetační proměnlivosti a původu lužních lesů. *Živa* 2, 56-59.
- Douda, J. (2010). The role of landscape configuration in plant composition of floodplain forests across different physiographic areas. *Journal of vegetation Science*, 21(6), 1110-1124. <https://doi.org/10.1111/j.1654-1103.2010.01213.x>
- Douda, J., Boublík, K., Doudová, J., & Kyncl, M. (2017). Traditional forest management practices stop forest succession and bring back rare plant species. *Journal of Applied Ecology*, 54(3), 761-771. <https://doi.org/10.1111/1365-2664.12801>
- Dynesius, M., & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, 266(5186), 753-762. <https://doi.org/10.1126/science.266.5186.753>
- Ellison, D., Morris, C. E., Locatelli, B., Sheil, D., Cohen, J., Murdiyarso, D., ... & Sullivan, C. A. (2017). Trees, forests and water: Cool insights for a hot world. *Global environmental change*, 43, 51-61. <https://doi.org/10.1016/j.gloenvcha.2017.01.002>

- Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M., & Zuleta, D. (2020). Climate-driven changes in the composition of New World plant communities. *Nature Climate Change*, 10(10), 965-970. <https://doi.org/10.1038/s41558-020-0873-2>
- Ferreira, L. V., & Stohlgren, T. J. (1999). Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia*, 120, 582-587. <https://doi.org/10.1007/s004420050893>
- Fischer, M., & Stöcklin, J. (1997). Local Extinctions of Plants in Remnants of Extensively Used Calcareous Grasslands 1950–1985: Extinciones Locales de Plantas en Remanentes de Pastizales Calcáreos de Uso extensivo entre 1950 y 1985. *Conservation biology*, 11(3), 727-737. <https://doi.org/10.1046/j.1523-1739.1997.96082.x>
- Garssen, A. G., Verhoeven, J. T., & Soons, M. B. (2014). Effects of climate-induced increases in summer drought on riparian plant species: A meta-analysis. *Freshwater Biology*, 59(5), 1052-1063. <https://doi.org/10.1111/fwb.12328>
- Gimmi, U., Poulter, B., Wolf, A., Portner, H., Weber, P., & Bürgi, M. (2013). Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking. *Landscape Ecology*, 28, 835-846. <https://doi.org/10.1007/s10980-012-9778-4>
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., ... & Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature climate change*, 2(2), 111-115. <https://doi.org/10.1038/nclimate1329>
- Gregory, S. V., Swanson, F. J., McKee, W. A., & Cummins, K. W. (1991). An ecosystem perspective of riparian zones. *BioScience*, 41(8), 540-551. <https://doi.org/10.2307/1311607>

- Hale, B. W., Alsum, E. M., & Adams, M. S. (2008). Changes in the floodplain forest vegetation of the lower Wisconsin River over the last fifty years. *The American Midland Naturalist*, 160(2), 454-476. [https://doi.org/10.1674/0003-0031\(2008\)160\[454:citffv\]2.0.co;2](https://doi.org/10.1674/0003-0031(2008)160[454:citffv]2.0.co;2)
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636-638. <https://doi.org/10.1126/science.1169640>
- Havrdová, A., Douda, J., & Doudová, J. (2023). Threats, biodiversity drivers and restoration in temperate floodplain forests related to spatial scales. *Science of the Total Environment*, 854, 158743. <https://doi.org/10.1016/j.scitotenv.2022.158743>
- Hédl, R. (2004). Vegetation of beech forests in the Rychlebské Mountains, Czech Republic, re-inspected after 60 years with assessment of environmental changes. *Plant Ecology*, 170, 243-265. <https://doi.org/10.1023/B:VEGE.0000021681.83068.53>
- Hédl, R., Kopecký, M., & Komárek, J. (2010). Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity and Distributions*, 16(2), 267-276. <https://doi.org/10.1111/j.1472-4642.2010.00637.x>
- Hédl, R., Bernhardt-Römermann, M., Grytnes, J. A., Jurasinski, G., & Ewald, J. (2017). Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. *Applied Vegetation Science*, 20(2), 161-163.
- Hodges, J. D. (1997). Development and ecology of bottomland hardwood sites. *Forest Ecology and Management*, 90(2-3), 117-125. [https://doi.org/10.1016/S0378-1127\(96\)03906-0](https://doi.org/10.1016/S0378-1127(96)03906-0)

- Honnay, O., Jacquemyn, H., Nackaerts, K., Breyne, P., & Van Looy, K. (2010). Patterns of population genetic diversity in riparian and aquatic plant species along rivers. *Journal of Biogeography*, 37(9), 1730-1739. <https://doi.org/10.1111/j.1365-2699.2010.02331.x>
- Humborg, C., Smedberg, E., Blomqvist, S., Mörth, C. M., Brink, J., Rahm, L., ... & Sahlberg, J. (2004). Nutrient variations in boreal and subarctic Swedish rivers: Landscape control of land-sea fluxes. *Limnology and Oceanography*, 49(5), 1871-1883. <https://doi.org/10.4319/lo.2004.49.5.1871>
- Janik, D., Adam, D., Vrska, T., Hort, L., Unar, P., Kral, K., ... & Horal, D. (2008). Tree layer dynamics of the Cahnov–Soutok near-natural floodplain forest after 33 years (1973–2006). *European Journal of Forest Research*, 127, 337-345. <https://doi.org/10.1007/s10342-008-0210-1>
- Johnson, S. E., Mudrak, E. L., & Waller, D. M. (2014). Local increases in diversity accompany community homogenization in floodplain forest understories. *Journal of Vegetation Science*, 25(3), 885-896. <https://doi.org/10.1111/jvs.12147>
- Johnson, S. E., Amatangelo, K. L., Townsend, P. A., & Waller, D. M. (2016). Large, connected floodplain forests prone to flooding best sustain plant diversity. *Ecology*, 97(11), 3019-3030. <https://doi.org/10.1002/ecy.1556>
- Jucker, T., Hardwick, S. R., Both, S., Elias, D. M., Ewers, R. M., Milodowski, D. T., ... & Coomes, D. A. (2018). Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global change biology*, 24(11), 5243-5258. <https://doi.org/10.1111/gcb.14415>

- Kapfer, J., Hédli, R., Jurasinski, G., Kopecký, M., Schei, F. H., & Grytnes, J. A. (2017). Resurveying historical vegetation data—opportunities and challenges. *Applied Vegetation Science*, 20(2), 164-171. <https://doi.org/10.1111/avsc.12269>
- Kirby, K. J., Goldberg, E. A., Isted, R., Perry, S. C., & Thomas, R. C. (2016). Long-term changes in the tree and shrub layers of a British nature reserve and their relevance for woodland conservation management. *Journal for Nature Conservation*, 31, 51-60. <https://doi.org/10.1016/j.jnc.2016.03.004>
- Klimo, E., Hager, H., 2001. The floodplain forests in Europe: Current situations and perspectives. European Forest Institute Research Report 10. Brill, Leiden, the Netherlands.
- Kopeć, D., Ratajczyk, N., Wolańska-Kamińska, A., Walisch, M., & Kruk, A. (2014). Floodplain forest vegetation response to hydroengineering and climatic pressure—A five decade comparative analysis in the Bzura River valley (Central Poland). *Forest Ecology and Management*, 314, 120-130. <https://doi.org/10.1016/j.foreco.2013.11.033>
- Kopecký, M., Hédli, R., & Szabó, P. (2013). Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology*, 50(1), 79-87. <https://doi.org/10.1111/1365-2664.12010>
- Kopecký, M., & Macek, M. (2015). Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, 21(3), 322-330. <https://doi.org/10.1111/ddi.12299>
- Lameire, S., Hermy, M., & Honnay, O. (2000). Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. *Journal of Vegetation Science*, 11(5), 695-704. <https://doi.org/10.2307/3236576>

- Lenoir, J., Gégout, J. C., Dupouey, J. L., Bert, D., & Svenning, J. C. (2010). Forest plant community changes during 1989-2007 in response to climate warming in the Jura Mountains (France and Switzerland). *Journal of Vegetation Science*, 21(5), 949-964. <https://doi.org/10.1111/j.1654-1103.2010.01201.x>
- Lite, S. J., Bagstad, K. J., & Stromberg, J. C. (2005). Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments*, 63(4), 785-813. <https://doi.org/10.1016/j.jaridenv.2005.03.026>
- Meier, A. J., Bratton, S. P., & Duffy, D. C. (1995). Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecological Applications*, 5(4), 935-946. <https://doi.org/10.2307/2269344> (1995)
- Menges, E. S., & Waller, D. M. (1983). Plant strategies in relation to elevation and light in floodplain herbs. *The American Naturalist*, 122(4), 454-473. <https://doi.org/10.1086/284149>
- Mezera, A., 1958. Středoevropské nížinné luhy II. Lesy českomoravských údolních niv, jejich historie a lesní hospodářství v lužních porostech. SZN, Praha.
- Mitsch, W. J., Taylor, J. R., & Benson, K. B. (1991). Estimating primary productivity of forested wetland communities in different hydrologic landscapes. *Landscape ecology*, 5, 75-92. <https://doi.org/10.1007/BF00124662>
- Morrison, L. W. (2021). Nonsampling error in vegetation surveys: understanding error types and recommendations for reducing their occurrence. *Plant Ecology*, 222(5), 577-586. <https://doi.org/10.1007/s11258-021-01125-5>

- Müllerová, J., Hédl, R., & Szabó, P. (2015). Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management*, 343, 88-100. <https://doi.org/10.1016/j.foreco.2015.02.003>
- Naaf, T., & Wulf, M. (2011). Traits of winner and loser species indicate drivers of herb layer changes over two decades in forests of NW Germany. *Journal of Vegetation Science*, 22(3), 516-527. <https://doi.org/10.1111/j.1654-1103.2011.01267.x>
- Naiman, R. J., & Rogers, K. H. (1997). Large animals and system-level characteristics in river corridors. *BioScience*, 47(8), 521-529. <https://doi.org/10.2307/1313120>
- Nilsson, C., Brown, R. L., Jansson, R., & Merritt, D. M. (2010). The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews*, 85(4), 837-858. <https://doi.org/10.1111/j.1469-185X.2010.00129.x>
- Oakes, L. E., Hennon, P. E., O'Hara, K. L., & Dirzo, R. (2014). Long-term vegetation changes in a temperate forest impacted by climate change. *Ecosphere*, 5(10), 1-28. <http://dx.doi.org/10.1890/ES14-00225.1>
- Ounissi, M., & Bouchareb, N. (2013). Nutrient distribution and fluxes from three Mediterranean coastal rivers (NE Algeria) under large damming. *Comptes Rendus Geoscience*, 345(2), 81-92. <https://doi.org/10.1016/j.crte.2013.02.002>.
- Petřík, P., Černý, T., Kolbek, J., Boublík, K. & Kopecký, M. (2009). Changes in forest vegetation induced by game impact in the Křivoklátsko Biosphere Reserve (Czech Republic). *Zprávy České Botanické Společnosti* 44 Materiály 24, 121– 135.

- Pilger, T. J., Gido, K. B., Propst, D. L., Whitney, J. E., & Turner, T. F. (2017). River network architecture, genetic effective size and distributional patterns predict differences in genetic structure across species in a dryland stream fish community. *Molecular ecology*, 26(10), 2687-2697. <https://doi.org/10.1111/mec.14079>
- Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., ... & Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science advances*, 3(1), e1600821. <https://doi.org/10.1126/sciadv.1600821>
- Pramova, E., Locatelli, B., Djoudi, H., & Somorin, O. A. (2012). Forests and trees for social adaptation to climate variability and change. *Wiley Interdisciplinary Reviews: Climate Change*, 3(6), 581-596. <https://doi.org/10.1002/wcc.195>
- Rackham, O. (2008). Ancient woodlands: modern threats. *New Phytologist*, 571-586. <https://doi.org/10.1111/j.1469-8137.2008.02579.x>
- Reczyńska, K., & Świerkosz, K. (2017). Compositional changes in thermophilous oak forests in Poland over time: do they correspond to European trends?. *Applied Vegetation Science*, 20(2), 293-303. <https://doi.org/10.1111/avsc.12290>
- Reinecke, J., Klemm, G., & Heinken, T. (2014). Vegetation change and homogenization of species composition in temperate nutrient deficient Scots pine forests after 45 yr. *Journal of Vegetation Science*, 25(1), 113-121. <https://doi.org/10.1111/jvs.12069>
- Riis, T., Kelly-Quinn, M., Aguiar, F. C., Manolaki, P., Bruno, D., Bejarano, M. D., ... & Dufour, S. (2020). Global overview of ecosystem services provided by riparian vegetation. *BioScience*, 70(6), 501-514. <https://doi.org/10.1093/biosci/biaa041>

- Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, 38(6), 546-555. <https://doi.org/10.1111/ecog.01131>
- Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., ... & Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of applied Ecology*, 55(1), 267-278. <https://doi.org/10.1111/1365-2664.12950>
- Schnitzler, A., Hale, B. W., & Alsum, E. (2005). Biodiversity of floodplain forests in Europe and eastern North America: a comparative study of the Rhine and Mississippi Valleys. *Biodiversity & Conservation*, 14, 97-117. <https://doi.org/10.1007/s10531-005-4056-2>
- Selwood, K. E., & Zimmer, H. C. (2020). Refuges for biodiversity conservation: A review of the evidence. *Biological conservation*, 245, 108502. <https://doi.org/10.1016/j.biocon.2020.108502>
- Strubelt, I., Diekmann, M., & Zacharias, D. (2017). Changes in species composition and richness in an alluvial hardwood forest over 52 yrs. *Journal of Vegetation Science*, 28(2), 401-412. <https://doi.org/10.1111/jvs.12483>
- Taverna, K., Peet, R. K., & Phillips, L. C. (2005). Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *Journal of ecology*, 93(1), 202-213. <https://doi.org/10.1111/j.0022-0477.2004.00965.x>
- Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environmental conservation*, 29(3), 308-330. <https://doi.org/10.1017/S037689290200022X>
- United Nations, 2015. *Transforming Our World: The 2030 Agenda for Sustainable Development*.

- Vellend, M., Brown, C. D., Kharouba, H. M., McCune, J. L., & Myers-Smith, I. H. (2013). Historical ecology: using unconventional data sources to test for effects of global environmental change. *American Journal of Botany*, 100(7), 1294-1305. <https://doi.org/10.3732/ajb.1200503>
- Verheyen, K., De Frenne, P., Baeten, L., Waller, D. M., Hédli, R., Perring, M. P., ... & Bernhardt-Römermann, M. (2017). Combining biodiversity resurveys across regions to advance global change research. *BioScience*, 67(1), 73-83. <https://doi.org/10.1093/biosci/biw150>
- Verheyen, K., Bažány, M., Chečko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P., ... & Baeten, L. (2018). Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science*, 29(5), 812-823. <https://doi.org/10.1111/jvs.12673>
- Vild, O., Roleček, J., Hédli, R., Kopecký, M., & Utinek, D. (2013). Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective. *Forest Ecology and Management*, 310, 234-241. <https://doi.org/10.1016/j.foreco.2013.07.056>
- Vild, O., Chudomelová, M., Macek, M., Kopecký, M., Prach, J., Petřík, P., ... & Hédli, R. (2024). Long-term shift towards shady and nutrient-rich habitats in Central European temperate forests. *New Phytologist*, 242(3), 1018–1028. <https://doi.org/10.1111/nph.19587>
- Vojík, M., & Boublík, K. (2018). Fear of the dark: decline in plant diversity and invasion of alien species due to increased tree canopy density and eutrophication in lowland woodlands. *Plant ecology*, 219, 749-758. <https://doi.org/10.1007/s11258-018-0831-5>

- von Oheimb, G., & Brunet, J. (2007). Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. *Acta Oecologica*, 31(2), 229-242. <https://doi.org/10.1016/j.actao.2006.12.001>
- Vrška T., Hort L., Adam D., Odehnalová P., Král K., & Horal D. (2006). Dynamika vývoje pralesovitých rezervací v ČR II – Lužní lesy (Cahnov-Soutok, Ranšpurk, Jiřina). Academia, Praha.
- Vymazalová, M., Axmanová, I., & Tichý, L. (2012). Effect of intra-seasonal variability on vegetation data. *Journal of Vegetation Science*, 23(5), 978-984. <https://doi.org/10.1111/j.1654-1103.2012.01416.x>
- Ward, J. V., Tockner, K., Arcsott, D. B., & Claret, C. (2002). Riverine landscape diversity. *Freshwater biology*, 47(4), 517-539. <https://doi.org/10.1046/j.1365-2427.2002.00893.x>
- Whited, D. C., Lorang, M. S., Harner, M. J., Hauer, F. R., Kimball, J. S., & Stanford, J. A. (2007). Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. *Ecology*, 88(4), 940-953. <https://doi.org/10.1890/05-1149>
- Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., ... & De Frenne, P. (2019). Seasonal drivers of understory temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28(12), 1774-1786. <https://doi.org/10.1111/geb.12991>
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., ... & Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, 368(6492), 772-775. <https://doi.org/10.1126/science.aba6880>

Chapter 10

Curriculum Vitae and List of Publications

Anežka Holešťová
Šumavská 2964/39, Ústí nad Labem 400 11
holestova@fzp.czu.cz
plant-ecology-lab-czu.com

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 life 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

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

Holešťová, 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., Holešťová, 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.