

SUMMARY OF THE PH.D. THESIS

**The role of secondary habitats in the preservation of
biodiversity**

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2020

Introduction

Technological advances in the second half of the 20th century have resulted in unprecedentedly rapid agricultural intensification worldwide, leading to a global-scale decline of the species and habitat diversity of ecosystems. Landscapes with a high proportion of natural grasslands have largely been converted into arable fields, built-up areas and forest plantations.

For instance, a large proportion of loess grasslands in Europe have been ploughed for cereal production because of their fertile chernozem soils. Today, this grassland type mainly occurs in small fragments (e.g., on ancient burial mounds, earthen fortifications, road verges or at the margins of arable fields) and its area is still shrinking.

The area and diversity of the European wet grasslands have also significantly declined in the last 300 years due to inappropriate management, drainage and river regulation. Along regulated rivers, wet grasslands can usually be found in the narrow and frequently disturbed (i.e., periodically flooded) floodplains between the river and the embankments.

A number of studies suggest that secondary habitats can act as refuges for native, endangered or vulnerable species, thus they may play key roles in the maintenance of biodiversity in transformed landscapes. For instance, city walls may provide valuable habitats for ferns, highway stormwater ponds for aquatic macroinvertebrates, graveyards for orchids, kurgans (i.e., burial mounds) for steppe species, roadside verges for endangered lizard- orchids and plantation forests for vulnerable plant species. Further studies show that linear anthropogenic structures (e.g., ditches, hedgerows, river embankments and road verges) have the potential to form dispersal corridors not

only for the native biota but also for many invasive species. Grasslands on embankments can be used as pastures or hay meadows and provide suitable habitats for pollinators. Although the area of secondary grasslands on river embankments is more than 15,000 ha in Hungary, data on their ecological function and conservation value are scarce.

We hypothesized that the secondary grasslands of river embankments have the potential to act as refuges for many plant species and provide important ecological functions that play a crucial role in sustaining the functionality of ecosystems within agricultural landscapes.

Karst dolines and their unique biota are particularly vulnerable to anthropogenic disturbances. For instance, road construction, overgrazing and nutrient addition by sheep have seriously threatened plants endemic to dolines in the Greek Archipelago biodiversity hotspot. Furthermore, many dolines in Europe are used as dumping grounds or have been filled with construction waste (in order to create new lands for highways, industrial facilities and residential areas), while others have been transformed into agricultural fields or gardens. Such disturbances would have reduced or eliminated the capacity of these dolines to be safe havens for biodiversity. Therefore, assessing the capacity of refugia to support biodiversity under anthropogenic climate change requires an understanding of the effects of anthropogenic disturbances.

We investigated the impact of anthropogenic disturbances on the conservation value of dolines in three European karst areas, where different levels and types of anthropogenic disturbances have been shaping the landscape for hundreds of years. Specifically, the following questions were addressed: Are there any differences between the number of cool-adapted, moist-adapted and high-conservation-importance

plant species between dolines and surrounding plateaus? Do different levels and types of anthropogenic disturbances influence the distribution patterns of such species in dolines?

Material and methods

Study I.

The study sites were located in the eastern part of the Great Hungarian Plain, in the proximity of the Körös and Maros Rivers. We chose a 100-km-long section of the Körös River and a 40-km-long section of the Maros River for vegetation sampling. The slopes of embankments were sown with seed mixtures of native grasses in order to reduce erosion and to produce fodder for livestock. At that time, natural grasslands were widespread in the vicinity of the rivers, and soils originating from these grasslands were also used for the construction of the embankments.

In order to obtain representative samples from the study sites, we applied a stratified random sampling approach. Both the secondary dry and wet grasslands on the upper two-thirds of embankments were sampled using three randomly placed 2 m × 2 m plots in both habitat types. For comparison, we selected 20 seminatural dry and 20 seminatural wet grassland patches within the study area. We randomly placed three 2 m × 2 m plots in each patch.

To evaluate the ecological functions and conservation value of secondary grasslands on river embankments, we compared them with the seminatural grasslands using the following metrics: species diversity, diagnostic species, phylogenetic diversity, functional diversity and functional trait distributions.

Study II.

The study area is a limestone karst landscape of about 30 km² in the western part of the Mecsek Mountains, located at an altitude between 250–500 m.

Two medium-sized dolines were selected with a funnel-shaped geometry. Dolines were about 70 m in diameter and about 14 m deep. Both dolines were sampled before logging (about 110 years old forests, in 2007) and 10 years after logging (in 2017), using the same method. We established a transect with north-to-south orientation across the dolines, traversing the deepest points. Transects began and ended on doline rims. Each transect consisted of 1 m×1 m plots spaced at 2-m intervals. We used permutational multivariate analysis of variance, diagnostic species and functional group comparisons for the assessment of the different habitats.

Study III.

Three karst regions were selected in Slovenia and Hungary, where the current vegetation in dolines has developed under varied disturbances. One study site was located in the Kras Plateau (Slovenia), one in the Mecsek Mountains, and two sites (forested and non-forested) in the Bükk Mountains (Hungary).

Prior to sampling, we classified dolines and adjacent plateaus at each site into ‘disturbance classes’ (little, medium and high disturbance) based on the effects of previous and current human activities. We classified disturbance within sites at three levels; the vegetation of ‘dolines with little disturbance’ (class D1) has developed under the lowest disturbance levels; while the vegetation of ‘dolines with high disturbance’ (class

D3) has developed under the highest disturbance levels. ‘Dolines with medium disturbance’(class D2) represent intermediate disturbance levels.

We established a transect with north to south orientation across each doline, traversing their deepest point. Transects began and ended on doline rims, their length varied between 37 and 127 m. For reference, a 89-m-long transect was established on each plateau. Transects consisted of 1×1 m plots spaced at 2 m intervals. We used one-way analysis of similarity (ANOSIM), diagnostic species and functional groups analysis for the comparison of the different habitats.

Results

Study I.

Both habitat types on embankments (i.e., secondary dry and wet grasslands) showed significantly higher Shannon diversity than their seminatural counterparts (seminatural dry and wet grasslands, respectively). The number of diagnostic species was also higher on the embankments: secondary dry grasslands had 25 and secondary wet grasslands had 29 species, whereas seminatural dry grasslands had only 12 and seminatural wet grasslands had 15 diagnostic species. Although the number of diagnostic species was higher in the secondary grasslands, the proportion of habitat-specific diagnostic species was higher in the seminatural grasslands. Secondary grasslands showed similar MPDs compared with the seminatural grasslands. In contrast, the difference was significant for MNTDs; secondary grasslands showed significantly lower MNTDs than seminatural ones. There was no difference between the Rao's index for secondary and seminatural grasslands, although there were some

single traits that, based on CWM analyses, showed significant differences between the seminatural and secondary habitats.

Study II.

A total of 72 vascular plant species were recorded in the plots. Five diagnostic species (one oak forest species and four beech and ravine forest species) were identified before logging and 15 (six oak forest species, three beech and ravine forest species, and six disturbance-tolerant species) after logging. NMDS ordinations showed that the compositional pattern of the vegetation changed significantly after logging.

Study III.

A total of 383 plant species were recorded in the 1263 plots. Fifteen diagnostic species differentiated between little disturbed habitats in dolines (D1) and on the plateau (D1R) in Kras, 9 in Mecsek, 9 at the forested site in Bükk and 32 at the non-forested site in Bükk. For disturbance classes (D1, D2 and D3), 6 diagnostic species were identified in Kras, 10 in Mecsek, 21 at the forested site in Bükk and 54 at the non-forested site in Bükk. The plots from little disturbed dolines (D1) and the plateau (D1R) were separated based on species composition along the PCoA axis 1 for all sites. Dolines with different disturbance classes (D1, D2 and D3) also differed in their species composition, but not between D2 and D3 in Kras. The number of cool-adapted species was significantly higher for little disturbed dolines (D1) than the plateau (D1R) for all sites, except for the forested site in Bükk. Overall, no consistent differences for the number of cool-adapted species were observed among the different disturbance classes. Although the

sets of cool- and moist-adapted species differed considerably, these two sets displayed very similar patterns of species richness with regard to disturbance classes. Little disturbed dolines (D1) on average had more species of high conservation importance than the plateau (D1R) for all sites.

Discussion and conclusions

According to the diagnostic species analyses, generalist species play an especially important role in the grasslands of embankments. Cosmopolitan species, nonindigenous species and weeds could initially colonize these fresh surfaces during the construction of the embankments simultaneously with the sown grasses and other species as founders; therefore, the higher abundances of generalist species on the embankments can be a legacy of this founder effect. The floodplains of the rivers are densely covered by invasive species and weeds, as the rivers can effectively disperse their propagules to these areas and the disturbance cycle of floods continuously creates new colonization gaps. Reconstruction works, dirt roads and the establishment of different flood regulation facilities also create bare surfaces where these species have the potential to colonize successfully once introduced. In addition, the habitats of these embankments are embedded in the matrix of agricultural land with a high perimeter–area ratio. These circumstances can provide good opportunities for many generalist species to survive on the embankments. Although the high species richness of generalist species significantly increased the Shannon diversity on the embankments; these species did not increase the functional diversity of the grasslands because of their similar functional traits. Therefore, the functional structure of these secondary grasslands is similar to that in the seminatural

grasslands of the landscape. Most studies agree that disturbance has the potential to decrease phylogenetic diversity. Based on the theory of environmental filtering and limiting similarity, the phylogenetically clustered structure of the secondary habitats can be expected, as disturbance may weaken the strength of competition. The MNTD analyses supported this theory, as the values of these indices were lower for the secondary grasslands on embankments than for the seminatural grasslands. It also means that the vulnerability of these secondary grasslands is higher and their resilience is lower against the invasion of alien species. Therefore, our results support the conclusion of recent studies showing that the precise assessment of the ecological function and conservation value of different habitats cannot solely be based on species- based diversity indices, as they are not sensitive to functional redundancy and other functional consequences of species identity. The Shannon diversity indices together with the diagnostic species and the MNTD analyses suggested that the reason for the higher diversity in these secondary grasslands is the higher proportion of generalist species that are functionally and phylogenetically more clustered compared with the species pool of the seminatural grasslands. Species with high SLA can respond rapidly to environmental changes (fast plants) because of their high efficiency of photosynthesis and fast growth. Thus, these species can be more successful on the river embankments where environmental conditions are less stable due to human disturbance and periodic management (mowing twice a year) than in their seminatural counterparts. One of the main ecosystem services of grasslands is hay production. Productivity often correlates positively with plant height, therefore the secondary grasslands on the embankments probably supply higher amount of hay compared with the seminatural grasslands. Moreover, the larger mean

SLAs in the grasslands on embankments indicate better quality of hay, because grazers prefer species with high nutritional values, which generally positively correlate with SLA. The longer flowering period and the presence of more insect pollinated plants in these secondary grasslands are favourable for the pollinator assemblages and also for the palynivores. This ecosystem service can support the maintenance of insect diversity, and can be beneficial for insect pollinated crop plants. The embankments of the investigated rivers are situated in agricultural landscapes; therefore, the colonization potential of many grassland specialist species (i.e., dry grassland and wet grassland species) is limited. Consequently, active restoration would be needed to ensure the establishment of these species on the embankments. To increase the number and abundance of valuable dry and wet grassland species in the grasslands of the embankments, hay transfer from seminatural habitats and sowing of regional seed mixtures would provide feasible solutions. Secondary grasslands on river embankments have the potential to act as refuge sites for many plant species and may provide important ecological functions in the future. Proper management practices are needed to improve the quality of these secondary habitats.

Dolines have the capacity to maintain the populations of vulnerable plant species and thus may function as safe havens or microrefugia during environmental changes, highlighting their importance for conservation. We demonstrated that anthropogenic disturbances play a significant role in determining the composition and diversity of plant species in dolines. While anthropogenic disturbance generally reduced the number of cool-adapted, moist-adapted and high-conservation-importance species, we documented that one type of human disturbance, the planting of *Picea abies* (as secondary habitats,

in Bükk), increased the number of cool-adapted and moist-adapted species supported in dolines. This highlights that management for conservation needs to consider the different impacts of various disturbances. Historic anthropogenic disturbances had considerable impacts on the species composition and the amount of vulnerable species in dolines. Generally, disturbances reduced the number of species that are cool-adapted, moist-adapted and of high conservation importance, reducing the conservation value of dolines. Several other studies have highlighted that climatically diverse habitats are extremely sensitive to anthropogenic disturbances and that their recovery from such disturbances may be slow or incomplete. We found that stronger disturbances that have a significant effect on the vegetation structure, such as intensive logging and invasion by *Calamagrostis epigejos*, can lead to significant declines of cool-adapted, moist-adapted and high-conservation importance plant species in dolines. Therefore, these disturbances seem to decrease the capacity of dolines to support vulnerable species and their potential to function as long-term microrefugia. This reduction in the conservation value of the dolines could be caused by changes to biotic (e.g., reduced species diversity and altered ecological interactions) and abiotic (e.g., altered light availability, moisture and temperature) characteristics. However, a detrimental impact on species that are cool-adapted, moist-adapted and of high conservation importance was not always observed. Our study has also illustrated that dolines have the capacity to function as habitat islands that facilitate the persistence of a high diversity of cool-adapted, moist-adapted and high-conservation-importance plant species and that this capacity is strongly influenced by local anthropogenic disturbances. Although anthropogenic disturbances generally decrease the conservation

value of dolines, they can also increase the capacity of dolines to function as microrefugia for cool-adapted and moist-adapted species under global warming. Therefore, a thorough understanding of the relationships between disturbances and species composition is necessary to successfully manage landscapes for the persistence of vulnerable species under global warming.

Publications covering the topics of the thesis

Bátori Z. *, Kiss P. J. *, Tölgyesi Cs., Deák B., Valkó O., Török P., Erdős L., Tóthmérész B., Kelemen A. (2020): River embankments mitigate the loss of grassland biodiversity in agricultural landscapes. *River Research and Applications* **36**: 1160-1170. IF: 1,916 (Q1)

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Kiss P. J., Tölgyesi Cs., Bóni I., Erdős L., Vojtkó A., Maák I. E., Bátori Z. (2020): The effects of intensive logging on the capacity of karst dolines to provide potential microrefugia for cool-adapted plants. *Acta geographica Slovenica* **60**: 37-48. IF: 1,341 (Q2)

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Cumulative IF: 30.48