Comparison of the floodplain forest floristic composition of two riparian corridors: species richness, alien species and the effect of water regime changes

Radomír Řepka, Jan Šebesta, Petr Maděra & Petr Vahalík

Department of the Forest Botany, Dendrology and Geobiocoenology and Department of Forest Management and Applied Geoinformatics, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, CZ-61300 Brno, Czech Republic; e-mail: repka@mendelu.cz

Abstract: Floodplain forests are sensitive to changes within the surrounding environment and contain the most highly invaded habitats. The overall aim of this study was to characterise floristic composition of floodplain forest along two different riparian corridors. The studied river ecosystems were influenced by human disturbances, but they have historically different hydrological management practices (e.g., damming and water regime management). We hypothesised that different hydrological management practices affect the composition and diversity of vegetation and influence multiple ecosystem functions and services in floodplain forests. A detailed study of the vascular plant species diversity of floodplain forests in the lower parts of two riparian corridors of the Thaya and Morava Rivers (South Moravia) was conducted. Altogether, 853 species of vascular plants were recorded, including 121 species of woody plants. We found 111 species that are protected by law or threatened according to the Czech Red List. We found 230 alien species, out of which 125 are archaeophytes and 105 are neophytes. Thirty-nine species are invasive; however, the most frequent group comprises naturalised archaeophytes (78). Differences in the effects of environmental factors on species richness and the proportions of alien and endangered species were tested using generalised linear models (GLMs). Differences in species composition in the two distinct riparian corridors were examined using non-metric multidimensional scaling (NMDS). Although only small differences were observed in the vegetation composition, we observed some differences in species richness and species composition between the riparian corridors. The most obvious difference was a higher proportion of alien species in the Morava River corridor than in the Thaya River corridor. In contrast, the proportion of endangered species richness was higher in the Thaya River corridor. We assume that the most probable explanation of the differences is the unique water management history for each river corridor.

Key words: floodplain forest; species diversity; alien species; riparian corridor; South Moravia

Introduction

A floodplain often represents a high biodiversity area in the European landscape (Ward et al. 2002). The species richness of certain organisms, such as vascular plants, often far exceeds that in adjacent upland habitats (Naiman et al. 1993, 2005; Tabacchi et al. 1996; Stohlgren et al. 1998). The biodiversity of a floodplain areas is generally considered very high (Klimo et al. 2008); this is due to the high heterogeneity of the environment in both the lateral and vertical directions, the high level of natural and anthropogenic disturbance and also the diversity of subsequent successions (Maděra et al. 2011). The important ecological functions of alluvial areas and their value to biodiversity conservation have made alluvial landscape conservation and restoration a high priority for ecosystem managers in many countries (Verry et al. 2000; Naiman et al. 2005).

Riparian plant communities typically comprise specialised and disturbance-adapted species within a matrix of less- specialised and disturbance adapted plant species (Naiman et al. 1997). Species diversity closely correlates with the diversity of floodplain forest habitats (Měkotová et al. 2006; Měkotová 2008). Riparian zones are often the ecosystems that are the most sensitive to changes within the surrounding environment (Lyon & Gross 2005). The current biodiversity of floodplains is a result of natural development and anthropogenic influences over recent decades (Thomas et al. 1979). Studies that address the species diversity of the South Moravian floodplains do yet not special focus on forest stands (Danihelka et al. 1995; Danihelka & Grulich 1996; Danihelka & Šumberová 2004). Vicherek et al. (2000) found 873 vascular plant species south of Lanžhot village over an confluence area Thaya-Morava Rivers of approximately 50 km^2 . A similar study was published by Schratt-Ehrendorfer (1999) in the Austrian part of the lower Morava River floodplain. Mölder & Schneider (2011) examined the floristic composition in three different parts of the Danube River and found that the species richness and eutrophication of floodplain communities increased in the direction of the river

flow. Schnitzler et al. (2007) ascertained that floodplain communities with rich species compositions occur across Europe.

There is one key negative factor in riparian systems: the invasion of alien plant species. Many of alien plants have been shown to significantly impact the composition and diversity of native plant communities (Pyšek & Prach 1993, 1994; Schnitzler et al. 2007; Chytrý et al. 2008; Lyon & Gross 2005; Maděra et al. 2013). A large number of studies that compare various habitat types confirmed that floodplain forests are one of the most invaded natural forest habitats (e.g., Chytrý et al. 2005, 2008; Petrášová et al. 2013). Floodplains are considered vulnerable to alien species (Hood & Naiman 2000; Harris et al. 2005) due to the combined influence of intensive human exploitation, a high degree of hydrological connectivity which facilitates the dispersal of propagules and the high spatial and temporal heterogeneity inherent to these systems. Globally, anthropogenic alterations to floodplain hydrological regimes have frequently resulted in riparian species invasions (Richardson et al. 2007). Floodplain forests are situated along rivers, which are important migration corridors (Boedeltje et al. 2004) for neophytes to colonise new territories (Pyšek & Prach 1993). Flooding not only disrupts native vegetation but also leaves bare soil for the establishment of new propagules and supplies new nutrients (Petrášová et al. 2013). The increase of neophytes may be caused by several factors, such as human land use intensification, the reduction and fragmentation of hardwood floodplain forests, and the increase in the transporting which affects the higher propagule pressure of neophytes during the last few decades (Walter et al. 2005; Von Holle et al. 2006; Schnitzler et al. 2007; Pyšek et al. 2010; Petrášová et al. 2013).

Modern hydrological changes have long affected the Morava River. Hydrological management has persisted since the 1930s in the Morava River and since the 1970s in the Thaya River; the management practices have decreased the groundwater level (Penka et al. 1991; Čermák et al. 2001) and practically eliminated floods in the study area. On contrary, the most elevated sandy sites were not changed by extremely long floods (Růžičková et al. 2004). We hypothesise that different hydrological management practices affect the composition and diversity of vegetation and influence multiple ecosystem functions and services in floodplain forests.

The general aim of our study is to assess and characterise species richness of floodplain forest vegetation along two riparian corridors in narrow strip to 1000 m from a river. We determine how the riparian corridors have influenced patterns of both native and alien species. Our objectives are to (1) characterise the tree and herb layer species diversity across two riparian corridors, (2) determine whether a particular river system (Thaya and Morava rivers) has an impact on species richness and spread of alien species, and 3) assess the relationship between the two riparian corridors, and their species diversity and floristic composition.

Fig. 1. Map of the study area with the analysed zone up to 1000 m from Morava and Thaya rivers marked by hatching.

Material and methods

The study area

The study area (Fig. 1) is the alluvial flatland of the lower watercourses of the Thaya and Morava Rivers between the Nové Mlýny village in the north-west and the Mikulčice village in the north-east. The southern point of the study area marks the confluence of the Thaya and Morava Rivers, which is south of the Lanžhot village. The study area is confined to a narrow strip along both Rivers up to 1000 m; we present the results of a detailed survey of floodplain forests over an area of 3745 ha (see Fig. 1). The areas of Thaya and Morava study strips are 2918 and 2387 ha, respectively. Proportion of forest is 60.7 % in the strip of Thaya River, forest comprises 82.2 % in the strip of Morava River. The study area belongs to the Lower Morava UNESCO Biosphere Reserve.

The study area is located in the southern part of the geomorphological unit called the Dolnomoravský úval basin (Thaya-Morava Floodplain) (Demek & Mackovčin 2006). Quaternary gravel is the geological substrate, which is covered by thick layers (up to 6 m) of alluvial sediments with loamy-clayey granularity and sandy elevations. Gley fluvisoils are in the area; gleys are typically in filled oxbows. The average annual temperature of the study area is 9.3◦ C and the cumulative average annual precipitation is 585 mm; climatologically, the area lies in the zone of warmest climate within the Czech Republic (Quitt 1975).

Data collection and processing

All vascular plants were recorded in the forest segments. Each segment corresponded to one stand group within the forest division; however, similar groups of segments were merged, and non-homogenous groups were divided. We used satellite photos with a actual forest stand map at the scale of 1:10000 (the current Forest Management Plan). The field survey was conducted in spring and summer between 2005 and 2013. Additionally, fresh clearings and young plantings

Table 1. Species diversity and proportions of alien and endangered species per segment in floodplain forests up to 1000 m from a river. The proportions of alien and endangered species were tested by GLM.

with a predominance of nitrophilous and clearing species were studied. Specimens of critical species were stored in the BRNL herbarium.

The field data were first transferred to the geodatabase. All maps of the terrain were digitised in the GIS environment (ArcGIS 10.2) to identify segments and obtain a better view of the species distribution. The resulting geodatabase of species was used to calculate diversity indices and establish other relationships. Thus, in addition to analysing the species diversity, the number of threatened species (categories of threat based on Grulich 2012) and the proportion of alien species were also identified (Pyšek et al. 2012a).

The effect of segment size on species diversity was first minimised (see Chytrý & Otýpková 2003; Dengler et al. 2008); the smallest and largest segments were removed from the dataset $(<0.3$ ha and >8 ha). The segments size was logarithmically transformed to produce a normal distribution. Linear regression compared the relationship of the species diversity medians to the segment size. To reveal the overall pattern of variation in species composition, we performed non-metric multidimensional scaling (NMDS) of all segments and dataset of a herb and woody species, calculated using the Bray-Curtis distances in two dimensions and with a maximum of 400 random starts. This analysis was done with the vegan package (Oksanen et al. 2013). We used generalised linear models (GLMs) in case of frequencies, as well as species richness and herb species differentiation between the riparian corridors. To evaluate fidelity, we used the "phi" coefficient (Chytrý et al. 2002) in the Juice software 7.0 (Tichý 2002). All statistical tests and analyses were performed in R software, version 3.0 (R Development Core Team 2013). Further, we examined the total number of species, the frequency of species in segments, and the proportions of alien, threatened and protected species. The nomenclature of vascular plants was used in accordance with Kubát et al. (2002).

Geographical information system and preparation of maps All analyses were performed by ArcGIS software version 10.2 (ESRI). The background data of the cartographic outputs are DIBAVOD (Digital Database for Water Management managed by T. G. Masaryk Water Research Institute), ArcCR500 (administrative geodatabase managed by Arc-Data Prague) and ESRI base maps.

Using geoinformation analyses, the closest distances from the rivers were calculated for all the centroids of the segments. Modelling of the biodiversity of the study area based on calculated values of the Shannon-Wiener index of all segments. The biodiversity was spatially interpolated by

a kriging process using a spherical semivariogram. The reason for using ordinary kriging was the structure of source data exactly matching the nature of this method. For ordinary kriging, rather than assuming that the mean is constant over the entire domain, we assume that it is constant in the local neighborhood of each estimation point (Clark 2000). The spatial distribution of alien species was interpolated using the same approach. The spatial resolution of the output images is 10 m, and the coordinate system is S-JTSK Krovak East-North.

Results

Species richness

Overall, a total of 732 herb and 121 woody species were found in the study area. The species richness was higher in the Thaya River than in the Morava River. Along the Thaya and Morava Rivers, a total of 627 and 609 herb species, respectively, and 107 and 92 woody species, respectively, were identified. No significant differences in species richness were found using Shannon's and Simpson's diversity methods between the Morava and Thaya Rivers (Table 1). Altogether, 104 unique herb species and 13 unique shrub and tree species were found in the Morava River alone; in the Thaya River 124 unique herb species and 27 unique shrub and tree species were found.

GLM analyses showed significant relationships between the affiliation of two riparian corridors and the richness of alien and endangered species. Table 1 provides a comparison of herb and total species richness and the proportions of alien and endangered species within the studied riparian corridors. In total, 230 alien species were found in the floodplain forests in the Morava and Thaya River corridors: 180 species in the Morava River and 199 species in the Thaya River forests. The Morava River corridor had a significantly higher proportion of alien species per segment than the Thaya River corridor. The affiliation with riparian corridors significantly influenced the endangered species richness (Table 1) but with the opposite effect – the proportion of endangered herb, shrub and tree species increased in the Thaya River corridor. Correlations between the number of alien species and the number

Comparison of floodplain forest floristic composition of two riparian corridors 211

Table 2. List of herb species by their fidelity to a particular river corridor and their frequencies.

of native species, calculated with individual riparian mean values, both were significant and positive. There was higher correlation coefficient in the Morava (0.80) then in the Thaya River (0.61). On the other hand, correlation between neophytes and the number of native species is proportionally much higher in the Thaya River (0.59) than in the Morava River (0.71).

Floristic composition

Differences in the floristic compositions of floodplain forest vegetation are shown in Fig. 2; we found two relatively overlapping assemblages in the riparian corridors using NMDS. The variation of those along the river corridors are significant ($F = 19.428$, $p < 0.05$). Nitrophilous species responsible for the river corridor affiliation are mainly present in the Morava River dataset, whereas vernal species and sciophytes (elements of Carpinion alliance) are mainly present in the Thaya River dataset (see Table 2). Of the total number of species, 18 are significantly more frequent in the Morava River corridor $(p < 0.05)$, and 22 species are significantly more frequent in the Thaya River corridor; the test results are shown in Table 2. Nitrophilous species, such as Agrostis stolonifera, Chaerophyllum bulbosum, Galeopsis speciosa, Taraxacum sect. Ruderalia, and Torilis japonica, mostly have high fidelity values in the Morava River corridor. Vernal herb species (grove species), such as Anemone ranunculoides, Corydalis cava, Gagea lutea, Pulmonaria officinalis, and Viola mirabilis, have the highest fidelity values in the Thaya River corridor. Some alien species were better represented in the Morava River corridor than in the Thaya River corridor. The most frequent alien species in the Thaya River corridor are Parthenocissus inserta and Galega officinalis. In the Morava River corridor, the significantly more frequent alien species are Aster lanceolatus, Erigeron annuus, Helianthus tuberosus and Oxalis fontana.

Fig. 2. The differences in species composition in the non-metric multidimensional analysis (NMDS) diagram. The black/grey polygons and circles represent the plots of the floodplain forests in the Thaya/Morava River floodplain.

GIS view of biodiversity and frequency of alien species Biodiversity was evaluated by the Shannon-Wiener index level in the river floodplains and is colour coded in the range of the min–max values in the map (Fig. 3). Our results show that the biodiversity of the study area varies from place to place, and it is arranged in a mosaic: the maximum diversity values occur in locations outside the direct influence of settlements, rather in clearcuts and younger forest stands that represent higher diversity (including nitrophilous and alien species). The lowest values of diversity are observed in locations with a share of non-forest areas (which we did not study) and where regular flooding occurs (near the eastern bank of the Thaya River, southwest of Lanžhot village).

Figure 4 shows a map of the accumulation of alien species in the study area: the highest strain of alien species is in the vicinity of settlements (most noticeable around the cities of Lednice, Břeclav and Lanžhot) and in areas with a higher occurrence of clearcuts with nitrophilous and alien species. The minimum number of alien species exists in places where are far less affected by humans, with a smaller proportion of clearcuts; a higher proportion of alien species occurs along the forest edges and roads (e.g., the large areas of floodplain between Břeclav and the confluence of the Morava and Thaya Rivers, the forest complex southeast of Mikulčice village and the Křivé jezero Nature reserve).

Discussion

The floristic compositions of two riparian corridors

Chytrý et al. (2010) described two basic floodplain lowland habitats on the alliance level (Alnion incanae, incl. hardwood forests of lowland river and *Salicion albae*, Willow-poplar forests of lowland river). We found that hardwood forest was the most frequent community in both floodplains of the Morava and Thaya Rivers. The floodplain vegetation was relatively homogenous and dominant species (Acer campestre, Aegopodium podagraria, Carex riparia, Deschampsia caespitosa, Ficaria verna, Glechoma hederacea, Quercus robur, Rubus caesius, and Urtica dioica) was common and shared across the both riparian corridors. Lyon and Gross (2005) described four floodplain community types in a study among three rivers, but the compositions of our assemblage exhibited similar dominant and common species. However, some species are significantly more frequent at one of the studied corridors (Table 2). Our study shows that nitrophilous and some alien species are more represented in the Morava River than in the Thaya River floodplain. The most likely explanation is a historical and current water management. Modern hydrological changes made in the 70s on both of the Rivers primarily caused decreases of the groundwater level (Penka et al. 1991). Hydrotechnical measures have decreased the mean range of the groundwater table level (Prax 1980; Penka et al. 1991; Čermák et al. 2001) and have practically eliminated floods. Since the 1990s, artificial and controlled spring flooding in some parts of the study area has been established. Restoration of a Lichtenstein water channels was performed in the Thaya River floodplain between 1990 and 1996 and in the Morava River floodplain between 1996 and 1999 (Hrib & Kordiovský 2004). It is known that fluctuations in the environment may lead to the easier establishment of alien species. The higher amount of nitrophilous and alien species in the Morava River floodplain may indicate the availability of unused resources caused by the fluctuation of nutrients due to the historic flooding and occurrence of disturbances, which is consistent with the theory of fluctuating resource availability (Davis et al. 2000). Moreover, in the region of the Thaya River hydrological management has continued in long tradi-

Fig. 3. Digital model of the biodiversity level in a forest stands of the study area using the Shannon-Wiener index.

tion of centuries. Therefore, consequences in vegetation composition of modern hydrological changes were not appeared in Thaya River as much as in Morava River floodplain. In accordance with Petrášová et al. (2013), we suggest that especially modern hydrological changes constituted more substantial modifications of environment which formed difference in vegetation. Beside this, flooding not only disrupts floodplain vegetation but also leaves bare soil for the establishment of new propagules and supplies new nutrients.

Species richness

Although there were only small differences in species

composition of floodplain vegetation between the two studied riparian corridors, however a few significant differences were found. The most marked disparity is the higher species richness of the Thaya River floodplain compared with the Morava River floodplain, as well as the lower alien species proportion in the Thaya River floodplain (see Table 1). Our results confirm the findings that floodplain forests harbour a number of alien species, which Mölder $\&$ Schneider (2011) explain by hydrodynamics, morphodynamics and anthropogenic impacts. The considerable differences in species richness between the studied areas cannot be linked to geographic position or climate. The catchments of the

Fig. 4. Digital model of alien species accumulation in a forest stands of the study area.

studied rivers may affect the floristic composition based on their distinct sources of flora. Beside this, the different species richness in the studied river corridors may be a result of the accumulation of diaspores in the Nové Mlýny water reservoir in the Thaya River floodplain and the lack of a reservoir in the Morava River floodplain. The Thaya River floodplain has a higher proportion of sandy elevations compared to the lower part of the Morava River. These elevated sites are sources of many endangered and protected species dependent on open-woodland habitats and elevated sandy sites belong to typical open habitats (Miklín & Čížek 2014) and they are inundated only seldomly (Růžičková et al. 2004).

Alien species

The overall proportions of alien species in the Thaya and Morava River corridors were almost identical $(27.2\% \text{ vs. } 27.9\%)$. However, the amounts of alien species per segment for the two studied rivers show significant differences: 17.7% in the Thaya River and 19.6% in the Morava River floodplains. The mean amount of alien species per segment is 19.5%, which is similar in values of studies of Tabacchi et al. (1996), Pyšek et al. (2012b) and Petrášová et al. (2013). We

found a higher proportion of alien species in the Morava River floodplains, where a longer history of modern water management exists (Čermák et al. 2001) and where spring flooding has been common during the last two decades. Pyšek et al. (2012b) reported that the proportion of alien species 14.6% to the permanently present Czech flora (excluding extinct natives and including only naturalized alien taxa); the authors also found that the proportion of neophytes in floodplain forests of the alliance Alnion incanae was $2.2 \pm 2.8\%$, in coverage $4 \pm 10\%$, which is the highest number within the forest communities of the Czech Republic. Our study shows higher average proportion of neophytes in the study area (8.8%).

A number of large-scale studies have confirmed that floodplain forests are one of the most invaded forest habitats (Chytrý et al. 2005, Pyšek et al. 2012b, Petrášová et al. 2013). The recent difference in the species richness and proportion of alien species of the floodplains of both studied rivers could be significantly influenced by unique water regime changes over the last 45 years and recent irrigation in some areas of the floodplain due to the revitalisation of channels. We also assume that the larger basin of Morava River, compared to the Thaya River basin, will be more disturbed and will have more resources of diaspores of alien species than the Thaya River. Another important factors in the floodplain of the Morava River are a higher proportion of clay particles in the alluvial soils and a lower percentage of sand elevations in the far broader floodplain than in the Thaya River (or elevations that are farther than 1000 m from the river). The Thaya River floodplain also engages the groundwater at a deeper level, which may explain why the floodplain dries more and consequently contains more elements of Carpinion alliance and thermophilous species than the Morava River floodplain. It is interesting that correlation between the numbers of neophytes and native species is proportionally higher in the Thaya corridor. We explain this disparity by higher proportion of urban landscape and denser human populations in the studied catchment of Thaya due to the closeness of a big city (Břeclav) (see Chytrý et al. 2008).

Vegetation changes of floodplain forests are partially structured by the reduction in the flood frequency, which helps to increase the abundance of sexually reproducing annual alien species at drier sites. It is known that disturbances facilitate invasions by eliminating or reducing the cover of competitors or by increasing resource levels (Davis et al. 2002). Alien species such as Aster lanceolatus, Erigeron annuus, Helianthus tuberosus and Oxalis fontana and some nitrophilous species were more frequent in the Morava River corridor. Our results are in accordance with Mölder $\&$ Schneider (2011) who found the same alien species in Danube flora. On the other hand, Pyšek & Prach (1993) presented other invasive species in riparian habitats in Central Europe: Impatiens glandulifera, Heracleum mantegazzianum, Reynoutria japonica and R. sachalinensis; none of these species poses significant problems in the study area. Chmura & Sierka (2006) also considered Impatiens parviflora to be an important invasive species in Polish floodplain forests. Similarly, on the Thaya River floodplain, this species is strongly present due to the higher proportion of sandy substrate in alluvial soil. Important invasive species in Morava River floodplain Aster lanceolatus possess a high capability for vegetative spread; moreover, the horizontal rhizome system of A. lanceolatus persists for many seasons in its native distribution area (Jedlička & Prach 2006). Clonal growth and the high production of diaspores (Pyšek et al. 2012) allow the spread of A. lanceolatus. Due to the higher disturbance in the Morava River floodplain, there are particular places where unused resources are available (see Davis et al. 2000) for the successful attaching of diaspores. Another cause of disturbances may be high logging intensity of forest stands. Miklín & Čížek (2014) documented that forests along the Thaya River are older than forests along the Morava River: more than 50% of forest stands along Morava River have been logged a replanted during the last four decades.

Species richness of aliens in large samplings units usually increases with that of native species because both species groups positively respond to increasing landscape heterogeneity and availability of different

habitats (Chytrý et al. 2005). Because of twice higher non-forest area along the Thaya River, we expect higher habitat heterogeneity there. Elton (1958) suggested that communities richer in native species tend to be more resistant against invasions by alien species. Chytrý el al. (2005) debated that this relationship (beside of habitat) depends on scale of the vegetation plots. In the present study higher correlation between alien and native species were found in the Morava than in the Thaya River corridor. Because of the almost same mean number of species between the study corridors we suppose that area along the Thaya River is more resistant against invasions. Despite of lower saturation of alien species in the Thaya than in the Morava River we assume that level of invasion is there on the upper limit due to the long history of traditional hydrological management in the Thaya River area.

Conclusions

Despite of homogenous vegetation of both studied river corridors we found significant differences in the species composition, species diversity and proportion of alien species between them. The most striking difference was a higher proportion of alien species in the Morava River corridor than in the Thaya River corridor. We explain these differences by the heterogeneity of habitats (particularly presence of sandy elevations and higher proportion of non-forest habitats along the Thaya River) and by variability of landscapes of both rivers. Further, we explain the differences by the historical water regime and modern hydrological changes which affects in particular Morava River area. Because of the almost same mean number of species in the study corridors we suppose that area along the Thaya River is more resistant to invasions. We assume that level of invasion is there on the upper limit due to the long history of traditional hydrological management in the Thaya River area.

Acknowledgements

The results were achieved thanks to financial support from the Faculty of Forestry and Wood Technology and the project of the National Agency for Agriculture Research entitled "Harmonization of forest management in lowland alluvia as a tool to preserve species diversity of vascular plants" (reg. no. QI92A031).

References

- Amanda L., Uowolo A.L., Binkley D. & Adair E.C. 2005. Plant diversity in riparian forests in northwest Colorado: Effects of time and river regulation. Forest Ecol. Manag. 218: 107–114.
- Archaux F., Chevalier R. & Berthelot A. 2010. Towards practices favourable to plant diversity in hybrid poplar plantations. Forest Ecol. Manag. 259: 2410–2417.
- Boedeltje G., Bakker J.P., Brinke A.T., Van Groenendael J.M. & Soesbergen M. 2004. Dispersal phenology of hydrochorous plants in relations to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. J. Ecol. 92: 786–796.
- Brewer J.S. 2010. A Potential Conflict between Preserving Regional Plant Diversity and Biotic Resistance to an Invasive Grass, Microstegium vimineum. Nat. Areas J. 30: 279–293.
- Chmura D. & Sierka E. 2006. Relation between invasive plant and species richness of forest floor vegetation: A study of Impatiens parviflora DC. Polish J. Ecol. 54: 417–428.
- Chytrý M. & Otýpková Z. 2003. Plot sizes used for phytosociological sampling of European vegetation. J. Veget. Sci. 14: 563–570.
- Chytrý M., Tichý L., Holt J. & Botta-Dukát Z. 2002. Determination of diagnostic species with statistical fidelity measures. J. Veg. Sci. 13: 79–90.
- Chytrý M., Pyšek P., Tichý L., Knollová I. & Danihelka J. 2005. Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77: 339–354.
- Chytrý M., Jarošík V., Pyšek P., Hájek O., Knollová I., Tichý L. & Danihelka J. 2008. Separating habitat invasibility by alien species from the actual level of invasion. Ecology 89: 1541–1553.
- Chytrý M., Kučera T., Kočí M., Grulich V. & Lustyk P. (eds) 2010. Katalog biotopů České republiky [Habitat catalogue of the Czech Republic], Ed. 2. AOPK, Praha, 445 pp.
- Clark I. & Harper W.V. 2000. Practical Geostatistics. Ecosse North Amer Llc., 442 pp.
- Čermák J., Kučera J., Prax A., Bednářová E., Tatarinov F. & Nadyezhdin V. 2001. Long-term course of transpiration in a floodplain forest in southern Moravia associated with changes of underground water table. Ecológia 20 (Suppl. 1): 92–115.
- Danihelka J. & Grulich V. (eds) 1996. Výsledky floristického kurzu v Břeclavi (1995) [The results of the floristic course in Břeclav town]. Zpr. Čes. Bot. Společ. 31 (Suppl.): 1–86.
- Danihelka J., Grulich V., Šumberová K., Řepka R., Husák Š. & Čáp J. 1995. O rozšíření některých cévnatých rostlin na nejjižnější Moravě [The distribution of some vascular plants in southern Moravia]. Zpr. Čes. Bot. Společ. 30 (Suppl.): 29–102.
- Danihelka J. & Šumberová K. 2004. O rozšíření některých cévnatých rostlin na nejjižnější Moravě II [The distribution of some vascular plants in southern Moravia, part II]. Příroda 21: 117–192.
- Davis M. A., Grime J. P. & Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Ecology 88: 528–534.
- De Ferrari C.M. & Naiman R.J. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. J. Veg. Sci. 5: 247–258.
- Demek J.& Mackovčin P. 2006. Zeměpisný lexikon ČR. Hory a nížiny. Ed. 2. vyd. AOPK, Praha, 582 pp.
- Dengler J., Chytrý M. & Ewald J. 2008. Phytosociology, pp. 2767–2779. In: Jørgensen S.E. & Fath B.D. (eds), Encyclopedia of ecology, Elsevier, Oxford.
- Grulich V. 2012. Red List of vascular plants of the Czech Republic: 3rd edition. Preslia 84: 631–645.
- Harris M. B., Tomas W., Mourao G., Da Silva C. J., Guimaraes E., Sonoda F. & Fachim E. 2005. Safeguarding the Pantanal wetlands: threats and conservation initiatives. Conserv. Biol. 19: 714–720.
- Hood G.W. & Naiman R.J. 2000. Vulnerability of riparian zones to invasion by exotic vascular plant species. Plant Ecol. 148: 105–114.
- Horák J. 1961. South-Moravian floodplain forests (Typological study). Ph.D. thesis. University of Agriculture and Forestry in Brno, 266 pp.
- Hrib M. & Kordiovský E. (eds) 2004. Lužní les v Dyjsko-moravské nivě. Moraviapress, Břeclav, 591 pp.
- Jedlička J. & Prach K. 2006. A comparison of two North-American asters invading in central Europe. Flora 201: 652– 657.
- Klimo E., Maděra P. & Kulhavý J. 2008. Floodplain forest of Southern Moravia, pp. 382–396. In: Klimo E., Hager H., Matič S., Anič I. & Kulhavý J. (eds), Floodplain forests of the temperate zone of Europe. Lesnická práce, Kostelec nad Černými lesy.
- Kubát K., Hrouda L., Chrtek J. jr., Kaplan Z., Kirschner J. & Štěpánek J. (eds) 2002. Klíč ke květeně České republiky. Academia, Praha, 927 pp.
- Lyon J. & Gross N.M. 2005. Patterns of plant diversity and plant– environmental relationships across three riparian corridors. Forest Ecol. Manag. 204: 267–278.
- Lyon J. & Sagers C.L. 1998. Structure of herbaceous plant assemblages in a forested riparian landscape. Plant Ecol. 138: $1 - 16$.
- Maděra, P., Šebesta, J., Řepka, R., Klimánek, M. (2011): Vascular plants distribution as a tool for adaptive forest management of floodplain forests in the Dyje river basin. J. Landsc. Ecol. 4: 18–34.
- Maděra P., Řepka R., Šebesta J., Koutecký T. & Klimánek M. 2013. Vascular plants diversity of floodplain forest geobiocoenosis in Lower Morava river basin (Forest district Tvrdonice), Czech Republic. J. Landsc. Ecol. 6: 33–63.
- Magee T.K., Ringold P.L. & Bollman M.A. 2008. Alien species importance in native vegetation along wadeable streams, John Day River basin, Oregon, USA. Plant Ecol. 195: 287– 307.
- McLane C.R., Battaglia L.L., Gibson D.J. & Groninger J.W. 2012. Succession of Exotic and Native Species Assemblages within Restored Floodplain Forests: A Test of the Parallel Dynamics Hypothesis. Rest. Ecol. 20: 202–210.
- Měkotová J. 2008. Biodiverzita v říční krajině, pp. 238–252. In: Štěrba O., Měkotová J., Šarapatka B., Rychnovská M., Kubíček F. & Řehořek V., Říční krajina a její ekosystémy. Univerzita Palackého v Olomouci, Olomouc.
- Měkotová J., Šarapatka B., Štěrba O. & Harper D. 2006. Restoration of a river landscape: biotopes as a basis for quantification of species diversity and evaluation of landscape quality. – Ecohydrol. Hydrobiol. Lett. 6: 43–51.
- Miklín J. & Čížek L. 2014. Erasing a European biodiversity hotspot: Open woodlands, veterantrees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO Biosphere Reserve. J. Nat. Conserv. 22: 35–41.
- Mölder A. & Schneider E. 2011. On the beautiful diverse Danube? Danubian floodplain forest vegetation and flora under the influence of river eutrophication. River Res. Appl. 27: 881–894.
- Naiman R.J. & Decamps H. 1997. The ecology of interfaces: Riparian zones. Ann. Rev. Ecol. Syst. 28: 621–658.
- Naiman R.J., Decamps H. & Mc Clain M.E. 2005. Riparia: Ecology, Conservation, and Management of Streamside Communities. Elsevier/Academic Press, New York, 448 pp.
- Naiman R. J., Decamps H. & Pollock M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3: 209–212.
- Paal J., Rannik R., Jeletsky E.M. & Prieditis N. 2007. Floodplain forests in Estonia: Typological diversity and growth conditions. Folia Geobot. 42: 383–400.
- Penka M., Vyskot M., Klimo E. & Vašíček F. (eds) 1985 and 1991. Floodplain forest ecosystem. Vol. 1 & 2. Academia, Praha, 466 & 632 pp.
- Petrášová M., Jarolímek I. & Medvecká J. 2013. Neophytes in Pannonian hardwood floodplain forests – History, present situation and trends. Forest Ecol. Manag. 308: 31–39.
- Planty-Tabacchi A., Tabacchi E., Naiman R.J., De Ferrari C.M. & Decamps H. 1996. Invasibility of species-rich communities in riparian zones. Biol. Conserv. 10: 598–607.
- Prax A. 1980: Studying the water cycle and soil water content dynamics in forest and substitute ecosystems of the floodplain and upland areas. Research report, University of Agriculture and Forestry in Brno, 119 pp.
- Pyle L.L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. Amer. Midl. Natur. 134: 244–253.
- Pyšek P., Bacher S., Chytrý M., Jarošík V., Wild J., Celesti-Grapow L., Gassó N., Kenis M., Lambdon P. W., Nentwig W., Pergl J., Roques A., Sádlo J., Solarz W., Vilà M. & Hulme P.E. 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. Glob. Ecol. Biogeogr. 19: 317–331.
- Pyšek P. & Prach K. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeogr. 20: 413–420.
- Pyšek P. & Prach K. 1994. How important are rivers for supporting plant invasions? pp. 19–26. In: De Waal L.C., Child L.E., Wade P.M. & Brock J.H. (eds), Ecology and Management of Invasive Riverside Plants. John Wiley & Sons Ltd., Chichester.
- Pyšek P., Danihelka J., Sádlo J., Chrtek J., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. 2012a. Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. Preslia 84: 155–255.
- Pyšek P., Chytrý M., Pergl J., Sádlo J. & Wild J. 2012b: Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. Preslia 84: 575–629.
- Quitt E. 1975. Mapa klimatických oblastí ČSR. Geografický ústav ČSAV, Brno, mapa v měřítku 1: 500 000.
- Richardson D., Holmes P.M., Elser K.J., Galatowitsch S.M., Stromberg J.C., Kirkman S.P., Pyšek P. & Hobbs R. J. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers. Distrib. 13: 126–139.
- Růžičková H., Banásová V. & Kalivoda H. 2004. Morava River alluvial meadows on the Slovak–Austrian border (Slovak part): plant community dynamics, floristic and butterfly diversity – threats and management. J. Nat. Conserv. 12: 157–169.
- Řepka R. & Maděra P. 2009. Rozšíření zavlečených druhů v nížinných luzích jižní Moravy – případ hvězdnice kopinaté Aster lanceolatus, pp. 100–105. In: Měkotová J. (ed.), Říční krajina 6, Sborník příspěvků z konference Olomouc 2009, Univerzita Palackého, Olomouc.
- Saccone P., Brun J.J. & Michalet R. 2010. Challenging growthsurvival trade-off: A key for Acer negundo invasion in European floodplains? Canad. J. Forest Res. 40: 1879–1886.
- Schnitzler A. 1997. River dynamics as a forest process: interaction between fluvial systems and alluvial forests in large European river plains. Bot. Rev. 63: 40–64.
- Schnitzler A., Hale B.W. & Alsum E. M. 2007. Examining native and exotic species diversity in European riparian forests. Biol. Conserv. 138: 146–156.
- Schratt-Ehrendorfer L. 1999. Zur Flora und Vegetation des ¨osterreichischen March- und Thaya-Tales, pp. 181–202. In: Fließende Grenzen. Lebensraum March-Thaya-Auen. Umweltbundesamt, Wien.
- Skalický V. 1988. Regionálně fytogeografické členění, pp. 103– 121. In: Hejný S. & Slavík B. (eds), Květena České republiky, vol. 1, Academia, Praha.
- Stohlgren T.J., Bull K.A., Otsuki Y., Villa C.A. & Lee M. 1998. Riparian zones are havens for exotic plant species in the central grasslands. Pl. Ecol. 138: 113–125.
- Štěrba O., Měkotová J., Šarapatka B., Rychnovská M., Kubíček F. & Řehořek V. 2008. Říční krajina a její ekosystémy. Univerzita Palackého v Olomouci, Olomouc, 391 pp.
- Tabacchi E., Planty-Tabacchi A.M., Salinas M.J. & Decamps H. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. Regul. Rivers: Res. Manag. 12: 367–390.
- Thomas J. W., Maser C. & Rodiek J. E. 1979. Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington. USDA For. Serv., Agric. Handb. 553, Washington DC, 512 pp.
- Tichý L. 2002. JUICE, software for vegetation classification. J. Veg. Sci. 13: 451–453.
- Tremoliéres M., Sanchez-Perez J.M., Schnitzler A. & Schmitt D. 1998. Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. Plant Ecol. 135: 59–78.
- Verry E.S., Hornbeck J.W. & Dolloff C.A. (eds) 2000. Riparian Management in Forests of the Continental Eastern United States. Lewis Publishers, New York, 432 pp.
- Vicherek J., Antonín V., Danihelka J., Grulich V., Gruna B., Hradílek Z., Řehořek V., Šumberová K., Vampola P. & Vágner A. 2000. Flóra a vegetace na soutoku Moravy a Dyje. Masarykova univerzita v Brně, 368 pp.
- Von Holle B., Joseph K.A., Largay E.F. & Lohnes R.G. 2006. Faciliation between the introduced nitrogen-fixing tree, Robinia pseudacacia, and nonnative plant species in the glacial outwash upland ecosystem of Cape Cod. MA. Biodiv. Conserv. 15: 2197–2215.
- Walter J., Ess F., Englisch T. & Kiehn M. 2005. Neophytes in Austria: Habitat preferences and ecological effects. Neobiota $6: 13-25$
- Ward J.V., Tockner K., Arscott D.B. & Claret C. 2002. Riverine landscape diversity. Freshwater Biol. 47: 517–539.
- Williams Ch.E. 2010. Survey of the alien flora of the Allegheny River island wilderness, Pennsylvania. Rhodora 112 (950): 142–155.

Received November 18, 2013 Accepted December 4, 2014