Wild bee (Apiformes) communities in contrasting habitats within agricultural and wooded landscapes: implications for conservation management

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Abstract

1 Semi-natural habitats are characterized by a high diversity of wildlife. However, other areas, e.g. old fields, can also play an important role in biodiversity conservation.

2 We assessed the species richness, abundance, and diversity of wild bees (Apiformes), including species of various functional groups in two contrasting and differently managed landscape types. For this study, we selected 15 xerothermic or sandy grasslands or extensively managed fresh meadows located in agricultural landscapes as well as 15 old fields located in wooded landscapes. The study sites differed in area, stage of succession, and management regime.

3 We did not detect any significant differences in total species richness, abundance, and diversity of Apiformes between the two landscape types, which suggests that both semi-natural habitats and old fields are highly attractive to bees. The two habitat types, however, differed in species composition and proportions of functional groups. We found that in wooded landscapes, eusocial, hive-nesting, and large-sized species increased in abundance.

4 The collected information on the preferences of Apiformes in respect of various habitats and landscapes makes it possible to protect and restore valuable habitats through the implementation of suitable methods of management, both locally and on the scale of landscapes.

Keywords Agricultural landscape, Apiformes, farmland, forest, functional diversity, old fields, semi-natural habitats, species diversity, wooded landscape.

Introduction

Bees (Hymenoptera: Apiformes) are an ideal taxonomic group for research on the conservation value of various habitats. They are undoubtedly the major providers of pollination services to wild and cultivated plant species (Potts et al., 2016), and, therefore, play a crucial role in functioning of ecosystems and human economy (Matias et al., 2017).

Wild habitats are of key importance for the protection and conservation of diverse and stable communities of pollinators (Mittermeier et al., 2003). Intensified destruction, fragmentation, and excessive isolation of natural and semi-natural habitats pose serious threats to biodiversity in Europe (Steppan-Dewenter & Tscharntke, 2001; Klein et al., 2004) and the availability of suitable nesting sites and substrates (Cane, 1991; Potts et al., 2015). At the landscape scale, the amount, distribution, and connectivity of habitats providing bees with resources are also important for their dispersion, density, and diversity (Rickert, 2004; Morandin & Winston, 2006; Kormann et al., 2015; Carré et al., 2017). Various functional groups of bees, determined by their traits, may react differently to changes in land use (Senior et al., 2013; Rader et al., 2014; Forrest et al., 2015; Twerd & Banaszak-Cibicka, 2019). Eusocial species (mostly Bombus spp.) can be more abundant in forest-steppe habitats as a result of land-use intensification, particularly conspicuous in agro-ecosystems and forest plantations (Steppan-Dewenter & Westphal, 2008).

Bees respond to spatial heterogeneity in habitats at different scales. At the local habitat scale, the occurrence of Apiformes is affected by habitat quality, such as the diversity and abundance of bee forage plants providing pollen and nectar (Steppan-Dewenter & Tscharntke, 2001; Klein et al., 2004) and the availability of suitable nesting sites and substrates (Cane, 1991; Potts et al., 2005). At the landscape scale, the amount, distribution, and connectivity of habitats providing bees with resources are also important for their dispersion, density, and diversity (Rickert, 2004; Morandin & Winston, 2006; Kormann et al., 2015; Carré et al., 2017). Various functional groups of bees, determined by their traits, may react differently to changes in land use (Senior et al., 2013; Rader et al., 2014; Forrest et al., 2015; Twerd & Banaszak-Cibicka, 2019). Eusocial species (mostly Bombus spp.) can be more abundant in forest-steppe habitats as a result of land-use intensification, particularly conspicuous in agro-ecosystems and forest plantations (Steppan-Dewenter & Westphal, 2008).

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than in open habitats (Banaszak & Twed, 2018). In contrast, most small-sized solitary bees prefer open habitats (Banaszak & Twed, 2018), whereas spatial isolation limits their distribution (Carrié et al., 2017). At least some bee species are affected not only by artificial barriers such as buildings, but also by natural barriers such as forests (Bhattacharya et al., 2003; Farwig et al., 2009). Understanding how changes in site conditions and landscape transformations modify the diversity of their functional features is necessary for the prediction of changes in bee communities (Lavorel & Garnier, 2002; Forrest et al., 2015; Twed et al., 2019). This will make it possible to protect and restore valuable habitats through the implementation of suitable methods of management, both at local habitat and landscape scales.

Semi-natural ecosystems are important components increasing pollinator diversity in farmlands and are classic source habitats (Jauker et al., 2009; Banaszak et al., 2017). Undoubtedly, this applies to meadows and dry grassland communities located in agricultural landscapes, including xerothermic and sandy grasslands, which are some of the rarest habitat types of western and central Europe, seriously threatened by ecological succession (Janíšová et al., 2011; Diacon-Bolli et al., 2012; Habel et al., 2013; Valkó et al., 2018). The conservation of these unique habitats is important for the European Union (EU, 1992). Equally valuable are the moderately moist meadows of the phytosociological alliance Arrenatherion, characterized by a high floristic diversity. Such habitats, shaped over ages by traditional management (e.g., burning, hay harvesting or livestock grazing) are important components of local biodiversity and play the role of refugia for many groups of organisms, e.g., bees, beetles, butterflies, hoverflies, and orthopterans (Sjödin et al., 2008; Fartmann et al., 2012; Lucas et al., 2017; Banaszak & Twed, 2018). Old fields are another habitat type with a high insect diversity (Steffan-Dewenter & Tscharntke, 1995; Kovács-Hostýnszki et al., 2011; Kuussaari et al., 2011; Mandelik et al., 2012). Many publications report that old fields in rural landscapes are important habitats for bees and provide pollination services to many crop plants (Decourtye et al., 2010; Toivonen et al., 2016). Some studies confirm (Steffan-Dewenter & Tscharntke, 2001) that their attractiveness depends primarily on the stage of plant succession, which in temperate climates, is always advancing towards forest communities, less diverse in terms of bee fauna (Taki et al., 2013; Banaszak & Twed, 2018).

Landscape shaped by long-term agricultural use is the dominant type in Poland and other European countries. However, the economic transformations observed in the last 20 years have led in many areas to changes in land use, so that many formerly arable lands are no longer farmed (Pointereaux et al., 2008). In Poland, setting aside of arable fields is primarily associated with reduced soil fertility, decreased profitability of agricultural production, changes in the employment structure in agriculture, and urbanization of rural areas (Orlowski & Nowak, 2004). This phenomenon is particularly intensive in extensively used forests, where inhabitants frequently abandon small patches of mid-forest open habitats formerly used for livestock grazing or as arable fields. This is also the case for Knyszyn Forest (total area 1267.02 km²), the second-largest forest in Poland (after Białowieża Forest). Abandoned farmlands are subject to ecological succession, which, in temperate climates, leads to the formation of forest communities (Banaszak & Twed, 2018); alternatively, they are afforested intentionally. The observed changes in land use will probably result in a loss of biodiversity, especially of species associated with open habitats (Faliński, 1986). That is why it seems necessary to intensify protection measures aimed at the conservation of diverse landscape structures. This is particularly important in simplified spatial units, such as landscapes of productive forests, in European climatic zones.

In our study we are testing the following hypotheses: (i) old fields located in wooded landscapes are equally attractive to bees as semi-natural habitats in agricultural landscapes; (ii) dominance of species and/or functional groups differs between wooded or agricultural landscapes due to their traits; (iii) increased forest cover and the presence of habitat barriers decrease species richness, abundance, and diversity of bees.

Materials and methods
Study sites

Our study sites were located in northern and north-eastern Poland (Fig. 1). We conducted research in two types of landscape: A = agricultural (arable fields ≥70% of site area); B = wooded (forests and groups of trees covering ≥70% of the site area). The study sites in farmlands were located in the Kuyavia region (Kujawy) and the Chelmno region (Ziemia Chelmnińska) in northern Poland, which are dominated by wheat, triticale, oilseed rape, and maize fields (Central Statistical Office of Poland, 2019). The woodland sites were situated in the Knyszyn Forest (Puszcza Knyszyska, north-eastern Poland), where forest communities cover 83.1% of the area, mostly fresh (= moderately moist) coniferous forest Carici digitatae-Piceetum (206.37 km², 26.2%), mixed coniferous forest Serratulo-Piceetum (1,12.51 km², 14.3%), and fresh pine forest Peucedano-Pinetum (93.98 km², 11.9%) (Łaska, 2008). In Kuyavia, soils are generally fertile, especially the complex of the so-called ‘Kuyavian black soils’, which cover large areas.

In contrast, soils in Knyszyn Forest are generally poor in nutrients, with large areas covered by loose, slightly clayey podzols formed on sand (Czerwiński, 1995).

We compared 15 habitats in farmlands (sites 1–15) and 15 in wooded landscapes (sites 16–30) (see Supporting information, Table S1). In the farmlands, we investigated xerothermic grasslands, sandy grasslands, and moderately moist meadows, in wooded landscapes we studied old fields, which were most similar in respect of site conditions (high insolation and, in most cases, a high diversity of light-demanding species, including bee forage plants). The sites varied in stages of ecological succession and area (2325–71424 m²). The old fields were formerly used for cultivation of cereals, mostly rye and buckwheat (about 5–10 years ago), but since then, they have been subjected to ecological succession. Old fields in wooded landscapes accounted for 0–20% of the total area. Flowering herbs in old fields were mostly synanthropic plant species, such as Anchnusa officinalis L. and Echium vulgare L. in wooded landscapes, and Achillea millefolium L. and Daucus carota L. in farmlands. The dominant grass species were Arrhenatherum elatius (L.) P.B. ex J. et C. Presl, Dactylis glomerata L., and Elymus repens (L.) Gould,
Figure 1 Map of the study areas (A1 and A2 = agricultural landscape; B = wooded landscape). [Colour figure can be viewed at wileyonlinelibrary.com].
while among woody species, *Pinus sylvestris* L. and *Picea abies* (L.) Karsten.

**Local environmental factors**

At each site, we determined the local environmental factors (predictors: C1-C5). All plant species were recorded in the areas, including the transects analysed. Floristic surveys were carried out twice: in spring (May) and in summer (July). On this basis, we estimated the proportion (of area) covered by flowering plants, which are potential sources of bee forage (C1). Simultaneously, we measured site area (C2) on the basis of aerial photographs on a scale of 1:5000, using the open-source Geographic Information System QGIS Desktop 2.18.21 (QGIS Development Team, 2019) and direct field research. Moreover, using a nominal scale, we determined the stage of succession (C3) as 0 = early succession (trees and shrubs <50% of site area) or 1 = late succession (trees and shrubs >50% of site area) and the management regime (C4) as 0 = no management or 1 = managed habitats (protection as a nature reserve or landscape park). Since previous studies indicate that at least some bee species are affected not only by artificial barriers such as buildings but also by natural barriers such as forests (Bhattacharya et al., 2003; Farwig et al., 2009), we also assessed the occurrence of habitat barriers (C5): 0 = open site, with only single shrubs/trees, no forest as flight barriers within 100 m; 1 = single houses or allotments with built structures or few shrubs/trees as low flight barriers within 100 m; 2 = dense forest and scrub. We calculated this variable based on the surrounding area at each cardinal direction (north, east, south, west) of the site’s borders. The scores of all four directions were summed up to obtain a single score for each site, with 0 being the lowest, and 8 being the highest possible score (after Fischer et al., 2016).

The characteristics of the study sites are presented in Table S1 (see Supporting information), while Table S2 (see Supporting information) lists the recorded bee forage plant species (producing pollen and nectar). Names of plant species follow the *Flora Europaea* (Rutkowski, 2004).

**Landscape factors**

At each site, we also determined landscape factors (predictors: C6 and C7). Landscape analysis was conducted on the basis of aerial photographs on a scale of 1:5000 and direct measurements in the field. Around each site, we designated a buffer zone of 200 m long and 1 m wide (Banaszak, 1980). We used an aerial photograph on a scale of 1:5000, using the open-source Geographic Information System QGIS Desktop 2.18.21 (QGIS Development Team, 2019) and direct field research. Moreover, using a nominal scale, we determined the stage of succession (C3) as 0 = early succession (trees and shrubs <50% of site area) or 1 = late succession (trees and shrubs >50% of site area) and the management regime (C4) as 0 = no management or 1 = managed habitats (protection as a nature reserve or landscape park). Since previous studies indicate that at least some bee species are affected not only by artificial barriers such as buildings but also by natural barriers such as forests (Bhattacharya et al., 2003; Farwig et al., 2009), we also assessed the occurrence of habitat barriers (C5): 0 = open site, with only single shrubs/trees, no forest as flight barriers within 100 m; 1 = single houses or allotments with built structures or few shrubs/trees as low flight barriers within 100 m; 2 = dense forest and scrub. We calculated this variable based on the surrounding area at each cardinal direction (north, east, south, west) of the site’s borders. The scores of all four directions were summed up to obtain a single score for each site, with 0 being the lowest, and 8 being the highest possible score (after Fischer et al., 2016).

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Where *H* is heterogeneity, *n*<sub>i</sub> is the area of individual types of aerial objects, and *N* is the total investigated area.

Forest cover in the landscape (%) is the area of forests and groups of trees in the buffer zone divided by the total buffer zone area (see Supporting information, Table S1).

**Insect sampling**

Field research was conducted in 2016 (six sites in farmlands), 2017 (15 sites in wooded landscapes), and 2018 (nine sites in farmlands). The phenological period in eastern Poland is delayed by approximately 2 weeks in relation to the central part of the country, and therefore, research was conducted in May and July (once a month) to collect the maximum number of both spring and summer species.

The insects were collected when the weather was favourable for bee activity, i.e., with no or little wind (<3 on the Beaufort scale) (Krauss et al., 2009). During our study, the temperature was always above 16°C, and on most days did not exceed 25°C.

At each site, bees were collected using the transect method (transects 200 m long and 1 m wide) (Banaszak, 1980). We used a sweep net by searching on flowers and in favourite nesting sites of bees. Bee collection along each transect lasted about 30 min. The number of delimited transects was adjusted to the site area: 0 < 10 000 m<sup>2</sup> (no more than two transects), 10 000–30 000 m<sup>2</sup> (no more than three transects), or >30 000 m<sup>2</sup> (no more than four transects). In total, 180 samples were taken, 90 in spring and 90 in summer (see Supporting information, Table S1). Bumblebees and other easily distinguished bee species were identified alive (McFrederick & LeBuhn, 2006). Other caught specimens were mounted and identified to species level. The species of the *Bombus lucorum*-complex (Bossert, 2015) are not distinguishable by morphological features, and *B. lucorum* and *B. terrestris* are easily confused (Wolf et al., 2010); therefore, data on the occurrence of bumblebees of the subgenus *Bombus* Latreille, 1802 = *Terrestrisbombus* Vogt, 1911 were summarized.

Functional and ecological classifications of bees followed earlier publications of our research team (Banaszak & Twerd, 2018; Twerd et al., 2019; Twerd & Banaszak-Cibicka, 2019). For each species, we determined social behaviour (solitary, eusocial, cleptoparasitic), nest substrate (soil, hive, cavity), floral specificity (oligolectic, polylectic), occurrence in Poland (rare vs. common), and body size (small <8 mm, medium 8–15 mm, large > 15 mm) (Table 1). Species names follow Kuhlmann et al. (2020) (see Supporting information, Table S3).

**Statistical analysis**

To assess the representativeness of the Apiformes caught in agricultural and wooded landscapes, and to analyse their species richness, we generated rarefaction curves (Gotelli & Colwell, 2001), using the EstimateS 9.1.0 software (Colwell, 2013). In addition, to estimate the true species diversity, we used the Chao 1 estimator (Chao, 1984) with 1000 randomizations.

The frequency of each species was expressed as percentage, calculated by dividing the number of sites of the given landscape type (agricultural/wooded) in which the species occurred
Nest substrate

lme4 package for the GLMMs (Bates conducted in R version 3.6.1 (R Core Team, 2019), using the modelswithandwithoutthetestedeffect.Alldataanalyseswere

relations was assessed with the likelihood-ratio test, comparing freedom method. Thesignificanceofspatialandtemporalcor-

ationsamong collected data, GLMMs with Poisson distribution

determine differences in species richness, abundance, and diver-

(GLM) was used to visualize the effects of the analysed factors

resulted in 208 species of Apiformes being recorded in farmlands,

by the total number of sites of this landscape type (agricul-

tural/wooded).

Numerical analysis of the collected data was performed using

the CANOCO software v. 4 (ter Braak & Šmilauer, 1998). To

assess the influences of the analysed environmental variables

(predictors: C1-C7) on bee occurrence, we used redundancy

analysis (RDA). Data on individuals were transformed logarith-

mically [log(x)]. To assess the significance of the tested variables

and canonical axes, a Monte Carlo permutation test with 1000

repeats was performed. We assessed only the influence of sta-

tistically significant variables (P < 0.05). A general linear model

(GLM) was used to visualize the effects of the analysed factors

on species richness, abundance and diversity of wild bees.

To determine the strength of the relationship of a species with

the given landscape (agricultural vs. wooded), we calculated the

indicator values (IndVal) of bee species recorded there (Dufrêne & Legendre, 1997). The IndVal method measures the strength

of the association of a given species with a given environment

on the basis of abundance and constancy of occurrence of the

species in samples. If IndVal was higher than 0.25, the

species was classified as strongly associated with the given

habitat. The significance of IndVals was confirmed by a Monte

Carlo test with 10 000 permutations. The above analyses were

performed in the R software environment (version 3.6.1; R Core

Team, 2019), using the vegan (Oksanen et al., 2011) and labdsv

(Roberts, 2010) packages.

Generalized linear mixed models (GLMMs) were applied to

determine differences in species richness, abundance, and diver-

sity of bees of the distinguished groups in agricultural and

wooded landscapes. To account for temporal and spatial corre-

lations among collected data, GLMMs with Poisson distribution

and canonical log link were used. Site, time, and observer were

considered as random effects, while landscape was considered as

fixed effect. In our model, the level recorded in farmland was the

reference level; P-values were calculated using Wald’s degrees

of freedom method. The significance of spatial and temporal cor-

relations was assessed with the likelihood-ratio test, comparing

models with and without the tested effect. All data analyses were

conducted in R version 3.6.1 (R Core Team, 2019), using the

lme4 package for the GLMMs (Bates et al., 2015).

Table 1 Description of the bee functional traits used in this study

| Trait                | Types   | Definition                                                                 |
|----------------------|---------|---------------------------------------------------------------------------|
| Social behaviour     | Solitary| Each female constructs her own nest and provides food for her offspring  |
|                      | Eusocial| Females nesting and breeding in colonies (e.g., bumble bees, some Halictidae species) |
| Nest substrate       | Soil    | Females lay their eggs in nests of specific host species                  |
|                      | Hive    | Nest is excavated in the soil (majority of species in Europe)             |
|                      | Cavity  | Nest is excavated in pithy stems and pre-made cavities                    |
| Floral specificity   | Oligolectic| Pollen specialists: Collect pollen from one plant family or genus     |
|                      | Polylectic| Pollen generalists: Forage from a very wide spectrum of unrelated plants for pollen |
| Occurrence in Poland | Rare    | Species that were assigned the threat category in Poland by Banaszak (2004) |
|                      | Common  | Species without the threat category by Banaszak (2004)                     |
| Body size            | Small < 8 mm| The mean full body length of females and males (frons to tip of the abdomen) were recorded in millimetres; for bumblebees, the size of female workers and queens were used for the analysis |
|                      | Medium 8–15 mm|                                                                      |
|                      | Large > 15 mm|                                                                      |

Results

Bee species composition

In total, we recorded 250 species of wild bees (Hymenoptera: Apoidea: Apiformes) of 38 genera, represented by 10 101 individuals. They account for about 52% of all bee species reported for Poland. In terms of species richness, the major families were Apidae (65 species; 26.0%), Halictidae (57; 22.8%), Megachilidae (51; 20.4%), Andrenidae (46; 18.4%), Colletidae (24; 9.6%), and Melittidae (7; 2.8%). In terms of abundance, most of the bees represented the families Apidae (4039 individuals; 40.0%), Andrenidae (2268; 22.5%), Halictidae (1687; 16.7%), Megachilidae (878; 8.7%), Colletidae (699; 6.9%), and Melittidae (530; 5.2%). In the collected material, we found 47 species (18.8%) that are infrequent in Poland. One of them, Amegilla quadrifasciata, is classified as critically endangered (CR) according to the Polish Red Data Book of Animals (Banaszak & Celary, 2004). Taxonomic and ecological characteristics of the bees recorded in the agricultural and wooded landscapes are summarized in the Supporting information (Table S3).

Species richness of bees in agricultural and wooded landscapes

In farmlands, 208 species of Apiformes were found, whereas in wooded landscapes, 176. The species accumulation curves did not reach saturation (Fig. 2), indicating that some species remained undetected. The expected species richness (Chao 1 estimator) in agricultural landscapes reached 240.10 (95% CI = 221.79–282.75) compared to 200.14 in wooded landscapes (95% CI = 185.31–238.60) (see Supporting information, Table S4).

Most of the species possible to detect in farmlands were recorded in the case of the Apidae, while the least of the Melitidiae. The same applies to wooded landscapes (see Supporting information, Table S4). After interpolation to the same number of recorded individuals, the families Colletidae, Andrenidae, Halictidae, Megachilidae, and Apidae were characterized by higher observed and estimated species richness in farmlands than in wooded landscapes (Fig. 3).
Factors affecting bee occurrence

Detailed RDA assessed effects of the analysed factors on bee species occurrence. We found that six of the variables affected it significantly: forest cover (C7), habitat barriers (C5), stage of succession (C3), management regime (C4), cover of bee forage plants (C1), and heterogeneity (C6) (Fig. 4 and Table 2). Visualization of the data with the use of GLM showed that species richness, abundance, and diversity of bees decreased with increasing values of factors such as C3, C5, and C7. Simultaneously, managed habitats located in heterogeneous landscapes were characterized by the highest values of the analysed indices (Fig. 4).

Indicator species of bees of agricultural and wooded landscapes

We distinguished 48 indicator species (IndVal method): 23 for agricultural landscapes and 25 for wooded landscapes (Table 3).
The abundance of indicator species associated with farmlands varied from 6 to 264 individuals at individual sites, while in wooded landscapes, it ranged from 10 to 587 individuals. Their frequency ranged from 33.3% to 86.7% in farmlands and from 33.3% to 100% in wooded landscapes (Table 3).

The genera *Andrena* and *Lasioglossum* were represented by the largest number of indicator species in farmlands (5 species each), with a total abundance of 490 and 242 individuals, respectively. In wooded landscapes, the genus *Andrena* included the largest number of indicator species (5 species, 147 individuals), followed by *Bombus* (4 species, 829 individuals) (Table 3).

**Taxonomic and functional diversity of bees (agricultural vs. wooded landscapes)**

In terms of species richness and abundance, species of the family Colletidae prevailed in wooded landscape as compared to agricultural landscape. By contrast, in agricultural landscapes, the Andrenidae reached higher species richness, abundance, and diversity, while for Halictidae, we observed higher species richness compared to wooded landscapes. On the other hand, both the abundance and diversity of species of the family Melittidae were higher in wooded landscape compared to agricultural

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**Figure 4** Ordination biplot diagram of redundancy analysis (RDA) for the Apiformes in agricultural and wooded landscapes. Vector labels refer to environmental variables. Eigenvalues: Axis 1–0.169; axis 2–0.076. The diagram explains 39.1% of the total variance (sum of all canonical eigenvalues: 0.391; sum of all eigenvalues: 1.000; 0.391/1.000 = 0.391, i.e., 39.1%). [Colour figure can be viewed at wileyonlinelibrary.com].

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lanscape. Also, bees of the family Apidae were more abundant there (Fig. 5 and Table 4).

Eusocial species were more diverse in farmlands, but their abundance was significantly higher in wooded landscapes. Furthermore, species nesting in cavities in farmlands reached higher values of species richness, abundance, and diversity, while soil-nesting species showed a higher abundance than in wooded landscape. Simultaneously, in agricultural landscape, higher values of diversity were recorded for hive-nesting species and small-sized bees. In contrast, the abundance of hive-nesting species and large-sized bees was significantly higher in wooded landscapes than in agricultural landscape. Similarly, species that are rare in Poland, in wooded landscapes reached higher species richness, abundance, and diversity, while in agricultural landscapes, common species prevailed (Figs 5 and 6 and Table 5).

Discussion

We found that old fields located in wooded landscapes are as attractive to bees as semi-natural habitats in farmlands. This was reflected in the lack of significant differences in species richness, abundance, and diversity of Apiformes between the compared landscape types (agricultural vs. wooded). This suggests that the different habitat types can be colonized by diverse bee communities, irrespective of the landscape context and the land use history (semi-natural habitats vs. old fields), as long as they provide the necessary environmental conditions (i.e., suitable sites for nesting, doing courtship flights, and feeding). We show that even in contrasting and very differently managed landscape types, the values of variables describing the structure of bee communities can be similar. Likewise, Harrison et al. (2019) did not find any significant differences in bee species richness and abundance among the three landscape types agricultural, wooded, and urban areas, with different levels of human disturbance. Similar to our study, these authors observed differences in species composition and occurrence of individual functional groups. The low difference in the overall species richness of bees, with simultaneous differences in species composition, confirms that some species tolerate or even prefer disturbed habitats (Dornelas et al., 2014; Newbold et al., 2015; Harrison et al., 2019).

Results of this study confirm the general rule that increasing forest cover and contribution of habitat barriers are associated with decreasing species richness, abundance, and diversity of bees. In this context, our results emphasize the importance of open habitats – at early stages of succession, with a high proportion of bee forage plants – for occurrence of Apiformes. Proper management of such areas can support maintaining of pollination services in both agricultural and wooded landscapes.

The influence of the above-mentioned factors concerned the whole area, irrespective of site location in the landscape. In our study, this was caused by both increasing forest cover and by changes in the dominant vegetation type. The wooded landscapes were dominated by communities of fresh coniferous forests, mixed coniferous forests, and fresh pine forests, relatively poor in bee forage plants (Cierzniak, 2003). We found that the major factor increasing the natural resources of bees was habitat management aimed to limit the succession of woody vegetation and to increase landscape heterogeneity.

Bold values were significant (P < 0.05). VIF = variance inflation factor.

Table 2 Results of stepwise selection of variables by redundancy analysis (RDA) and a Monte Carlo permutation test – Analysis of significance of effects of the studied variables on the occurrence of different species of Apiformes

| Variable                                      | Results of redundancy analysis and Monte Carlo test | Level of significance | Variance | % of explained variance | VIF |
|-----------------------------------------------|---------------------------------------------------|-----------------------|----------|-------------------------|-----|
| C7: Landscape buffer: Forest cover            |                                                   | 0.001                 | 0.16     | 5.217                   | 8.835 |
| C5: Occurrence of habitat barriers            |                                                   | 0.001                 | 0.13     | 4.137                   | 5.011 |
| C3: Stage of succession                       |                                                   | 0.001                 | 0.12     | 3.946                   | 3.827 |
| C4: Management regime                         |                                                   | 0.001                 | 0.11     | 3.725                   | 3.954 |
| C1: Cover of bee forage plants                |                                                   | 0.001                 | 0.09     | 2.970                   | 2.811 |
| C6: Landscape buffer: Heterogeneity           |                                                   | 0.004                 | 0.08     | 2.519                   | 2.117 |
| C2: Site area                                 |                                                   | 0.582                 | 0.03     | 0.906                   | 1.206 |

Wild bees of agricultural and wooded landscapes

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Table 3 Associations of individual species with the studied landscapes (A = agricultural; B = wooded): Comparison of statistically significant indicator values (IndVal > 0.25) for indicator species of wild bees

| Landscape type | Species              | IndVal | P   | A: Abundance | A: Frequency (%) | B: Abundance | B: Frequency (%) |
|---------------|----------------------|--------|-----|--------------|------------------|--------------|------------------|
| A             | Colletes daviesanus  | 0.759  | 0.001 | 78           | 86.66            | 11           | 33.33            |
|               | Andrena vaga         | 0.745  | 0.003 | 264          | 43               |              |                  |
|               | Lasioglossum pauxillum | 0.679 | 0.010 | 91           | 25               | 46.66        |                  |
|               | Bombus hortorum      | 0.689  | 0.009 | 81           | 80.00            | 13           | 60.00            |
|               | Andrena nitida       | 0.733  | 0.001 | 28           | 73.33            |              |                  |
|               | Lasioglossum calceatum | 0.606 | 0.036 | 72           | 15               | 46.66        |                  |
|               | Osmia bicorinis      | 0.586  | 0.008 | 28           | 7                | 20.00        |                  |
|               | Colletes cunicularius | 0.560 | 0.041 | 84           | 26               | 40.00        |                  |
|               | Andrena helvola      | 0.666  | 0.002 | 47           | 66.66            |              |                  |
|               | Andrena ventralis    | 0.666  | 0.002 | 78           |                  |              |                  |
|               | Nomada lathburiana   | 0.633  | 0.006 | 114          | 6                | 20.00        |                  |
|               | Heniades truncorum   | 0.613  | 0.002 | 23           | 2                | 6.66         |                  |
|               | Halictus quadriinctus | 0.606 | 0.019 | 70           | 7                | 33.33        |                  |
|               | Lasioglossum lucidulum | 0.535 | 0.031 | 49           | 12               | 40.00        |                  |
|               | Halictus rubicundus  | 0.500  | 0.046 | 15           | 5                | 33.33        |                  |
|               | Osmia bidentata      | 0.517  | 0.030 | 25           | 60.00            | 4             | 20.00            |
|               | Ceratina cyannea     | 0.494  | 0.048 | 14           | 3                |              |                  |
|               | Andrena synadelpha   | 0.400  | 0.016 | 73           | 40.00            |              |                  |
|               | Lasioglossum aeratum | 0.400  | 0.021 | 6            |                  |              |                  |
|               | Lasioglossum parvulum | 0.400 | 0.015 | 24           |                  |              |                  |
|               | Osmia aurulenta      | 0.400  | 0.019 | 36           |                  |              |                  |
|               | Coelioxys elongata   | 0.333  | 0.043 | 14           | 33.33            |              |                  |
|               | Hoplitis papaveralis | 0.333  | 0.045 | 8            |                  |              |                  |
| B             | Epeolus variegatus   | 0.918  | 0.001 | 9            | 26.66            | 102          | 100.00           |
|               | Bombus ruderarius    | 0.916  | 0.001 | 3            | 20.00            | 159          |                  |
|               | Bombus pascuorum     | 0.743  | 0.001 | 203          | 100.00           | 587          |                  |
|               | Dasypoda hirtipes    | 0.637  | 0.046 | 88           | 80.00            | 155          |                  |
|               | Melitta leporina     | 0.813  | 0.003 | 33           | 73.33            | 223          | 93.33            |
|               | Colletes biocadians  | 0.782  | 0.001 | 25           | 46.66            | 130          |                  |
|               | Trachusa byssina     | 0.866  | 0.001 | —            | —                | 81           | 86.66            |
|               | Andrena hattorfiana  | 0.768  | 0.001 | 6            | 13.33            | 47           |                  |
|               | Anthidium punctatum  | 0.800  | 0.001 | —            | —                | 25           | 80.00            |
|               | Colletes marginatus  | 0.800  | 0.001 | —            | —                | 21           |                  |
|               | Tetraloniella salcanae | 0.733 | 0.001 | —            | —                | 105          | 73.33            |
|               | Anthidium strigatum  | 0.559  | 0.034 | 9            | 40.00            | 29           |                  |
|               | Coelioxys concideae  | 0.559  | 0.041 | 9            | 46.66            | 29           |                  |
|               | Pararugus calcaratus | 0.638  | 0.008 | 4            | 13.33            | 89           | 66.66            |
|               | Colletes similis     | 0.507  | 0.016 | 5            | 20.00            | 16           |                  |
|               | Nomada roberjeotiana | 0.541  | 0.005 | 3            | 13.33            | 28           | 60.00            |
|               | Nomada flavopicta    | 0.529  | 0.020 | 4            | 20.00            | 30           |                  |
|               | Megachile versicolor | 0.504  | 0.046 | 4            | 26.66            | 21           |                  |
|               | Andrena nigriceps   | 0.533  | 0.003 | —            | —                | 18           | 53.33            |
|               | Andrena assimilis    | 0.466  | 0.007 | —            | —                | 50           | 46.66            |
|               | Andrena thoracica    | 0.466  | 0.007 | —            | —                | 18           |                  |
|               | Bombus humilis       | 0.466  | 0.005 | —            | —                | 73           |                  |
|               | Andrena denticulata  | 0.400  | 0.016 | —            | —                | 14           | 40.00            |
|               | Bombus schrencki     | 0.333  | 0.042 | —            | —                | 10           | 33.33            |
|               | Hylaeus nigritus     | 0.333  | 0.037 | —            | —                | 22           |                  |

Species frequency (%) is the proportion of study sites (within the given landscape type) where the species was recorded.

Spring was largely provided by *Salix* spp., found near lakes and small watercourses, as well as fruit trees growing singly or in larger groups. Many of the bee species nesting in the ground prefer permeable sandy or loamy soils, with good light conditions (Cane, 1991), which prevailed in agricultural landscapes. Another important factor is the occurrence of many suitable nesting sites, in particular sandy dirt roads, without vegetation, which are favourable for nest aggregations. Many of the *Andrena* species are solitary, but have a highly gregarious behaviour, sometimes aggregating hundreds of nests within
one square meter (Michener, 2007). Simultaneously, roadsides elevated above the surface of roads and fields are usually drier, while small escarpments at the borders between roadsides and fields are favourable for soil nests. Also, grassland habitats in agricultural landscapes are often dominated by Halictidae; many of them are thermophilous species, which nest in open, sunny habitats (Banaszak et al., 2006; Banaszak & Twerd, 2018).

We found that in wooded landscapes, eusocial, hive-nesting, and large-sized species increased in abundance. This was due to the large contribution of Bombus spp., which often avoid sunny sites and prefer forest-steppe habitats (Banaszak & Twerd, 2018). More shaded sites provide shelter for large-sized species, which are less active at higher temperatures, in contrast to small-sized bees (Danforth et al., 2019). The species richness

Figure 5 Effect of landscape type on species richness and abundance (mean ± SE) of wild bee families and on bees grouped based on functional characteristics: Behaviour and nest substrate. White = agricultural landscape; grey = wooded landscape. *P < 0.05; **P < 0.01; ***P < 0.001.
Table 4 Effects of landscape type (agricultural vs. wooded) on species richness, abundance, and diversity of wild bees

| Wild bees       | Richness                        | Abundance                     | Diversity (Shannon index) |
|-----------------|---------------------------------|-------------------------------|---------------------------|
|                 | Estimate ± CI                  | Z                              | P                         | Estimate ± CI                  | Z                              | P                         |
| Total           | 0.90 ± 1.16                     | −1.43                          | 0.152                     | 1.29 ± 1.39                   | 1.54                           | 0.123                     | −0.15 ± 0.19                  | −1.49                          | 0.137                     |
| Family          |                                 |                               |                           |                                 |                               |                           |                                 |                               |                           |
| Colletidae      | 1.55 ± 1.53                     | 2.02                           | **0.044**                 | 2.07 ± 1.59                   | 3.07                           | **0.002**                 | 0.22 ± 0.34                   | 1.26                           | 0.206                     |
| Andrenidae      | 0.83 ± 1.27                     | −2.50                          | **0.033**                 | 0.74 ± 1.67                   | −2.15                          | **0.032**                 | −0.41 ± 0.38                  | −2.13                          | **0.033**             |
| Halictidae      | 0.79 ± 1.25                     | −2.09                          | **0.037**                 | 0.94 ± 1.68                   | −0.24                          | 0.811                     | −0.19 ± 0.30                  | −1.26                          | 0.209                     |
| Melittidae      | 1.32 ± 1.59                     | 1.18                           | 0.237                     | 3.26 ± 1.84                   | 3.79                           | <0.001                    | 0.13 ± 0.15                   | 1.98                           | **0.047**             |
| Megachilidae    | 0.86 ± 1.46                     | −0.78                          | 0.434                     | 1.17 ± 1.73                   | 0.56                           | 0.576                     | −0.28 ± 0.42                  | −1.30                          | 0.192                     |
| Apidae          | 1.03 ± 1.24                     | 0.30                           | 0.763                     | 2.37 ± 1.58                   | 3.72                           | <0.001                    | −0.08 ± 0.23                  | −0.66                          | 0.509                     |

The table shows results of generalized linear mixed models (GLMMs), taking into account spatial and temporal correlations among the collected data; bold estimates indicate significant effects ($P < 0.05$).

Figure 6 Effect of landscape type on species richness and abundance (mean ± SE) of wild bees grouped based on functional characteristics: Floral specificity, body size, and occurrence in Poland. White = agricultural landscape; grey = wooded landscape. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. © 2020 The Authors. Agricultural and Forest Entomology published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

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Table 5 Effects of landscape type (agricultural vs. wooded) on species richness, abundance, and diversity of functional groups and species with defined characteristics

| Ecological characteristics | Agricultural vs. wooded landscape | Abundance | Diversity (Shannon index) |
|----------------------------|-----------------------------------|-----------|--------------------------|
|                            | Richness Estimate ± CI Z P        | Abundance Estimate ± CI Z P | Diversity Estimate ± CI Z P |
| Behaviour                  |                                    |           |                          |
| Solitary                   | 0.90 ± 1.15 -1.45 0.146            | 0.91 ± 1.33 -0.64 0.523      | -0.21 ± 0.29 -1.38 0.167    |
| Eusocial                   | 0.98 ± 1.29 -0.12 0.902            | 2.18 ± 1.31 5.65 <0.001      | -0.41 ± 0.22 -3.63 <0.001   |
| Cleptoparasitic            | 0.94 ± 1.43 -0.36 0.720            | 1.06 ± 1.78 0.19 0.849       | 0.04 ± 0.38 0.21 0.836      |
| Nest substrate             |                                    |           |                          |
| Soil                       | 0.92 ± 1.15 -1.20 0.231            | 0.90 ± 1.34 -1.79 0.037      | -0.18 ± 0.29 -1.17 0.241    |
| Cavity                     | 0.70 ± 1.31 -2.58 0.010            | 0.66 ± 1.63 -1.68 0.043      | -0.28 ± 0.24 -2.21 0.027    |
| Hive                       | 0.99 ± 1.27 -0.12 0.904            | 2.58 ± 1.44 5.07 <0.001      | -0.21 ± 0.21 -1.90 0.047    |
| Floral specificity         |                                    |           |                          |
| Oligolectic                | 1.06 ± 1.26 0.51 0.607             | 1.48 ± 1.54 1.71 0.073       | -0.13 ± 0.33 -0.78 0.435    |
| Polylectic                 | 0.86 ± 1.17 -1.96 0.750            | 1.22 ± 1.38 1.19 0.233       | -0.18 ± 0.20 -1.78 0.076    |
| Body size                  |                                    |           |                          |
| Small                      | 0.95 ± 1.33 -0.37 0.708            | 1.22 ± 1.53 0.90 0.547       | -0.28 ± 0.24 -2.24 0.025    |
| Medium                     | 0.96 ± 1.19 -0.50 0.615            | 1.11 ± 1.35 0.70 0.482       | -0.21 ± 0.27 -1.48 0.138    |
| Large                      | 0.78 ± 1.39 -1.43 0.153            | 2.34 ± 1.62 3.46 0.001       | -0.17 ± 0.21 -1.59 0.112    |
| Occurrence                 |                                    |           |                          |
| Rare                       | 1.99 ± 1.99 1.96 0.039             | 2.59 ± 2.73 2.26 0.003       | 0.36 ± 0.35 2.01 0.044      |
| Common                     | 0.86 ± 1.15 -2.11 0.035            | 1.23 ± 1.38 -2.29 0.007      | -0.17 ± 0.19 -1.98 0.046    |

The table shows results of generalized linear mixed models (GLMMs), taking into account spatial and temporal correlations among collected data; bold estimates indicate significant effects (P < 0.05).

of bumblebees in both landscapes, however, was comparable: 14 species in farmlands and 18 in wooded landscapes. Extensively cultivated plots, such as coniferous forest plantations or arable fields, are often visited by large bees because they can fly long distances and thus can use various types of plant cover, both as nesting sites and for foraging (Osborne et al., 2008; Hagen et al., 2011). This applies mostly to polylectic bees, which can make use of a wide spectrum of flowering plants as their food sources. The strong isolation of favourite sites in wooded habitats limits the possibilities of migration of small-sized species, which feed within a radius of 150–600 m from their nesting sites (Gathmann & Tscharntke, 2002). That is why small-sized bees prevailed in the habitats located in agricultural landscapes, which in this case, were characterized by a higher degree of heterogeneity as compared to wooded habitats. This study, solitary bees constituted the majority of this group.

The faunistic value of a given area is determined mostly by the number of recorded rare species (Williams, 2000), but these species do not have any significant effect on their ecosystem services. We found that rare species in Poland, in wooded landscapes, reached higher species richness, abundance, and diversity. In contrast, farmlands were dominated by common species. Similar conclusions have been drawn by Harrison et al. (2019), who found fewer rare bee species in agricultural than in wooded landscapes. In our study, this probably resulted from the fact that Knyszyn Forest is a unique ecosystem, characterized by a significantly lower level of human disturbance than farmlands of central Poland.

Some studies confirm that sufficiently large semi-natural habitats, including protected areas, are crucial for the survival of pollinators in farmlands (Hendrickx et al., 2007; Billeter et al., 2008) and thus for the provision of pollination services (Klein et al., 2007; Kremen et al., 2007). Results of the present study show, however, that a similar role can be played also by old fields. In agreement with Banaszak and Cierziak (2002), we did not detect any significant relationship between the area of study sites and species richness, abundance, and diversity of bees, at least within the analysed scale from 0.23 to 7.14 ha. This means that even small areas can be attractive to bees. This important finding should be taken into account in landscape planning and management, concerning both agricultural and wooded landscapes.

Conclusions

The protection of semi-natural habitats should consist of activities aimed to restore or continue extensive farming in meadows of high conservation value. In old fields, it is also important to consider the possibility of transforming them into partly protected ‘ecological areas’. A detailed analysis of the factors that tend to increase insect diversity in agricultural and wooded landscapes makes it possible to develop guidelines aimed to improve the quality of those areas for the local fauna, including threatened species. One of the ways to reach these aims is the indication of gene resources.

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Data availability statement

The data that support the findings of this study are openly available in [Mendeley Data] at https://data.mendeley.com/datasets/p6v5b9ct9v/draft?ar=2f96d02f-36f9-45e3-a032-d23d9ae0b598, reference number [doi:10.17632/p6v5b9ct9v.2].

Supporting information

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

Appendix S1: Supporting Information

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