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Ecological intensification in a Hungarian agricultural landscape: Effects of low-disturbance, diverse wildflower habitats on the pollinator community

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PhD thesis booklet

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BACKGROUND AND OBJECTIVES

Insect pollination is one of the most important ecosystem services from an economic and conservation perspective. Flower visitation by insects provides pollination of many wild plants, as well as higher yields, improved crop quality and higher crop safety of many cultivated crops. To maintain adequate pollination of crops in agricultural landscapes, a large and diverse pollinator community is required, which in addition to honeybees (*Apis mellifera*) also requires the presence of various wild pollinator species such as solitary wild bees, bumblebees, butterflies and hoverflies. However, both domesticated and wild pollinators are in decline worldwide, threatening food security, human well-being and the proper functioning of terrestrial ecosystems in general. Pollinator declines in agricultural landscapes are mainly caused by farming practices such as monoculture and pesticide use. In addition, the loss, fragmentation and degradation of semi-natural habitats that can provide reliable resources for pollinators to feed and nest is a major threat. In contrast, intensively cultivated arable fields, plantations and grasslands, which are expanding, cannot maintain sufficient numbers and diversity of pollinator communities, while being highly dependent on the pollination services they provide.

Agri-environmental schemes and ecological intensification practices have been developed to mitigate the negative impacts of agriculture and maintain biodiversity, including wild pollinators. Some of these practices, such as organic farming may reduce crop yields, while others take areas out of production through set-aside or the creation of wildflower margins. These ecological intensification practices may seem to reduce the productivity of agricultural production. However, in addition to their crucial role in conservation and biodiversity enhancement, these interventions can increase pollinator abundance and diversity, and thus improve crop yields and ultimately profit. In addition to these benefits, farmers in the European Union can receive additional agricultural support under the Common Agricultural Policy (CAP, the EU's agricultural subsidy system) to encourage such environmentally friendly interventions. However, the effectiveness of these interventions are often questionable from a conservation point of view and needs to be improved.

The establishment of wildflower plantings is a widely used practice, mostly in the form of wildflower strips along the edges of fields. The purpose of annual wildflower strips is only to increase the flower resources, while areas maintained for several years also provide nesting, overwintering and sheltering habitat for various species, including pollinating insects. Wildflower plantings are primarily focused on the needs of pollinators and can therefore have a positive impact on their abundance, species richness or species composition. However, their effectiveness can be strongly influenced by a wide range of factors, such as the surrounding landscape composition, their size and spatial configuration, their age, seasonal variations within the year, their management, the composition of the seed mixture used and the floral resources of plants from the soil seed bank. Scientific research on this topic has been limited so far mainly to the Western and Northern parts of Europe and North America, while a significant knowledge gap has been identified in the research on the efficiency and dynamics of wildflower plantings established in agricultural landscapes in East-Central Europe. These agricultural landscapes in East-Central Europe are located in quite different climatic, landscape, historical and socio-cultural contexts, and often in more diverse environments, compared to the intensively studied Western European countries. Therefore, studies in the East-Central European region are essential for the proper adaptation of Western European practices to make efficient use of limited financial resources.

Objectives:

Our aim was to answer the following questions by transect walk sampling and flower resources assessment:

i) How did the flower resources of sown and not sown plant species change after planting, and what changes did this induce in the abundance and species richness of wild pollinator groups in wildflower plantings?

ii) How did the landscape context, spatial configuration and age of wildflower plantings, seasons and their interactions affect flower resources and the abundance and species richness of pollinator insects?

iii) What practical recommendations can be provided for the establishment of future wildflower plantings as an improvement of agri-environmental schemes in East-Central Europe?

In addition to the above mentioned direct objectives of the dissertation, a number of additional local and landscape sampling methods were used to investigate the long-term and landscape-scale effects of wildflower plantings. Among these sampling methods, preliminary results from trapnest sampling are presented in the Dissertation, with the aim of examining the first two years after establishment and answering the following questions:

i) Which cavity-nesting Hymenoptera species used trapnests?

ii) What proportion of nests were built by each hymenopteran species group?

iii) Which kleptoparasitic species appeared and to what extent did they control the nesting species?

MATERIALS AND METHODS

The study area and the experimental setup

Our studies were carried out in the central part of Hungary, in the Solti-sík, in the administrative districts of Dunavecse, Újsolt, Solt and Harta. We selected areas managed by the Állampusztai Mezőgazdasági és Kereskedelmi Kft. This area is mainly dominated by agricultural production, with a significant share of arable land.

At the end of 2019, 24 landscape plots with a radius of 500 m were designated by the Lendület Ecosystem Services Research Group. Considering landscape complexity, half of the landscape plots were in homogeneous and the other half in heterogeneous agricultural landscapes. The proportion of semi-natural habitats in the homogeneous landscape plots was below 10%, while in the heterogeneous landscape plots, it was above 40%.

The landscape plots were grouped in triples. Altogether, 8 landscape plot triplets were selected, half of which were in homogeneous and half in heterogeneous agricultural landscapes. Each triplet contained three different landscape plots: in the middle of one of them we established a half hectare (50*100 m) wildflower field, in the middle of the other one we sowed 3 smaller (24*70 m) wildflower strips of half a hectare in total, about 100-150 m apart. The third landscape plot served as a control, where we did not sow any wildflower planting, but covered a similar landscape context to the other two "treated" landscape plots.

The wildflower plantings were established by sowing a seed mixture of diverse, native plant species in the beginning of 2020. The seed mixture came from András Máté's garden (vadviragvilag.hu) and was specially formulated for our study from seeds of 32 native flowering plant species. The two main criteria for the selection of plant species were to best support a wide range of pollinator insects throughout the season and to be able to maintain their longevity under an extensive management regime.

We treated the areas by mowing and removing the biomass. In the first two years, all 32 plantings (8 fields and 24 strips) were mowed in the autumn, and from the third year onwards, each year in early summer, in mid-June, half of each planting was mowed and then the other half in the following year. Thanks to careful planning and management, the wildflower plantings have resulted in diverse flower resources over the years.

Sampling methods

The main objective of our study was to assess the changes in vegetation, in flower resources and in the number of individuals and species of different pollinator groups and the community composition of the different pollinator groups over the years, both locally and at the landscape scale, following the establishment of wildflower plantings. Several different sampling methods were used every year from the year of establishment (2020) onwards, up to several times a year, to obtain a sufficiently comprehensive picture of the changes in the vegetation and the different groups of pollinators. Botanical surveys, Malaise trapping and transect walk sampling (in the wildflower plantings and from 2022 in the surrounding area) and flower resource assessment were carried out twice a year in the sown areas. In addition to this, trapnests were set for landscape-scale sampling and pollinator communities were surveyed once a year with yellow pan traps. This dissertation presents in detail the results of the first two years (2020-21) of transect walk sampling and flower resources assessment in wildflower plantings. In addition, the results of the trapnest sampling of the same period and the flower visitation experiences of the four years (2020-23) are also described descriptively.

The design of the experiment and the monitoring of vegetation, floral resources and pollinators were carried out in cooperation between HUN-REN ÖK ÖBI Lendület Ecosystem Service Research Group, MATE VTI Department of Zoology and Ecology and Dorcadion Kft. The project involved researchers, students and volunteers of the Research Group and the Department. I was actively involved in the designing, development of the sampling protocol, organisation and conduct of the samplings in the field, data organisation, publication and management of the sites. My doctoral thesis summarises the results of two samplings that I coordinated and carried out during the first two years after establishment.

Transect walk sampling

During the transect walk sampling, pollinator insects (solitary and social wild bees, hoverflies, butterflies, honeybees and other pollinators) were surveyed along two parallel transects in all wildflower plantings. The survey was completed in 15 minutes on the wildflower fields at 75 m and in 5 minutes on the strips at 25 m. Wild bees and hoverflies were captured for species-level identification, while other pollinator groups were recorded at a higher taxonomic level. The survey was not conducted in control landscape plots.

Flower resource assessment

In parallel with the transect walk sampling, flower resource assessment was carried out each time. Along the transects, the actually flowering, insect-pollinated plant species were recorded in 1*1 m quadrats. For each flowering plant species, the number of flowers or inflorescences actually open and the number of flowers per inflorescence were recorded. Quadrats were marked at the start point of transects and every 12.5 m from there. The same sampling effort was applied to all landscape plots: 12 quadrats were measured per landscape plot.

Trapnest sampling

Trapnest sampling allows us to sample the cavity-nesting hymenopterans throughout the year (from March to September) at the landscape level and to obtain biological information (e.g., parasitism, the survival rate of broods) in addition to data on the number of individuals and species. The trapnests were made from a bundle of rolled-up pieces of reeds, placed in PVC tubes, fixed in pairs with wire to a 140 cm high wooden pole and protected from rain and strong sunlight with a roof. Trapnests were placed in all 24 landscape plots, including the controls. We placed pairs of trapnests at 6 points every 80 m along a linear landscape component (road, tree line) away from the centre of the landscape plot, at a total of 144 locations.

After collection, the trapnests were initially stored in the open air and then, from the first freezing evenings, in a cooling chamber at a constant low humidity under 4°C. In early January, we started processing the previous year's traps, selecting one trap per trapnest pair. The work was carried out according to a protocol and guide written by me, and all data, including all characteristics of the nests found in the reeds, were recorded in a pre-made online spreadsheet and folder system. The nesting species and their kleptoparasites were identified at the species level.

Statistical analysis

The abundance of wild bees (solitary wild bees and bumblebees), butterflies and hoverflies (hereafter: **wild pollinators**) was analysed using generalised linear mixed models (GLMM) with negative binomial distribution and log link function based on transect-level data. For the models, flower abundance and species number were averaged per quadrat. Log-flower abundance, number of flowering plant species (as continuous variables), year (i.e., age of wildflower plantings), season (early summer or mid-summer), spatial configuration (one large field or three smaller strips) and landscape context (homogeneous or heterogeneous), the latter two in interaction with season or year, were incorporated into the model as fixed effects. The unique identifiers of landscape plots, study units and transects were considered as nested random effects.

In models describing the number of pollinator species, data were pooled at the landscape plot level. In these models, we included cumulative flowering plant species numbers and flower abundances per landscape plot as fixed effects. The Poisson distribution (log-link) modeling for the hoverflies and the negative binomial distribution for the wild bee models provided a better fit based on tests using the Akaike Information Criterion (AIC). Fixed effects were the same as in the abundance models, with landscape plot identifiers used as random effects.

Similarly, flower abundance and species numbers were modeled using landscape plot level data. We differentiated between sown and not sown flowering plant species and considered their interaction with season and year. We were unable to achieve an acceptable model fit in the flower abundance models using GLMMs, and therefore present these results as descriptive.

The PERMANOVA method was used to investigate the community composition of the plant and pollinator communities (wild bees and hoverflies combined) observed in all landscape plots during the four sampling occasions. To visualize community composition, we performed non-metric multidimensional scaling (NMDS) restricted to two dimensions using the Bray-Curtis Diversity Index.

All analyses and visualisations were done using R 4.1.3. GLMMs were created using glmmTMB 1.1.3.

RESULTS

Transect walk sampling and flower resource assessment

Flower resources (2020-21)

During the flower resource assessment, 92 flowering plant species were observed at the time of transect walk sampling in the first two years after establishment, of which 17 were sown (8 species in the first year and 16 in the second) and 75 were not sown. In the first year, not sown plant species provided significantly larger and more species-rich floral resources, whereas the sown plant species contributed slightly to the floral resources directly after establishment. However, the flower abundance and species number of the sown species increased steadily and significantly at each sampling occasion (year by year, season by season), taking over the dominance of the flower resources from not sown species by mid-summer of the second year.

Pollinator abundance and species numbers (2020-21)

During the first two years of our surveys, a total of 4486 wild pollinators (2283 wild bees, 1252 hoverflies, 951 butterflies) were recorded, of which 1468 wild bees and hoverflies were captured for species-level identification. A total of 110 species of wild bees (104 solitary wild bee species and 6 bumblebee species) and 16 species of hoverflies were recorded. The number of observed pollinators increased during each sampling round in the two years after establishment. However, the years, seasons, flower resources and spatial configuration of wildflower plantings, and the influence of landscape context varied among the different pollinator groups.

Wild bee abundance increased significantly year by year, season by season, with flower abundance and flower species number, and was higher in heterogeneous agricultural landscapes in general, but significantly higher in homogeneous landscapes in mid-summer. Species numbers also increased between years and seasons, and with increasing flower abundance.

Butterfly abundance was higher in heterogeneous agricultural landscapes and increased between years, and this increase was even more pronounced in heterogeneous landscape contexts.

In the case of **hoverflies**, an overall decline in abundance and species number was observed between years and seasons, but the rate of decline between seasons was smaller in the larger wildflower fields and their abundance increased with flower abundance.

Community composition (2020-21)

Year and season had the greatest effect on the community composition of flowering plant species in the final PERMANOVA model. Landscape context showed a significant interaction with the spatial configuration of wildflower plantings, but only a weaker effect. Different years showed significant separation in the NMDS plot.

In the final model, year also had the most significant effect on pollinator community composition. This variable was followed by the number of flowering plant species and landscape context, although with weaker effects. Different years showed some degree of separation on the NMDS graph, while no clear patterns were seen in landscape context.

Flower visitation (2020-23)

During transect walk sampling, we observed flower visitation by all pollinator groups on a total of 113 plant species in the four years following planting, 22 of which were sown species. Wild pollinators visited flowers of 101 plant species, of which 20 were sown species. The number of flower visits by wild pollinators, after an extraordinary increase in the first year (843 in the first year and 1656 in the second), showed a decrease in the third year (960) and in the fourth year (497).

In the first year, a significant proportion of the flower visitation was observed on flowers of not sown plant species. In the second year, and especially from the third year onwards, the dominance of sown species in terms of flower visitation was obvious.

On average over the 4 years, 6 of the 10 most visited plant species were sown species, and 8 of the 15 most visited were sown. Thus, the order of flower visitation for wild pollinators was the following (sown species in bold): 1. ***Cephalaria transsylvanica,*** 2. ***Salvia nemorosa***, 3. *Polygonum aviculare*, 4. *Anthemis austriaca*, 5. ***Dianthus pontederae*** 6. *Carduus acanthoides*, 7. *Matricaria chamomilla,* 8. ***Centaurea cyanus***, 9. ***Seseli varium*** and 10. ***Onobrychis arenaria***. They were followed by 11. ***Echium vulgare***, 12. *Reseda lutea*, 13. *Fallopia convolvulus*, 14. ***Salvia austriaca*** and 15. *Tripleurospermum inodorum*. In seasonal classification, it was possible to distinguish between species that provide flowers in early summer, mid-summer and both.

Each wild pollinator group preferred different plant species for feeding at different frequencies. Butterflies (79.8%), but especially bumblebees (82.2%), visited the sown species in high proportions. However, solitary wild bees (49.2%) and hoverflies (35.0%) also frequently visited other flower sources in addition to sown plant species. The vast majority of flower visits by honeybees were observed on sown plant species (84.9%) and 53.6% of other pollinators were observed on sown plant species.

Trapnest sampling (2020-21)

Half of the nests and brood cells were made by wild bees (49.1% and 51.3%) and the other half by wasps (50.9% and 48.7%) in the trapnests. A total of 6437 nests and 22985 brood cells were recorded in the two years after establishment. Wild bees made a total of 3158 nests and 11793 brood cells in the two years, and wasps made 3279 nests and 11192 brood cells in total. In the second year, both wild bees and wasps built slightly fewer nests and brood cells. Only mason bees (*Osmia spp*.) of the family Megachilidae and *Solierella* species of the family Crabronidae showed a significant increase in the number of nests and brood cells between the two years.

The identified **wild bee** species were from 5 genera of 2 families. From the family of Megachilidae: *Osmia spp.*, *Megachile spp.*, *Anthidium spp*. and *Heriades spp*.; and from the family of Colletidae: *Hylaeus spp.* colonised trapnests.

The identified species of **wasps** came from 15 genera of 4 families. The most abundant nest-building wasps were the Crabronidae family (*Trypoxylon*, *Solierella*, *Passaloecus*, *Nitela*, *Psenulus* and *Astata* species); the Pompilidae family (*Agenioideus*, *Dipogon*, and *Auplopus* species); several genera of wasps from the subfamily Eumeninae; and the family Sphecidae (*Isodontia mexicana*). The largest number of trapnests (61.0% of wasps' nests) were made by species that collected paralysed spiders to feed their offspring.

Kleptoparasites come from a wide range of arthropod taxa, but the largest number of Hymenoptera were identified, followed by flies (Diptera) and beetles (Coleoptera). Amongst the hymenopterans, the cuckoo bees of cavity-nesting wild bees, the Chrysididae species, *Sapyga quinquepunctata* (Sapygidae), *Melittobia acasta* (Eulophidae) were present, as well as other wasps. Larvae of the fly *Cacoxenus indagator* were present exclusively in the nests of megachilid bees, and a small number of Tachinidae flies were also identified. Many nests were heavily damaged by the larvae of the Trichodes apiarius. The vast majority of bee nests were damaged. Beetle species belonging to the family Dermestidae (e.g., *Megatoma undata*) were also present, but in most cases, they were found to play a secondary role, feeding on organic matter remains.

DISCUSSION AND RECOMMENDATIONS

Transect walk sampling and flower resource assessment

Our main results from transect walk sampling and flower resource assessment showed that wildflower plantings not only increased local pollinator abundance and species richness in the years after establishment, but that sown wildflower plantings in flower-poor (homogeneous) landscapes were particularly attractive to wild bees during the flower-poor (mid-summer) period of the year. This effect can be explained by the greater contrast in flower resources between the surrounding landscape and the wildflower planting, which was further enhanced by the mid-summer increase in wild bee abundance. We also found that, in addition to flower abundance, flower species number also had a positive effect on pollinator abundance. Furthermore, not sown flowering plant species from the soil seed bank contributed significantly to the higher number and diversity of flower resources in wildflower plantings.

Flower resources (2020-21)

In the first two years, after the establishment of the wildflower plantings, the available flower resources increased steadily. Of the 32 species in the seed mix, 17 species were recorded to flower, 8 in the first year and 16 in the second. In the following years the dominance of sown species increased.

In the first year, annual and biennial species dominated the flower resources, but from the second year, perennial species started to dominate. However, not only the sown species but also other wild plant species contributed to the flower resources, probably largely from the soil seed bank. These are usually arable weeds with a pioneer strategy, which can efficiently utilise nutrients accumulated in temporarily uncultivated fields. Therefore, it is important to take into account the potentially more diverse soil seed bank when planning future wildflower plantings in these less intensively cultivated European regions (East-Central Europe, South-East Europe and Eastern Europe).

Perennial sown species have excellent competitive ability against annual weed competitors, and several of the annual sown species have excellent self-seeding potential (e.g., *C. transsylvanica*) and therefore good competitive ability. As a result, the flower abundance and species richness of the sown plant species increased sharply in the second year, while the number of not sown species showed a steady decline. This result underlines the importance of proper species selection for the seed mixture, especially for perennial wildflower plantings.

Pollinator abundance and species numbers (2020-21)

Similarly to several previous studies, we have shown a general positive effect of wildflower plantings on pollinators in the studied agricultural landscape of East-Central Europe. The increase in pollinator communities can be explained by: i) increased availability of flower resources, ii) a suitable, native and diverse seed mixture, and iii) less disturbed nesting and shelter habitat. However, the different groups of wild pollinator insects (wild bees, butterflies and hoverflies) responded differently to the studied variables. These different responses can probably be explained by the different foraging and nesting strategies of each pollinator group. In general, wild bees use a "central-place foraging" strategy, whereas butterflies and hoverflies are generally not "central-place foragers" and their larvae rely on different food sources (phytophagous, aphidophagous, entomophagous, saprophagous, etc.) than adults with good dispersal ability (flower visitors).

Wild bee abundance and species number increased between years and seasons, supporting the general positive expectations for wildflower plantings mentioned above. Previous studies have shown that agri-environment schemes are generally more effective in supporting biodiversity in simple (simple; 1-20% semi-natural habitats) than in complex (>20% semi-natural habitats) and cleared (<1% semi-natural habitats) agri-environment landscapes. However, our results suggest that the positive impact of wildflower plantings on the target insect community (pollinators) was in this case much more independent of landscape context. Wildflower plantings were also able to effectively support wild bee communities in heterogeneous agricultural landscapes (40-60% semi-natural habitat), not only in homogeneous ones (1-10% semi-natural habitat), suggesting that despite the improved availability of habitat for wintering, nesting and foraging in the landscape, wildflower plantings may still provide an important additional resource capacity for a potentially more diverse wild bee community. This can encourage farmers and decision-makers to apply and support the establishment of wildflower plantings as an agri-environmental practice, regardless of the landscape context. Furthermore, both flower abundance and species number had a positive effect on the wild bee abundance, and the number of flower species also had a positive effect on the wild bee species number, highlighting the importance of the diversity of flower resources.

One of our key findings was that wildflower plantings in homogeneous agricultural landscapes were extremely attractive to wild bees in mid-summer. This was probably because there was a greater contrast in flower resources between wildflower plantings and flower-poor landscapes during this period. This suggests that wildflower plantings are more likely to be successful in heterogeneous agricultural landscapes, but that there is a much greater need to create these flower-rich habitats in homogeneous agricultural landscapes, particularly in the flower-poor and high wild bee abundance mid-summer period.

Perennial wildflower plantings can therefore serve as foraging and shelter habitat, attracting and aggregating wild bees from surrounding lands. However, if they find other flowers resources outside the wildflower plantings, especially in insect-pollinated crops, they may spread out into adjacent habitats and pollinate them (spillover effect). They thus provide an economically beneficial ecosystem service.

The **butterflies** responded similarly to the wild bees: their abundance increased after establishment (year by year) and in line with the increase in the number of flower species. Previous research has already shown that butterfly populations increased in areas where agri-environment schemes increased flower abundance and the proportion of less disturbed habitats in the landscape, and a similar pattern was observed in wildflower plantings. It suggests that the most important predictor of change in butterfly abundance is the number of flowering plant species, and that their populations can increase year by year after establishment if wildflower plantings provide flowering resources for several years. We found that, like wild bees, butterflies were more strongly associated with heterogeneous landscapes, probably because surrounding semi-natural habitats, especially grasslands, may support more abundant and diverse populations of butterflies. These habitats are also important because butterfly larvae are attached to different food sources (plants) than their imagines, as we have taken into account in composition of our seed mixture.

Hoverflies showed opposite trends to wild bees. They generally responded positively to flower abundance, but both abundance and species numbers decreased significantly from the first to the second year and from early summer to mid-summer. These results were rather unexpected, as i) the succession of wildflower plantings was also associated with an overall increase in flower abundance for the hoverflies, and ii) they were also in contrast to previous studies that found positive effects of wildflower plantings on hoverflies. We, therefore, conclude that the significant decrease in the abundance and species number of hoverflies was not due to the introduction of wildflower plantings, but may have been due to changes in other factors, most likely seasonality and unfavourable weather conditions.

Previous studies showed that the size of wildflower plantings has little or no effect on the hoverflies, probably due to the high mobility of the adults. Our results, however, show that the decline in the abundance and species number of hoverflies from early to mid-summer was less pronounced in larger, contiguous wildflower fields than in several smaller strips. This may suggest that larger fields may be more effective at supporting hoverfly communities during unfavourable periods and conditions than smaller strips of the same overall size. Although the "single large or several smaller" dilemma suggests that several smaller wildflower patches may support biodiversity better than a single large patch, we found larger fields are more favourable for hoverflies in interaction with seasons.

Community composition (2020-21)

Floral plant communities differed almost completely on each of the four sampling occasions, and pollinator community composition followed this change, but with some delay and overlap. Such a drastic change in the floral assemblage can be explained by the emergence of perennial plants and the natural succession of habitats. The slower response of pollinators to significant changes in flower resources is probably explained by i) the seasonality of plant-pollinator systems, ii) the generalist behaviour of some pollinator species, and iii) the effect of the availability of floral and nesting resources in previous years on pollinator insect populations, which are highly interannual. In other words, the effect of the changing composition of floral resources on pollinator communities is delayed, i.e. there is a buffer effect in the plant-pollinator system.

Flower visitation (2020-23)

In the first year, as the flower resources were dominated by not sown species, the majority of flower visitations were also observed on not sown plant species, indicating that flowering plants emerging from the soil seed bank are an important flower resource for pollinators. The most commonly visited flowering plant species were native or archeophyte species that appeared to be suitable for native wild pollinators. The importance of the not sown flowering plant species lies in their ability to provide an immediate flower resource following establishment and in their abundance. Frequently visited flowering plants that emerge from the soil seed bank should therefore be considered as providing effective support for pollinators, or as something that may be worth considering for integration into future seed mixtures.

From the second year onwards, more than half (55.8%) of the flower visits by wild pollinators were observed on sown species. For the third and fourth years, the proportion of visitations of sown species increased even further. Some sown species played a prominent role in our seed mixture in terms of flower visitation, the main reasons for which could be: i) they provided a high amount of flower resources (e.g., *C. transsylvanica*), ii) they provided flower resources during the crucial mid-summer period of the year when flower resources were scarce (e.g., *S. varium*), iii) they were particularly attractive to certain pollinator groups (e.g., *Silene viscosa, Dianthus pontederae*), or iv) a specific preference of pollinators for them (as shown by the fact that they were particularly frequently visited despite their low flower abundance, e.g., *C. cyanus*). The visitation of sown species was over-represented in mid-summer, highlighting that the importance of sown plants (and generally the use of seed mixes), compared to not sown species, is also due to the fact that they offered a flower source for pollinators during a critical flower-poor period. *C. transsylvanica* was a particularly important species, with a third of all flower visits in the second year being recorded on flowers of this species, and it was also among the most visited plants in the following years. Its importance lies in its mass flowering ability at a period of the year when there are few floral resources available to pollinators at the landscape level.

Based on the high - and increasing over the years - rates of flower visitation of the sown plant species, native plants seemed to be suitable for the establishment of efficient pollinator-focused wildflower plantings. Compared to neophyte species, native species have the additional advantage that, when used, they do not pose the risk of invasion, which is already a serious problem in the region, and native perennial flowering plant species are more supportive of native specialist pollinator species. However, it is important to note that, following the principle of precaution, native plant species should originate from the narrowest possible region from the place of establishment.

The sown plant species were visited to different extents by pollinator groups. Based on these results, it appears that the species of the seed mixture were mainly adapted to the flower preferences of bumblebees and butterflies. One in two flower visits of solitary wild bees occurred on sown species, indicating that this group was also strongly supported by the seed mixture, but these species also visited flowers of not sown plants with the same intensity. Only one-third of the flower visits by the hoverflies were observed on sown species, and they were more attracted to the flowering plants from the soil seed bank. Therefore, an important aspect for further development of this seed mixture may be to add plants that are attractive to solitary wild bees and hoverflies too. Honeybees also visited the flowers of the sown plants in high numbers. The three species that stand out for honeybees (*C. transsylvanica, S. nemorosa and S. austriaca*) could therefore provide beekeepers with additional economic benefits. Not because of the large quantities of honey, but rather because of the behaviour of the families. In the case of continuous carrying, there is no need to feed and there is no competition for food between families, the so-called "rablás" in Hungarian.

Trapnest sampling (2020-21)

A wide range of cavity-nesting hymenopterans in the study area greatly used the trapnests. The number of nests made in reeds and the number of brood cells within nests were equally divided between wild bees and wasps.

Wild bees clearly play an important role in ecosystems by providing a pollination service. Their importance is reflected in the pollination of both cultivated crops and wild plants. The role of **wasps** in agro-ecosystems is not as obvious as it is for bees. The literature generally considers this group as effective or potential 'biocontrol' agents. This is of course also true for a significant proportion of the wasp species found in our trapnests. However, more than half of the nests and brood cells (61.0%; 58.1%) made by wasp species that feed their offspring with spiders (T*rypoxylon spp., Passaloecus spp.* and Pompilidae species) are more difficult to assess from an ecosystem service perspective, as they control individuals of an arthropod group that are themselves effective biological control agents. However, they have an important bioindicator role.

Among the **kleptoparasites**, species of Chrysididae family, *Sapyga quinquepunctata*, *Melittobia acasta*, *Cacoxenus indagator* and *Trichodes apiarus* were present in high numbers and destroyed the brood cells of the nest-building species. Parasitism of nests was variable, but overall, parasites were found in a quarter of nests and 13% of brood cells. This proportion is slightly lower than in previous studies in more diverse habitats.

NEW SCIENTIFIC RESULTS

1. I have played a crucial role in establishing an experimental setting that allows long-term monitoring of the effects of wildflower plantings at local and landscape scales in an understudied East-Central European region.

2. I have demonstrated that (in the studied Hungarian agricultural landscape dominated by arable cultivation) flowering plant species from the soil seed bank can provide diverse and significant floral resources for pollinator insects, complementing and enriching the species of the wildflower seed mixture, especially in the first and to a lesser extent in the second year after establishment.

3. I have demonstrated that large perennial wildflower plantings dominated by native flowering plant species (regardless of spatial arrangement) attract (and provide habitat for) a wide range of wild pollinator species in large numbers and their positive impact increases with the age of the planting.

4. I have proved that the landscape context influences the abundance of pollinator communities in wildflower plantings. Wildflower plantings in heterogeneous agricultural landscapes (>40% semi-natural habitat) attracted significantly more wild bees and butterflies, and butterfly abundance increased more intensively with age in heterogeneous landscape contexts.

5. However, I have also found that in mid-summer, in homogeneous agricultural landscapes, (i.e., in flower-poor periods and landscape contexts), sown wildflower plantings attracted and maintained a

particularly high wild bee community. I thus demonstrated the significant effect of the contrast in flower resources between the landscape and wildflower plantings on wild bees, and highlighted the importance of such interventions that increase mid-summer flower resources in homogeneous agricultural landscapes.

6. I have also indicated that the abundance of wild pollinators responds positively not only to an increase in the amount of flower resources but also to an increase in the number of flowering plant species, with varying intensities between different pollinator groups.

7. My results show that the spatial configuration of wildflower plantings (with the same total area) had no local effect on pollinators, but it interacted with the season in the case of hoverflies: the decrease in hoverfly abundance between seasons was more moderate in the larger wildflower fields than in the smaller ones.

PUBLICATIONS

Publications directly related to the dissertation:

Bihaly, Á. D., Piross, I. S., Pellaton, R., Szigeti, V., Somay, L., Vajna, F., Soltész, Z., Báldi, A., Sárospataki, M. & Kovács-Hostyánszki, A. (2024) Landscape-Wide Floral Resource Deficit Enhances the Importance of Diverse Wildflower Plantings for Pollinators in Farmlands. *Agriculture Ecosystems and Environment,* 367(15), 108984. https://doi.org/10.1016/j.agee.2024.108984

Báldi, A., Pellaton, R., **Bihaly, Á. D.,** Szigeti, V., Lellei-Kovács, E., Máté, A., Sárospataki, M., Soltész, Z., Somay, L. & Kovács-Hostyánszki, A. (2022) Improving ecosystem services in farmlands: the beginning of a long-term ecological study with restored flower-rich grasslands. *Ecosystem Health and Sustainability*, 8(1), 2090449. https://doi.org/10.1080/20964129.2022.2090449

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Publications related to the subject of the dissertation:

Lajos, K., Samu, F., **Bihaly, Á. D.,** Fülöp, D., & Sárospataki, M. (2021) Landscape structure affects the sunflower visiting frequency of insect pollinators. Scientific Reports, 11(1), 8147. https://doi.org/10.1038/s41598-021-87650-9

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Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sárospataki, M., Saure, C., Raffa, B., Vaskor, D., **Bihaly, Á.** & Pywell, R.F. (2017) Population responses of wild bees to oilseed rape neonicotinoid seed treatments in Hungary, Germany and the UK. NERC Environmental Information Data Centre. https://doi.org/10.5285/b75b40f6-cdb1-4bfd-a599-bd2e171512e7