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Forest and grassland habitats support pollinator diversity more than wildflowers and sunflower monoculture

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Abstract

1. Intensively managed agricultural landscapes often lack suitable habitats to support diverse wildlife, particularly harming pollinator communities. Besides mass flowering crops, remnant patches of natural and semi-natural vegetation may play a key role in maintaining and conserving biodiversity. Yet, the effects of different natural habitats, including forests and grasslands, on different pollinator communities are poorly understood at the landscape scale.

2. We examined the abundance, richness, and diversity of wild bees and hoverflies, two key pollinator groups, across a land-use gradient spanning forest edges, grassland, wildflower strips, and sunflower monoculture. We also examined the distribution of hoverfly larvae trophic guilds and wild bee nesting traits across the above-mentioned land-use gradient. Finally, we evaluated the impact of landscape structure (forest, grassland, and water cover in the surrounding landscape) on pollinator community composition.

3. Our results indicate that forest and grassland habitats supported a higher abundance and greater richness of pollinators than wildflower strips and sunflower monocultures. Furthermore, hoverflies were more sensitive to habitat and floristic homogenization than wild bees. Sunflower and wildflower habitats also hosted a lower diversity of larvae trophic guilds and wild bee nesting guilds as compared to forests and grasslands.

4. Our study suggests that conserving and restoring forest and grassland habitats within agricultural mosaics may serve as the main 'refuge' for wild pollinators.

KEYWORDS
bees, habitat types, hoverflies, intensive agriculture, landscape composition, pollination

INTRODUCTION

Intensive agricultural production—the 'green revolution'—that started in the second half of the 20th century has caused major landscape changes on a global scale, including habitat homogenization, biodiversity decline and erosion of ecological functions (Henle et al., 2008), with profound effects on pollination (Dainese et al., 2019) and life-support systems. Homogenous landscapes subjected to intensive agricultural production lack diverse foraging resources as well as nesting habitats that would support

diverse pollinator communities (Biesmeijer et al., 2006; IPBES, 2016; Zattara & Aizen, 2021). In contrast, maintaining landscape heterogeneity is known to positively support the diversity of wild pollinators (Fisher et al., 2017; Lorandi et al., 2023; Nery et al., 2018; Ricotta et al., 2003). Considering the global agricultural expansion rates and pollinator declines, it is of utmost importance to understand how to limit and halt the impact of habitat disruption/loss resulting from agricultural practises on pollinators.

In temperate regions, wild bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) are the most important pollinators of both wild plants (Doyle et al., 2020; Larson et al., 2001; Vanbergen et al., 2013) and agricultural crops (Inouye et al., 2015; Jauker & Wolters, 2008; Larson et al., 2001; Rader et al., 2020; Ssymank et al., 2008). However, the majority of studies addressing the effects of agricultural land use on pollinator species composition are mostly limited to wild bees (Bailey et al., 2014; Senapathi et al., 2017). Thus, our knowledge of broader pollinator diversity presently does not extend to key groups, such as hoverflies (Doyle et al., 2020; Jauker et al., 2009; Proesmans et al., 2019), which also act as biocontrol agents of aphids in crops (Bellefeuille et al., 2019; Ramsden et al., 2017; Wotton et al., 2019) and decomposers of organic waste (Morales & Wolff, 2010). Understanding how different wild insect pollinators respond to different habitat types in agricultural landscapes is key to improving conservation of pollinator communities and land management.

Increasing evidence points to the key role of trees and shrubs integrated into crop farming, including riparian forest buffers, hedgerows, windbreaks, shelterbelts, and alley cropping, in pollinator feeding, reproduction and survival (Morandin & Kremen, 2013; Kremen & M'Gonigle, 2015; Kay et al., 2019; Bentrup et al., 2019; Varah et al., 2020). Yet, different taxonomic groups are differently impacted by landscape structure due to largely diverse ecological traits (Jovičić et al., 2017; Moquet et al., 2018), particularly those related to the ecological and feeding requirements of larvae. Species-specific response of wild pollinators to different land use pressures, such as mowing (Meyer et al., 2017), grazing (Lazaro et al., 2016; Oleques et al., 2019) and plant diversity (Losapio et al., 2016) highlight that pollinator persistence depends on traits that characterise very few favourable habitats (Brown et al., 2020; Devictor & Jiguet, 2007; Ekroos et al., 2013; Hall et al., 2019; Miličić et al., 2020). For instance, solitary wild bees thrive in forests within an agricultural matrix, specifically in the early stages of forest development rich in floral resources and nesting sites (Centrella et al., 2020; Hanula et al., 2015; Roberts et al., 2017; Rubene et al., 2015). On the other hand, saproxylic hoverflies depend on well-established forests and abundant sources of large, dead trees (Maritano, 2020; Reemer, 2005; Ricarte et al., 2009). For instance, as large saprophagous hoverflies are closely associated with water during their development, greater species richness could be expected in areas with a greater number of riparian sites (Keil et al., 2008), while species with phytophagous larvae developing on the underground storage organs of plants can often be found in habitats with a higher proportion of agricultural land

(Jovičić et al., 2017). Yet, little is known about the effects of different components of landscape structure on different pollinator communities.

Although mass-flowering crops can increase the abundance of generalist pollinators (Westphal et al., 2003), when grown extensively at the landscape scale, they tend to negatively affect the taxonomic richness and abundance of pollinators, particularly bees (Shaw et al., 2020; Todd et al., 2016). Short term benefits of abundant floral resources provided by mass-flowering crops are diminished by agrochemical toxicity (Henry et al., 2012; Stanley et al., 2015) and an increase in pathogen prevalence (Tuerlings et al., 2022). Spontaneously established or sown wildflower strips in close proximity to mass-flowering crops offer diverse nectar and pollen resources pre- and post-crop flowering (Maurer et al., 2022), while also providing nesting and overwintering habitats (Holland et al., 2017).
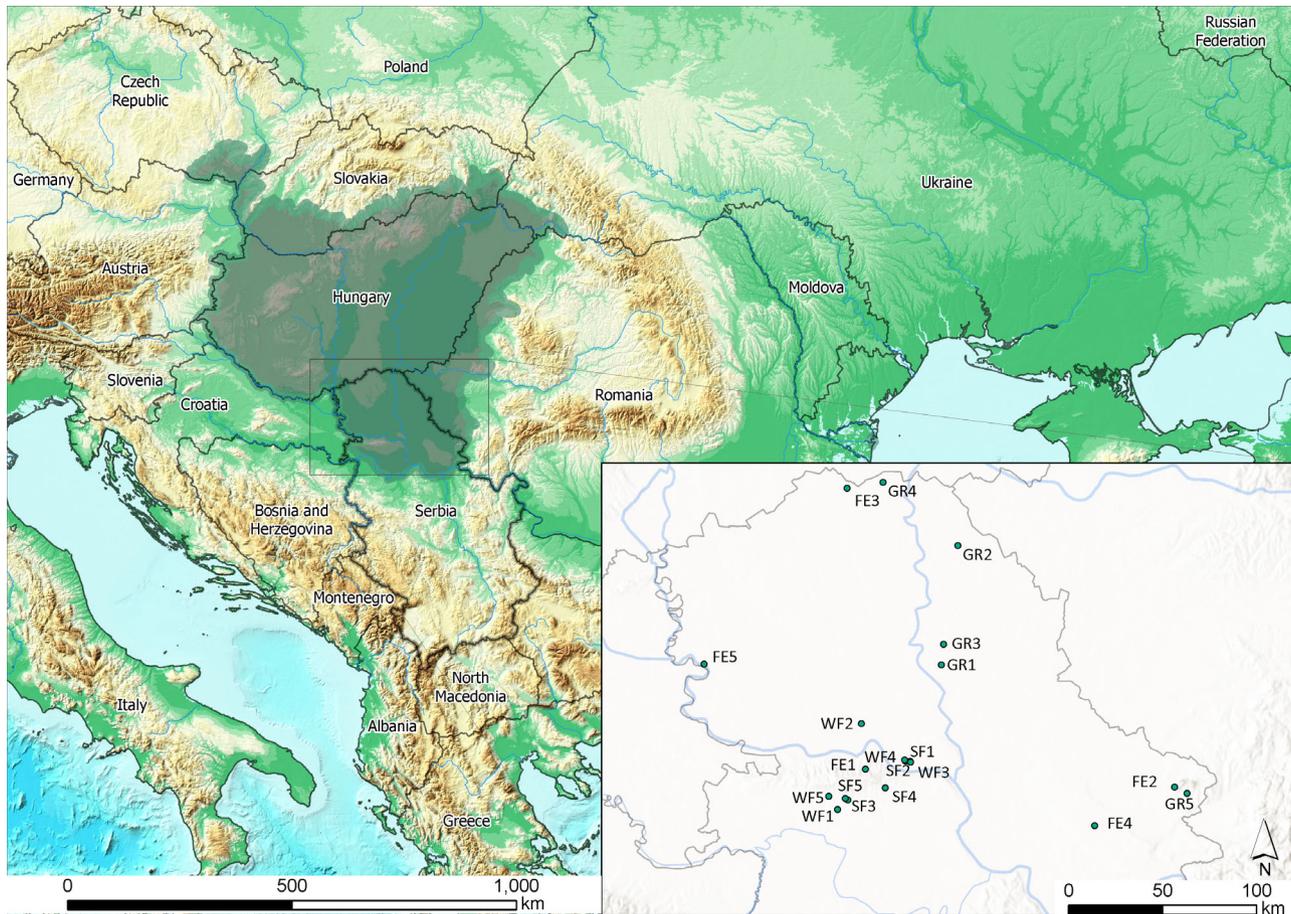
In this study, we examine the response of bee and hoverfly species to different land use types in an agricultural setting and assess the impact of the surrounding landscape and management on their distribution and community composition. Our aim is to address two main questions: (1) How do habitat type and landscape composition affect pollinator abundance, richness, diversity and community composition? (2) How does landscape composition affect the distribution of hoverfly larvae trophic guilds and wild bee nesting traits?

We hypothesise that forest edges and forest fragments increase pollinator abundance and diversity. As forests would provide more resources (qualitatively and quantitatively) compared to grasslands, wildflower strips and sunflower fields for both larvae and adults, we also hypothesise that the diversity of hoverfly larvae trophic guilds and wild bee nesting traits increase with forest edges and fragments. Finally, we expect that pollinators respond in different ways to different habitats, with wild bees being more diversified in grasslands than in forests.

MATERIALS AND METHODS

Study site

The study was carried out in Vojvodina province (8.345 sq mi area) in Serbia (Figure 1). The area is characterised by an intensively managed agricultural lowland landscape, 80% of which is covered by monoculture field crops. The entire Vojvodina territory lies in the Pannonian ecoregion (Figure 1), a flat basin surrounded by the Carpathian Mountains, Alps and Dinarides. Such a shielded position of the Pannonian plain and various climatic influences have resulted in distinct vegetation and soil, a diverse range of habitats and a high level of species diversity (Ács et al., 2015; European Commission, 2010). The climate of the region is typically continental, with extreme temperature variations (Feddema, 2005). Vojvodina generally has about 600 mm annual precipitation. Although primarily agricultural land, it also features the remains of typical Pannonian forest steppes. The main reservoirs of biodiversity in Vojvodina are small fragments of managed grasslands, steppes, riparian sites and continental salt marshes as well as two

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FIGURE 1 Map showing the distribution of the 20 sampling sites within Vojvodina region in Serbia. Each site is designated with the following abbreviations: FE, forest edge; WF, wildflower strip; SF, sunflower field; GR, grassland. Pannonical ecoregion is highlighted in grey colour.

major forest sites, Fruška gora and Vršački breg, which provide habitat and abundant additional resources for a great variety of wildlife (Vujić & Glumac, 1994; Vujić & Šimić, 1994). Besides offering a wide choice of floral resources and nesting places to pollinators, these forest habitats are less exposed to agricultural chemicals, one of the main contributors to the global pollinator decline (Evans et al., 2018; Main et al., 2020; Moquet et al., 2018), in comparison to the sunflower fields and wildflower strips in their surroundings (Markov et al., 2016).

We randomly selected 20 sites reflecting four land use and habitat types, namely: five forest edge sites (FE), five grassland sites (GR), five sunflower field sites (SF), and five wildflower strips (WF) (Figure 2). Sites within the same habitat type were at least 1 km apart to account for the foraging distance of hoverflies and bees (Rotheray et al., 2009; Zurbuchen et al., 2010). The high compositional independence between habitat types minimised the potential effects of spatial autocorrelation on the obtained results. Forest edges were on the margins of natural, mixed deciduous forests as well as deciduous forest plantations, whereby two sites were located at the edge of oak-hornbeam and mixed beech forests, one was situated at the edge of a poplar forest, and two sites were at the edge of a cultivated black locust forest (Table S1). This

means that all forest edge sites had a forest interior in their extension. Sampling was performed at 1 to 2 m distance from the forest margin, which is characterised by early succession stages subjected to both southern and western exposure and containing around 5% of bare ground. Natural grasslands were represented by dry steppes, mostly populated by graminoid species, while also including scattered herbs, shrubs and trees in different small percentages. In grassland sites, herbaceous vegetation covered approximately 90% of the ground. They are subjected to a combined management regime (grazing and mowing) and are unaffected by agricultural practices. All forest edge and grassland sites were under nature conservation measures, whereas all sunflower field sites were characterised by mass flowering crop monocultures and were located in large fields treated with systemic and selective herbicides as well as soil insecticides. Those sunflower monocultures were therefore devoid of wild plants' ground cover. Wildflower strips were sparsely scattered, situated 100 to 400 m near crops, with herbaceous cover spontaneously established from the soil seed bank. They are mowed twice a year and were previously part of the massive flowering crops. Vegetation was represented by grasses and forbs of relatively low plant diversity with few dominant species. Within wildflower strips consisting mostly

FIGURE 2   Photographs of representative land cover types: (a) sunflower; (b) wildflower strip; (c) forest edge; (d) grassland.

of perennial plants, only plant species with the highest flower cover were identified (Table S1).

POLLINATOR SAMPLING

To assess bee and hoverfly abundance and diversity, standardised transect walks and sweep nets were used. Specimens were sampled in three temporal replicates within sunflower fields and five replicates in plots of other land use types along 300 × 1 m belt transects. The same transects were used for repeated visits. The observer walked the transect at a steady pace (10 m/min) for 30 min within each repetition. The same transect walks were conducted for each site and repetition. Samplings were conducted between 09:00 and 13:00 on sunny days with temperatures above 15°C and little or no wind. Pollinators were identified to the species level, either directly in the field or in the laboratory (bumblebee queens were not sampled but identified on the field). All data was collected in 2013, whereby sunflower fields were surveyed during sunflower blooming in late June and July while all other sites were surveyed in April, May, June, July and October. No data collection was conducted in August and September due to high temperatures, low flower abundance and hence low pollinator activity. Data were pooled across the season at the plot level ($n = 20$).

ENVIRONMENTAL VARIABLES

We selected the following three landscape properties due to their effects on pollinator distribution (Miličić et al., 2020; Moquet et al., 2018): forest, grassland and water cover in the surrounding area expressed in km^2 and converted to a percent value (%). Forest cover encompasses both interior forest and forest edge. The interior forest area is an important habitat for forest specialists, cavity nesting and saproxylic species, which are dependent on high amounts of dead and rotting wood used for nests or egg deposition habitats. Forest, grassland and water cover were calculated in a 1 km buffer zone around the centre of each transect using the Corine Land Cover (CLC) 2018 (V2020) classes: CLC classes 311, 312, 313, 324 and 244 for forests; CLC classes 231 and 321 for grasslands; and CLC classes 511, 512, and 411 for water. Data were processed in ArcGIS Pro 3.0. We chose buffer zones of 1 km, considering that both wild bees and hoverflies generally disperse over very short distances of several hundred metres
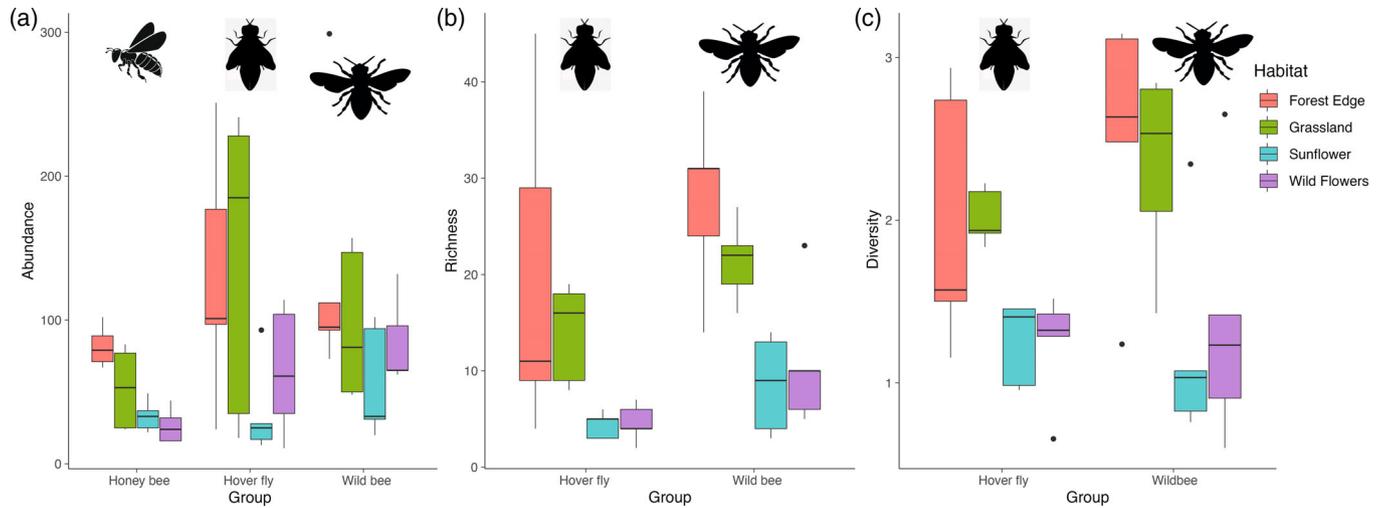
FIGURE 3 Summary of the effects of different habitats (forest edge in red, grassland in green, sunflower in light blue, wildflower strips in purple) on (a) pollinator abundance, (b) richness, and (c) Shannon diversity.

(Gathmann & Tscharntke, 2002; Kleijn & Van Langevelde, 2006; Meyer et al., 2009; Westphal et al., 2006; Wratten et al., 2003; Zurbuchen et al., 2010), excluding migration events for the very small number of occasionally and strongly migratory hoverfly species.

DATA ANALYSIS

We used a regression approach to test the effects of land use type on pollinator abundance, richness and diversity, whereby pollinator taxa were assigned to honeybee, wild bee and hoverfly groups. In each plot and for wild bees and hoverflies, we calculated: (1) abundance, that is, the total number of individuals; (2) richness, that is, the total number of species as an index of alpha-diversity; and (3) diversity, as the Shannon index of complexity that encompasses both abundance and richness. For honeybees, we calculated their abundance in each plot (as species diversity would be meaningless).

Separate Generalised Linear Models (GLMs) were built with pollinator abundance (negative binomial distribution), pollinator richness (negative binomial distribution), and pollinator diversity (normal distribution) as response variables (three separate models). In each model, we tested the effects of pollinator group (categorical) and land use type (categorical: forest, grassland, wildflower strips, and monoculture), and their interactions, as well as grassland cover (continuous), forest cover (continuous) and water cover (continuous) both separately and in interactions with pollinator group. Each model looks like $Y = a + \beta_p X_p \times \beta_h X_h + \beta_p X_p \times \beta_l X_l + \epsilon$, where Y is either pollinator abundance, richness or diversity, β_p is the parameter for pollinator groups, β_h the parameter for land use type, and β_l the parameter for landscape structure. GLMs were fitted using the template model builder with *glmmTMB* R package (Brooks et al., 2017). To account for data heteroscedasticity between different pollinator groups, we included the pollinator group as a dispersion parameter in the model, allowing the residual variance to vary among groups.

Next, we assessed: (1) The importance of predictors by estimating the amount of variance explained in the response variables based on the findings yielded by type-II analysis-of-deviance tests included in the *car* R package (Fox & Weisberg, 2019); (2) The strength of predictors by computing Cohen's *f* effect size for partial sums of squares using the *effectsize* R package (Ben-Shachar et al., 2020); (3) The direction of the relationships between predictor and response variables by estimating the GLM-template model builder (TMB) parameters along with their standard errors and significance tests (R Core Team, 2022); (4) Model overdispersion by comparing the variance of the observed raw residuals against the variance of the simulated residuals using the *testDispersion* function in *DHARMa* R package (Hartig, 2022). Finally, to compare the abundance, richness and diversity of each pollinator group across land use types, we ran contrasts of estimated marginal means from each GLM with *p*-values adjusted according to the Tukey method using the *emmeans* R package (Lenth, 2022).

Since hoverfly distribution is closely associated with both adult and larval traits, we also examined the abundance of hoverfly larvae trophic groups across investigated land use types, which is particularly useful when analysing the impact of agricultural landscapes (Meyer et al., 2009; Moquet et al., 2018). For this purpose, in accordance with the approach adopted by other authors (Speight, 2020; Speight et al., 2015), we considered the following five trophic groups: saproxylic, phytophagous developing in roots, phytophagous developing in bulbs, zoophagous, and saprophagous. In addition, we examined wild bee nesting traits across the investigated land cover types by considering four different nesting traits: ground nesters, renters, cavity nesters and wood nesters.

RESULTS

We surveyed 4681 pollinator specimens, 1855 of which were wild bees, 968 were honeybees, and 1858 were hoverflies. Land use type had significant, strong effects on pollinator abundance overall
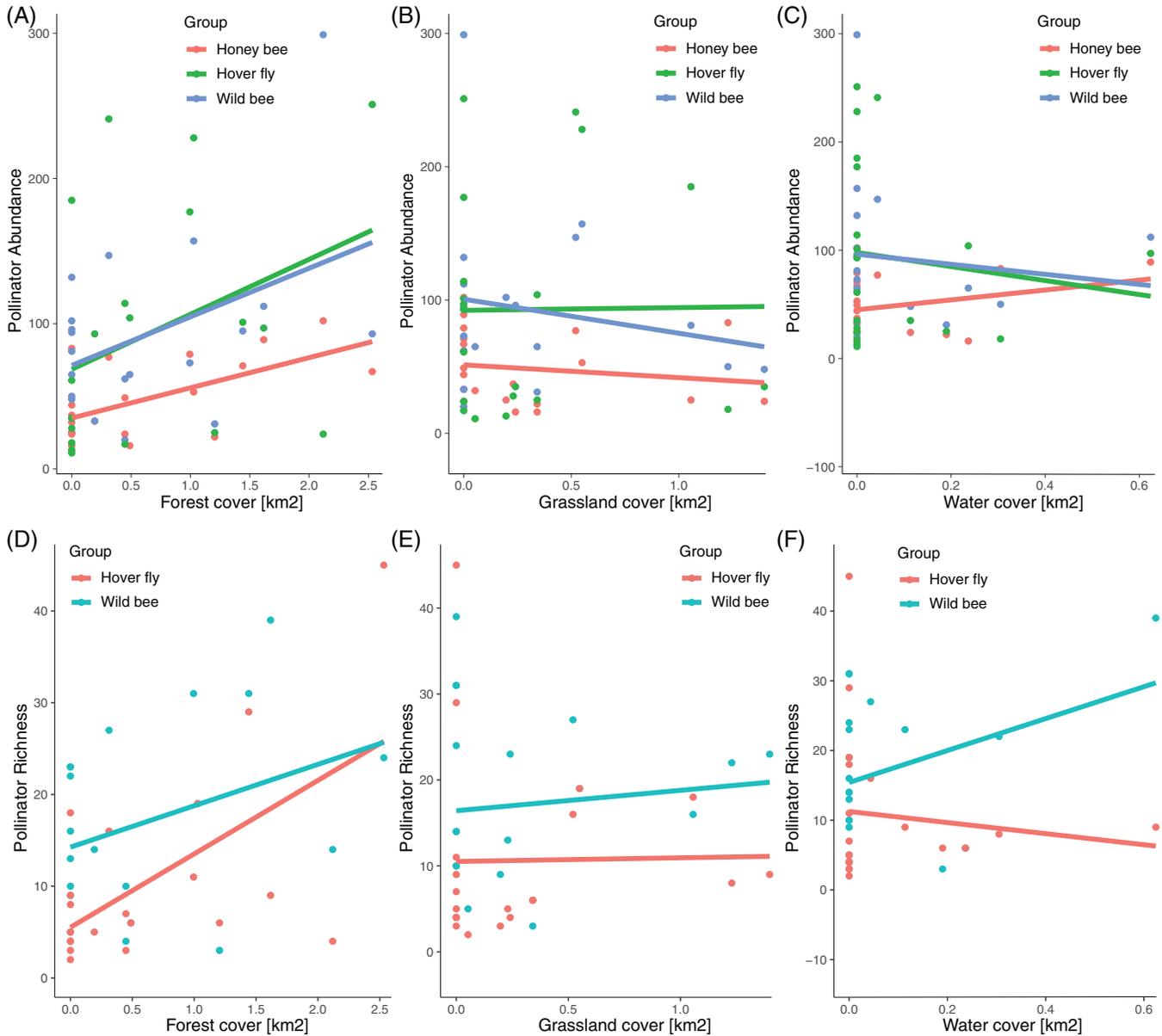
FIGURE 4 Relationship between abundance and richness of different pollinator groups (honey bee in red, hover fly in green, wild bee in light blue) and landscape structure (forest, grassland and water cover expressed in km^2 in the surrounding area of 1 km).

($f = 0.72$; $p < 0.001$; Figure 3a). Across pollinator groups, forest edges and grasslands significantly increased pollinator abundance relative to sunflower monoculture ($\beta = 0.95$, $p = 0.001$ and $\beta = 1.25$, $p < 0.001$, respectively), whereas wildflowers had no significant differences ($\beta = -0.30$, $p = 0.126$). Although the effects of land use type on abundance did not vary among pollinator groups ($f = 0.35$; $p = 0.149$; Table S3), the abundance of pollinators increased from monocultures to wild flowers for wild bees and hoverflies but not for honeybees, ($\beta = 1.02$, $p = 0.031$; $\beta = 0.67$, $p = 0.583$, respectively). Furthermore, the percentage of land cover with grassland in the surrounding transects significantly affected pollinator abundance ($f = 0.54$, $p = 0.003$), whereby, forest and water cover were not significant ($f = 0.16$, $p = 0.263$; and $f = 0.09$, $p = 0.182$, respectively) (Figure 4).

We identified 133 species of bees and 82 species of hoverflies (Table S2). Land use type had significant, strong effects on both pollinator richness ($f = 1.24$; $p < 0.001$; Figure 3b) and pollinator diversity ($f = 1.00$; $p = 0.005$; Figure 3c). Although pollinator richness responds to land use type in similar ways across groups ($f = 0.13$; $p = 0.397$), significant interactions were observed between land use type and pollinator group identity for pollinator diversity ($f = 0.23$; $p = 0.039$). Forest edges and grasslands increased pollinator richness ($\beta = 0.79$, $p = 0.094$ and $\beta = 1.20$, $p = 0.023$, respectively) as compared to sunflower monoculture. Instead, there were no significant differences observed between wildflower strips and sunflower monoculture ($\beta = 0.16$, $p = 0.680$). Similar results were obtained for pollinator diversity (Table S8). Furthermore, in both cases of richness and
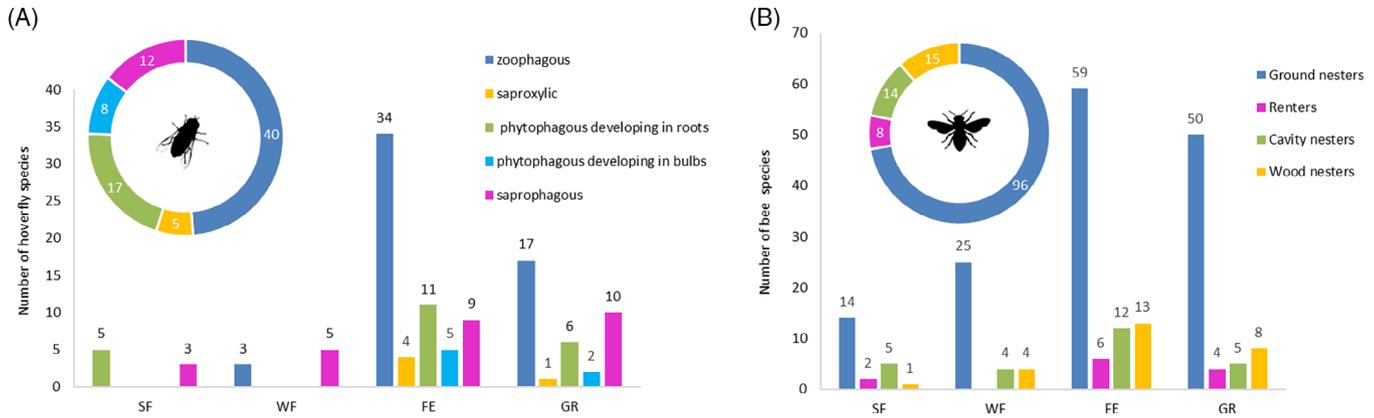
FIGURE 5 (a) hoverfly larvae trophic groups across different site types (SF, sunflower monoculture; WF, wildflower strip; FE, forest edge; GR, grassland) represented by column charts; (b) wild bee nesting traits across investigated site types (SF, sunflower monoculture; WF, wildflower strip; FE, forest edge; GR, grassland) represented by column charts. Doughnut charts represent (a) hoverfly larvae trophic groups in the whole hoverfly dataset, and (b) wild bee nesting guilds in the whole wild bee dataset.

diversity, forest cover exhibited different effects on wild bee and hoverfly richness ($f = 0.53$; $p = 0.001$; $f = 0.42$; $p = 0.005$, respectively; Figure 4). The main idiosyncrasies were associated with the stronger increase in hoverfly richness and diversity with increasing forest cover as compared to wild bees ($\beta = 1.01$, $p = 0.001$ and $\beta = 1.04$, $p = 0.005$, respectively).

We also found variation in the hoverfly larvae trophic groups across different land use types (Figure 5a). Zoophagous hoverflies predominated in the total sample (Figure 5a), as well as at forest sites. Unsurprisingly, as many as 80% of the total number of saproxylic hoverflies included in the analysis were found in forest habitats. The study sample contained 12 saprophagous species, 83% of which were observed at grassland sites. In contrast, phytophagous hoverfly species (both developing in roots and bulbs) were only found in forest edges and grasslands. As for wild bee nesting traits, we found that ground nesters (70%) and wood nesters (11%) were dominant nesting types in the wild bee data set (Figure. 5b). Among the investigated land cover types, forest edges had the highest number of species within each nesting type.

DISCUSSION

Habitat and biodiversity loss due to intensive agriculture, especially monoculture and pesticides, impact the environment and wildlife, including pollinator decline (Moquet et al., 2018; Meyer et al., 2009). We demonstrated that diverse floral resources as well as the number of different habitat types are key in supporting populations and diversity of both bee and hoverfly pollinators. Although these species may respond differently to reductions in habitat diversity, our results demonstrate that all pollinators responded with increased abundance and richness to both the presence and the cover of forest and grassland habitats. However, there is no evidence to support the expectation that wildflower strips close to monocultures increase pollinator diversity. These results indicate that limiting both habitat fragmentation

and the extent of monoculture farming is required to support diverse pollinators. Increasing habitat subdivision on a landscape scale may affect pollinators by directly reducing the availability of suitable habitats (via the erosion of the species–area relationship) and indirectly by reducing the diversity and quality of flower resources.

Our results confirm previous observations for wild bees (Kennedy et al., 2013; Vanbergen et al., 2013) and hoverflies (Cole et al., 2017; Rodríguez-Gasol et al., 2020; Schirmel et al., 2018). Although the abundance of both pollinator groups is significantly higher within forest edges and grassland habitats compared to wild-flower strips and sunflower fields, we observed that bees were more tolerant than hoverflies to floristically impoverished sites. Concurring with Ricarte et al. (2011) and Proesmans et al. (2018), we confirmed that forests act as the main reservoirs of hoverfly and bee species within agricultural landscapes. Notably, our findings indicate that the abundance and richness of different pollinator species are positively correlated with forest-edge habitats. This is not surprising, given that larger forests usually contain microhabitats in greater abundance, hence providing greater diversity of nesting places (Ferreira et al., 2020; Ouin et al., 2006; Roberts et al., 2017; Taki et al., 2007), which have the capacity to maintain a wider range of pollinators with more heterogeneous nesting requirements and behaviours. In addition, forests with well-developed herbaceous ground layers offer abundant forage resources, particularly in the spring.

Although few authors noted that agricultural areas can preserve bee diversity at levels similar to or even higher than (preserved) forests (Harrison et al., 2018; Schüepp et al., 2012; Winfree et al., 2007, 2011), our findings counter these limited assertions and support the vast majority of published research showing that (intensive) agriculture decreases species diversity. Such discrepancies may be due to several reasons, one of which is the type of agriculture studied. For instance, conventional monoculture and ecological farming have completely different effects on biodiversity (Gonthier et al., 2014). Moreover, the amount and size of habitat patches likely differed across investigated habitat types. In particular, the region in the focus

of our investigation exhibits low diversity in habitat types, which would decrease the local pollinator community size even further. Consequently, our results emphasise the need for a more careful assessment of patch-level structural factors in a large area under highly intensive agriculture.

Grasslands host a variety of microhabitat types, including scrub patches and water sources. In addition, they offer diverse floral resources and nesting sites for many ground nesters that prefer short vegetation, ultimately increasing pollinator diversity and supporting the development and sustainability of pollination networks (Robinson et al., 2018). Managed grasslands with high wild floral diversity adjacent to forest sites are of particular importance, as these habitats offer both nesting and foraging resources.

Markedly lower diversity of pollinators in wildflower strips in comparison to grassland and forest edges may be attributed to distance of wildflower strips from large forested sites, as the main reservoirs of source populations, and low amount of suitable surrounding habitat. Wildflower strips are surrounded by agricultural fields and heavily dependent on dispersal from source populations that thrive in and nearby forest sites, as our results have shown. Although we can presume that wildflower strips' geometry (width, length and size) as well as flower diversity, is not adequate to support viable and diverse pollinator populations, this remains to be further investigated. As pointed out by De Cauwer et al. (2005), inadequate management of wildflower strips and surrounding habitat radically decreases floral quality over time. Investigated wildflower strips are not sown for insect conservation and consequently, the mowing regime is not tailored to promote plant species richness and floral abundance, but is conducted only for maintaining aesthetics. In addition, it is worth considering other contributing factors that led to lower pollinator diversity in these habitats, such as close proximity to roads, repetitive disturbance in nearby agricultural sites, and possibly pesticide spray drift (Fischer & Moriarty, 2011; Fitch & Vaidya, 2021).

As for the early-season mass-flowering crops, such as sunflowers, even though they provide abundant pollen and nectar resources, this supply is very short term due to their short flowering time of around 20 days (Schellhorn et al., 2015) and poor nutritional value (Somerville & Nicol, 2006; Tasei & Aupinel, 2008; Nicolson & Human, 2013). The sudden shortage of pollen after sunflower bloom is even more pronounced in areas lacking wild plant resources due to heavy herbicide use, which is the case in the region in focus of our study. Dietary diversity is vital for the maintenance of insect pollinators' immune systems (Leach & Drummond, 2018; Vaudo et al., 2015) and is a key driver of population health.

A long history of intensive agricultural production in northern Serbia has resulted in the adaptation of a small number of species that temporarily feed on mass flowering crops, such as sunflowers. For instance, the abundance of the hoverfly *Philhelius pedissequus* (Harris, 1776) is expected to have a higher association with sunflower monoculture than with other habitats, due to its tolerance and potential adaptation to agricultural intensification. Yet this is just one of more than a 100 species, most of which are adversely affected by monoculture. This negative impact is also supported by a clear decline in the

life history traits of pollinators, given that only two hoverfly trophic groups (zoophagous and saprophagous species) occur in sunflower fields and wildflower strips, whereas forest edges and grasslands support five groups (including saproxylic species, phytophagous species developing in roots, and phytophagous species developing in bulbs).

Diverse micro-habitats are of the utmost importance for most of the hoverfly species, and their benefits are especially evident in the forest edges, where almost 80% of the hoverfly species included in our study were found. Moreover, forest edge sites favour saproxylic hoverfly species, considered specialists (Herrault et al., 2016; van Veen, 2004), while neither sunflower fields nor wildflower strips were suitable habitats for these species. Indeed, hoverfly larvae feeding reflects the level of species specialisation (Aguirre-Gutiérrez et al., 2016; Miličić et al., 2021). On the other hand, generalists, such as zoophagous hoverfly species, constituted the majority of our study sample and were distributed evenly across the land cover types because they can more easily find alternative resources in less suitable habitats (Biesmeijer et al., 2006). The ecological requirements of saprophagous hoverflies were best fulfilled at grassland sites, where they could inhabit diverse microhabitats. In particular, the existence of moist microhabitats in which these hoverfly species could lay their eggs (Rotheray & Gilbert, 1999) is vital for their development.

As our findings revealed, forest edges also support the highest species richness of wild bees within four nesting types, indicating that they offer the widest choice of nesting habitats within the agricultural landscape. Our research findings are likely to be representative of the whole Pannonian region due to the same specific regional and habitat features as well as land use history.

In conclusion, our results provide evidence that large and diversified habitats devoid of agriculture are crucial for harbouring diverse pollinator communities. Not only reducing agrochemical input, but also limiting the land areas under monoculture is imperative for meeting the essential habitat and resource requirements of pollinators. Therefore, future conservation and management efforts need to consider the expansion and preservation of forests, extensive grasslands and adequately managed wildflower habitats in order to sustain vital pollination services in agricultural landscapes with extensively grown mass flowering crops.

AUTHOR CONTRIBUTIONS

DV: conceptualization, data analysis and paper writing. GL: statistical analysis, interpretation and paper writing. MM: ArcGIS calculations and map design. SP: paper writing and review. ZMR: data collection. SMS: data collection. JJ: data preparation, literature, and paper review. AV: supervision and funding acquisition. All authors reviewed the results and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors claim no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

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

Table S1. Vegetation characteristics across investigated sites. Each site is designated with the following abbreviations: FE, forest edge; WF, wildflower strip; SF, sunflower field; GR, grassland

Table S2. The abundance of wild bee and hoverfly species across investigated land cover types

Table S3. Summary of model parameters assessing the effects of habitat, grassland cover, forest cover, water cover in the surrounding landscape on the pollinator abundance across pollinator groups

Table S4. Contrasts (estimated marginal means) among habitat types across pollinator groups for pollinator abundance

Table S5. Summary of model parameters assessing the effects of habitat and grassland, forest and water cover in the surrounding landscape on the pollinator richness across pollinator groups

Table S6. Contrasts (estimated marginal means) among habitat types across pollinator groups for pollinator richness

Table S7. Summary of model parameters assessing the effects of habitat and grassland, forest and water cover in the surrounding landscape on pollinator diversity (Shannon index) across pollinator groups

Table S8. Contrasts (estimated marginal means) among habitat types across pollinator groups for pollinator diversity (Shannon index)

Appendix S1. Supporting Information