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Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and surrounding landscape in European arable fields

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Abstract

Farmland species provide key ecological services that support agricultural production, but are under threat from agricultural intensification and mechanization. In order to design effective measures to mitigate agricultural impact, simultaneous investigations of different taxonomic groups across several regions are required. Therefore, four contrasting taxonomic groups were investigated: plants, earthworms, spiders and bees (wild bees and bumblebees), which represent different trophic levels and provide different ecological services. To better understand underlying patterns, three community measurements for each taxonomic group were considered: abundance, species richness and species composition. In four European regions, ten potential environmental drivers of the four taxonomic groups were tested and assigned to three groups of drivers: geographic location (farm, region), agricultural management (crop type, mineral nitrogen input, organic nitrogen input, mechanical field operations and pesticide applications) and surrounding landscape in a 250 m buffer zone (diversity of habitats in the surroundings, proportion of arable fields and proportion of non-productive, non-woody habitats). First, the variation in abundance, species richness and species composition from 167 arable sites was partitioned to compare the relative contribution of the three groups of drivers (geographic location, agricultural management and surrounding landscape). Second, generalized linear mixed-effects models were applied to estimate the effect of the individual explanatory variables on abundance and species richness. Our analysis showed a dominant effect of geographic location in all four taxonomic groups and a strong influence of agricultural management on plants, spiders and bees. The effect of the surrounding landscape was of minor importance and inconsistent in our data. We conclude that in European arable fields, the avoidance of mineral nitrogen and pesticides is beneficial for biodiversity, and that species protection measures should take into account regional characteristics and the community structure of the investigated taxonomic groups.

Keywords

Abundance, Species richness, Species composition, Partitioning of variation, BioBio

1. Introduction

Although the production of agricultural goods depends, in part, on ecological services provided by farmland species, human activities often impair biodiversity (Hector and Bagchi, 2007; Sachs et al., 2009). Intensive agricultural management may deplete beneficial species that contribute to, for example, soil fertility, decomposition, biological control or pollination (Costanza et al., 1997). Such species are particularly threatened in arable fields, which face regular disturbances due to intensive management for optimized resource use and crop protection (Matson et al., 1997; Robinson and Sutherland, 2002).

Agri-environment schemes are implemented to mitigate the pressure on biodiversity and to promote farmland species. While they have frequently been shown to benefit farmland species, the magnitude of the effects has varied among studies (Batáry et al., 2010; Gibson et al., 2007). These ambiguous results have been attributed to differences in taxonomic groups, study regions and scales of investigation (Bengtsson et al., 2005). In addition, several studies have concluded that more detailed insights into the drivers of farmland species could be achieved if both landscape characteristics and management practices were considered (Batáry et al., 2011; Chaplin-Kramer and Kremen, 2012; Concepción et al., 2012a; Schweiger et al., 2005; Tscharntke et al., 2005).

Many studies of farmland species have been limited to only one or a few popular taxonomic groups. However, the effects of agricultural management and of landscape characteristics on a particular taxonomic group are likely to depend on its specific resource needs, such as food or habitat requirements (Aviron et al., 2009; Báldi et al., 2013; Kleijn et al., 2006; Schuldt and Assmann, 2010). In order to promote agricultural practices with targeted benefits for biodiversity, it is therefore important to evaluate their impacts on multiple taxonomic groups. Further, it may also be important to evaluate multiple community measurements such as abundance, species richness and species composition, as these may have different specific effects on ecological services (Isbell et al., 2011) and different sensitivities to the agricultural environmental drivers (Jeanneret et al., 2003; Worthen, 1996).

Here, we investigated plant, earthworm, spider and bee (wild bee and bumblebee) communities in 167 arable fields across four European regions. The four taxonomic groups were chosen because they have different habitat and food requirements, provide a range of ecological services and occupy different trophic levels. Plants, as primary producers and sessile organisms, depend on light, water and nutrients available on site. Plant abundance and species richness in arable fields have been found to decrease due to management intensity (mineral nitrogen input, pesticide applications) in numerous studies, e.g. Hyvönen and Salonen (2002) and Rassam et al. (2011). Further, plant diversity, mainly in field edges, is enriched by a higher amount of semi-natural habitats in the surrounding landscape (Concepción et al., 2012b; Kovács-Hostyánszki et al., 2011). Earthworms, as detritivores and soil organisms, contribute to soil fertility. They are positively affected by the application of solid manure, mulches and reduced tillage (Chan, 2001). Spiders are a widely distributed and highly abundant group of predators for which several studies have emphasized the significance of (perennial) vegetation structure (e.g. Gibson et al., 1992 or Schmidt and Tscharntke, 2005). Wild bees and bumblebees act as pollinators and are highly mobile. They depend on a continuous pollen and nectar supply in the wider landscape and on appropriate nesting sites (e.g. Kremen et al., 2007).

We tested how plant, earthworm, spider and bee communities in the same arable fields responded to explanatory variables representing geographic location, agricultural management and surrounding landscape. For all communities, abundance, species richness and species composition were considered to gain more information on community patterns than one measurement alone could provide. The four taxonomic groups were expected to differ in their responses, and that these differences were reflected in existing or missing correlations among the taxonomic groups. However, because arable fields are predominantly shaped by agricultural practices for the purpose of crop production, we hypothesized that management variables have a significant effect on the four taxonomic groups, independent of geographic location and surrounding landscape.

2. Materials and methods

2.1. Study sites

Data collection was part of the EU-FP7 project BioBio, which investigated and proposed a set of biodiversity indicators applicable for European farmland monitoring (Herzog et al., 2012). This study investigated 167 arable fields from four European regions: Marchfeld (Austria), Southern Bavaria (Germany), Gascony (France) and Homokhátság (Hungary).

Each region was an environmentally homogeneous area, representing either typical arable cropping or a combination of arable cropping and grassland-based livestock farming (Table 1). In each region of approximately 1000 km^2, between 14 and 16 study farms, half of them organic and half non-organic, were randomly selected. The whole area of these farms was mapped by classifying different habitat types according to primary life forms, environment and management (Bunce et al., 2008). One of four crop categories was assigned to each arable field: winter cereals, spring cereals, forage crops (e.g. lucerne, grass-clover) and others (e.g. oilseed rape). For each available crop category per farm, one field was randomly selected for species sampling.

2.2. Species sampling

In each randomly selected arable field, species of the four taxonomic groups were sampled from spring to early autumn in 2010 according to standardized protocols (Dennis et al., 2012). Sample locations were chosen such that edge effects were avoided. Plant surveys were conducted once, in a plot of 10 x 10 m. All species were recorded and their respective cover estimated. Cultivated crop species were excluded from the analysis except the forage crops. Earthworms were collected at three random locations per field, at one time. A solution of allyl isothiocyanate (0.1 g/l) was poured into a metal frame of 30 x 30 cm in order to encourage earthworms to move to the surface. Subsequently, earthworms were collected by hand from a 20 cm deep earth core. Identification and counting of earthworms species was conducted in the lab. Non-clitellates (juveniles and subadults) were excluded from the analysis. Spiders were sucked from the surface at three dates during the season from within five randomly located circular areas of 35.7 cm diameter per field using a modified leaf blower. The samples were frozen and adults were identified in the lab. Wild bee and bumblebee species were sampled during good weather conditions, i.e. during periods of sunshine when it was not too windy and the temperature was higher than 15 °C. Bees were sampled on three dates with a handheld net along a 100 x 2 m transect traversing the plant survey plot for 15 min, except in the Marchfeld region, where bees were sampled only twice due to bad weather. Honeybees (*Apis mellifera)* were excluded from the analysis.

2.3. Response variables

Three community measurements were calculated as response variables: abundance, species richness and species composition. Abundance was expressed as the percentage cover for plants and the total number of individuals per field for earthworms, spiders and bees. Species richness was calculated as the total number of species in a field. Species composition was quantified as the species list for each taxonomic group, accounting for abundance per field.

2.4. Explanatory variables

Potential environmental drivers were divided into three groups of variables for (1) geographic location, (2) agricultural management and (3) surrounding landscape.

Geographic location: Two variables, farm (fields belonged to 61 farms) nested within region (four groups), were assigned to each investigated field as descriptors of general geographic conditions. The variable farm accounted for general features of the farm (e.g. location, overall farming intensity or the crop rotation system). The variable region incorporated characteristics such as climatic conditions, soil properties and large-scale landscape features (e.g. exclusively arable cropping or mixed farming, occurrence of forest or water bodies) as well as historic processes of landscape changes.

Agricultural management: For all investigated fields, management practices in 2010 were recorded in structured interviews with farmers. Since a large number of agricultural management variables were partially correlated, we pre-selected the five that were only weakly correlated using correlation coefficients and variance inflation factors, according to Borcard et al. (2011). The final group of agricultural management variables consisted of: crop type, amount of mineral nitrogen (N) fertilizer applied, amount of organic nitrogen (N) fertilizer applied, number of mechanical field operations and number of synthetic and natural pesticide applications. For the analysis, we regrouped the original division of four crop types into six crop types according to sowing time and management practices (winter cereals, spring cereals, Fabaceae, forage plants, maize/sunflower and miscellaneous crops such as oilseed rape, potato or sugar beet). Winter cereals were the most abundant crop type, followed by forage plants and maize/sunflower (Table 2). In general, fields with Fabaceae and forage plants were less intensively managed regarding N input and pesticide applications than fields sown with miscellaneous crops and maize/sunflower. In order to detect the specific drivers (e.g. mineral N input or pesticide applications) of community structures, organic and non-organic fields were not separated in the analysis. The N input and the mechanical field operations were remarkably high in Southern Bavaria (Table 2). Pesticides were applied on 58 of the 167 fields, 34 fields were treated more than once. Pesticides were mainly herbicides, fungicides and rarely insecticides, retardants or molluscicides.

Surrounding landscape: Based on aerial photographs, the landscape composition was recorded in a buffer zone around each investigated field. The radius of the buffer zone was set at 250 m as a compromise for the four contrasting taxonomic groups (Gaba et al., 2010; Schmidt et al., 2008; Zurbuchen et al., 2010). Initially, the buffer zone was subdivided into nine habitat categories, and the estimates of percentage of habitat cover were used to calculate a Shannon diversity index H (based on the natural logarithms) of the surrounding habitats for each field. Then, the percentage cover of four aggregated habitat groups was calculated: (a) arable fields, (b) grasslands, (c) woody habitats (forest, scrub and woody crops) and (d) non-productive, non-woody habitats (urban area, sparsely vegetated ground, aquatic habitats, emergent hydrophytes or helophytes). Similar to agricultural management variables, the number of surrounding landscape variables was reduced to three: diversity of habitats in the surroundings, proportion of arable fields and proportion of non-productive, non-woody habitats (Table 2).

2.5. Data analysis

The relative roles of the three groups of explanatory variables were calculated: geographic location, agricultural management and surrounding landscape on the three response variables per taxonomic group.

Partitioning of variation was used to quantify the variation in abundance, species richness and species composition due to the three groups of explanatory variables (Borcard et al., 2011). The three groups were not fully independent of each other; therefore, some variation was explained jointly by two or by all three groups. The percentages of variation due to a single group of explanatory variables or a combination of groups were reflected in the adjusted R^2, which were calculated by partial redundancy analysis (RDA). Significance of percentages allocated to single groups was assessed based on 999 permutations (Legendre and Legendre, 2012). Because partitioning of variation relies on linear regressions, the univariate response variables, abundance and species richness, were log-transformed after adding a constant $c = 0.5$ (½ of the smallest non-zero value). Species composition data, as multivariate response variables, were Hellinger transformed (Legendre and Gallagher, 2001).

Generalized linear mixed-effects models were used to analyse effects of the individual explanatory variables on abundance and species richness. Since the response variables were over-dispersed with respect to a Poisson model, we assumed that they followed a negative binomial distribution. Bee data contained more than 60% zeros. Therefore, we applied models that accounted for zero-inflation. Agricultural management and surrounding landscape variables were treated as fixed effects, and interactions among fixed effects were included when significant. Region was included as a random intercept in all models. If, as an additional random intercept, farm improved the fit of the model significantly, it was included, also. The influence of individual crop types was tested against the most abundant crop type, the winter cereals. Models were reduced based on the AIC (Akaike information criterion) corrected for small samples (Burnham and Anderson, 2002). The significance of the reduced models was assessed with sequential likelihood-ratio tests.

Correlations in abundance, species richness and species composition among the four taxonomic groups, were calculated separately for all four regions based on untransformed species data. For abundance and species richness, Spearman's rank correlation coefficients were calculated in order to account for the non-normal distribution of the data. Procrustes rotation was used to test for correlations among the species compositions of the four taxonomic groups (Legendre and Legendre, 2012).

All analyses were performed in R 2.15.3 (R Development Core Team, 2012) using packages vegan 2.0-6, vennerable, plotrix, glmmADMB 0.7.3, AICcmodavg 1.27 and lmtest.

3. Results

In the entire set of 167 arable fields, 2,565 adult earthworm individuals, 1,967 adult spider individuals and 343 bee individuals were found. We identified 292 plant species, 19 earthworm species, 158 spider species and 72 wild bee and bumblebee species. The complete species lists and the number of fields in which they occurred are provided in Appendices S2, S3, S4 and S5 in Supplementary Material. In the Gascony region, the highest number of species was recorded for all four taxonomic groups (Fig. 1). For plants, 5% of all species occurred in all four regions and covered 30% of the area investigated (167 x 100 m^2). Five common species in all four regions with a high overall abundance were *Chenopodium album, Cirsium arvense, Convolvulus arvensis*, *Lolium perenne* and *Medicago sativa*. For earthworms, the most common species were *Allolobophora caliginosa* and *A. rosea*, which accounted for 55% of all earthworm individuals. For spiders, 4% of all species were recorded in all regions, and these made up 34% of the total spider abundance. The spider species *Erigone dentipalpis*, *Meioneta rurestris* and *Pachygnatha degeeri* were highly abundant and are among others listed by Schmidt and Tscharntke (2005) as so called agrobionts, i.e. species that "invariably dominate spider communities in crop fields over large parts of Europe." One bumblebee species, *Bombus terrestris*, was common in all regions, accounting for 13% of all bee individuals.

3.1. Plants

Variation in plant abundance of non-crop species was primarily explained by agricultural management (22%) and geographic location (18%), but not by surrounding landscape (Fig. 2). Variation in plant species richness was mainly explained by combinations of geographic location, agricultural management and surrounding landscape. None of the groups of explanatory variables explained a significant percentage of the variation independently of other variables. The variation in plant species composition was equally well explained by geographic location (10%) and agricultural management (10%), but not by surrounding landscape.

The generalized linear mixed-effects model revealed a negative effect of mineral N input and a positive effect of organic N input on plant abundance (Table 3). The interaction of organic N input and the proportion of arable fields in the surroundings was negative. This indicated that the positive effect of the combination of the both variables was weaker than the sum of the two variables. Crop type was also important: plant abundance in winter cereal fields was significantly lower than in forage fields and was significantly higher than in maize/sunflower fields. Mineral N input and pesticide applications had a negative effect on plant species richness (Table 4). Further, the interactions of mineral N input and pesticide applications and of mineral N input and mechanical fields operations were significantly positive. Thus, the detrimental effect of the two involved variables in combination was weaker than the sum of them. Plant species richness was significantly higher in winter cereal fields than in maize/sunflower fields, and the diversity of habitats in the surroundings had a positive effect.

3.2. Earthworms

Variation in earthworm abundance, species richness and species composition was predominantly explained by geographic location at percentages of 55%, 47% and 21%, respectively (Fig. 2). Neither agricultural management nor surrounding landscape explained a significant percentage of variation in earthworm communities independently.

Also in the mixed models, none of the agricultural management and surrounding landscape variables had a significant effect on earthworm abundance and species richness (Table 3 and 4).

3.3. Spiders

Variation in spider abundance, species richness and species composition was similarly significantly explained by geographic location (11%, 12% and 10%, respectively) and agricultural management (9%, 6% and 6%, respectively), but not by surrounding landscape (Fig. 2).

The mixed model indicated a positive effect of organic N input on spider abundance and species richness (Table 3 and 4). Furthermore, spider abundance and species richness were significantly higher in forage fields than in winter cereal fields, and maize/sunflower fields harboured significantly fewer spider species than winter cereal fields.

3.4. Bees

Variation in bee abundance and species richness was largely explained by geographic location (22% and 15%, respectively) but not by agricultural management or surrounding landscape (Fig. 2). Bee species composition was highly variable and none of the groups of explanatory variables tested had a significant effect.

The mixed models showed a negative effect of pesticide applications on bee abundance and species richness (Table 3 and 4). Mineral N input affected bee species richness negatively. Both, abundance and species richness, were higher in forage fields than in winter cereal fields. Furthermore, habitat diversity as well as the proportion of arable fields and the proportion of non-productive, non-woody habitats in the surroundings decreased bee abundance and species richness. The interaction of habitat diversity and the proportion of non-productive, non-woody habitats was positive for bee abundance and species richness and the interaction of the proportion of arable fields and the proportion of non-productive, non-woody habitats also for species richness. This indicated that the detrimental effect of the two involved variables in combination was weaker than the sum of them.

3.5. Correlations

Correlations between the four taxonomic groups differed between regions (Table 5). If significant, all correlations within abundances and species richness values were positive except one significantly negative correlation between plant and earthworm species richness in the Homokhátság region. Significant correlations were most frequently found between plants and bees. A few positive correlations were found between plants and spiders, between earthworms and spiders and between spiders and bees.

4. Discussion

4.1. Abundance, species richness and species composition

In plant communities, the patterns of explained variation differed strongly among abundance, species richness and species composition. For example, plant abundance responded to crop type far more than plant species richness responded. This can be explained by the fact that the crop type governed the dominance of a small number of very common weed species, in particular *Avena fatua* and *C. arvense*, as well as the forage crops *M. sativa, Trifolium pratense* and *Lolium multiflorum*, but affected the presence or the absence of all other species to a lesser degree. A similarly low impact of crop type on plant species richness was also reported by Fried et al. (2008). Nevertheless, a high percentage of variation in plant species richness was jointly explained by geographic location, agricultural management and surrounding landscape, indicating that explanatory variables had combined effects. For example, plants species richness increased with a higher diversity of habitats in the surroundings and a lower mineral N input.

In the faunistic communities, the patterns of explained variation were relatively similar for abundance, species richness and species composition. One exception was the variation in bee species composition that appeared to be largely unrelated to the investigated explanatory variables. A reason for this exception might be that the few, non-empty bee samples were highly divergent and therefore, no structure in bee assemblages was detected. Generally, if explanatory variables explained variation in species composition of the faunistic groups, it was reflected in abundance and species richness. This is in contrast to findings of Báldi et al. (2013) which showed that species compositions of several taxa, including spiders and bees, responded to environmental drivers in grassland fields but their species richnesses did not. We hypothesize that species communities in arable fields are subject to greater and more frequent fluctuations, and beneficial conditions might be too short to establish intensive interactions between species. Therefore, we would expect such interactions to result in relatively stable species compositions, which would respond differently to environmental factors considering species richness or species composition.

Whereas it was obvious that the consideration of abundance, species richness and species composition provided complementary information for plants, the three community measurements for the faunistic groups provided similar results. The similarity among the community measurements is an important result, because it indicates that species community structures might depend on species mobility and disturbance frequencies in habitats.

4.2. Responses of taxonomic groups

Plant abundance and species richness were diminished by management intensity, in line with Hyvönen and Salonen (2002) and Rassam et al. (2011). Fields with higher mineral N input had lower plant abundance and species richness than fields with additional or exclusive organic N input or fields that were not fertilized. The positive effect of organic N input should not be interpreted as a univariate relationship but as an additive effect. Its negative interaction with the proportion of arable fields in the surrounding landscape indicated that plant abundance in fields located in a homogeneous landscape of arable cropping benefited less from organic fertilization. Pesticide applications were detrimental for plant species richness. Crop type also affected plant communities probably due to crop-specific management practices and direct competition for water, nutrients and light. Similar to Pysek et al. (2005), maize/sunflower fields had lower plant abundance and species richness than cereal fields. Furthermore, plant species richness increased with the diversity of surrounding habitats, in accordance with Gabriel et al. (2005) who found higher plant species richness of arable fields in structurally more complex landscapes. Contrastingly, Bohan and Haughton (2012) and Marshall (2009) found no effect of margin strips or landscape context on weed diversity in the centre of arable fields, but did report a small effect in field edges. We assume that our result was related to a comparatively low management intensity (e.g. in the Homokhátság region), in which species with wind-dispersed seeds were abundant and succeeded to germinate within fields (compare also Concepción et al., 2012b and Tscharntke et al., 2005).

Earthworms rely on habitat and food resources at a local scale due to their restricted mobility. Not surprisingly, an effect of the surrounding landscape was lacking. However, in contrast to our expectations, we did not find a significant effect of management variables in our data. Generally, earthworms are considered vulnerable to management practices that lead to mechanical damage, increased susceptibility to predation (e.g. after cultivation), loss of an insulating layer of vegetation and a decreased food supply (Edwards and Bohlen, 1996). Indeed, abundant literature highlights the detrimental effect of inversion tillage on earthworms (e.g. Paoletti et al., 2010). The absence of significant effects in our study might be due to the relatively coarse description of management practices. In addition, the two most abundant earthworm species (the endogeic *A. caliginosa* and *A. rosea*), which accounted for more than half of all earthworm individuals, are known to be rather insensitive to agricultural management (Paoletti, 1999).

Spider communities were found to be closely related to vegetation structure, as this provides specific microclimatic conditions, shelter and food resources (Gibson et al., 1992). Crop type also had a major effect on spider communities. The highest spider abundance and species richness were found in forage crops. Furthermore, high spider abundance and species richness under organic N input might be caused by a positive influence of organic fertilizer on epigeal arthropods, which contributed to the food supply of spiders, as mentioned in Purvis and Curry (1984). In agreement with Batáry et al. (2008), the surrounding landscape had no effect on spider abundance, which could be due to the restricted spatial scale under investigation, because landscape factors measured over larger distances have been observed to significantly affect spiders (Drapela et al., 2008; Schmidt et al., 2008).

In our study, the direct link between plant and bee species communities was evident because the same management variables, mineral N input and pesticide applications, affected abundance and/or richness of both taxonomic groups negatively in accordance with Kremen et al. (2007) and Goulson et al. (2008). As most of the pesticides were herbicides, an indirect effect on bees via plants was suggested. However, very likely direct impacts of insecticides intensified this effect (Brittain et al., 2010; Whitehorn et al., 2012). All tested surrounding landscape variables had a negative effect on bee abundance and species richness. The negative effect of the proportion of arable fields was in line with Holzschuh et al. (2010) who found more bees in landscapes with high proportions of non-crop habitats. Surprisingly, bee abundance also decreased with a higher diversity of surrounding habitats. Steffan-Dewenter (2003) discussed this issue and noted the importance of specific habitat types in the surroundings, an aspect later studied by Carré et al. (2009), who found a decrease in bee abundance with a higher amount of surrounding forest patches, which could act as barriers. In our case, diversity of surrounding habitats was correlated with the area of woody elements in the surroundings, which suggests a similar underlying pattern.

Identical drivers acting on the four taxonomic groups were expected to result in positive correlations between the different groups. The highest agreement among drivers occurred between plant and bee communities (crop type, mineral N input and pesticide applications) and was indeed reflected in several correlations between these two groups. Correlations between plants and spiders and between spiders and bees were weak and primarily due to crop type. Correlations between plant and earthworm species richness occurred in the Homokhátság region. Interestingly, earthworm species composition was significantly correlated to spider species composition in the Marchfeld region and in Southern Bavaria, and earthworm abundance was positively correlated to spider abundance in the Marchfeld region. One reason could be that both, earthworms and spiders, were affected by the structure of the soil surface, especially soil cover by plant litter. Litter provided food resources for earthworms and for other detritivores involved in decomposition, which might then be hunted by spiders (Purvis and Curry, 1984).

4.3. Group-specific explanatory power of agricultural management

Since arable fields are highly disturbed habitats, a direct effect of agricultural management on plant, earthworm, spider and bee communities in arable fields seems plausible. Indeed, all four investigated taxonomic groups were dominated by only a few species, and these occurred frequently under high management intensity. Nevertheless, we expected agricultural management to act as a filter for the large number of uncommon or rare species, independent of geographic location and surrounding landscape. This was shown in plant abundance, plant species composition and all measurements of spider communities. Furthermore, individual agricultural management variables had significant impacts on plant species richness, bee abundance and bee species richness. In contrast, earthworm communities were largely unaffected by the agricultural management variables that were available in this study. However, in agreement with other studies across several regions (e.g. Concepción et al, 2012b; Báldi et al., 2013), the majority of variation in species communities was explained by region (in the geographic location variables group). This demonstrated that farmland species communities were samples of the regional species pool driven by agricultural management and surrounding landscape variables (Tscharntke et al., 2005).

5. Conclusions

This is a rare study that investigated contrasting taxonomic groups in arable fields across several European regions. The consideration of abundance, species richness and species composition clearly contributed to an information gain regarding community structures and allowed us to separate general from taxon-specific effects. As expected, plant, earthworm, spider and bee communities differed in their responses to geographic location, agricultural management and surrounding landscape. One of the strongest general results of this study was the clear detrimental effect of mineral N input and pesticide applications on plant or bee abundance, respectively, as well as on species richness of plants and bees. Besides the significant agricultural management effects, this study revealed the predominant effect of geographic location, pointing out that regional conditions should be taken into account when designing measures to promote farmland species.

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Table 1

Geographic coordinates, environmental and agricultural characteristics of the study regions.

Region	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Country	Austria	Germany	France	Hungary
Latitude (°)	48.3	48.4	43.4	46.7
Longitude (°)	16.7	11.3	0.8	19.6
Altitude (m asl)	140-180	350-500	197-373	93-168
Climate	Pannonian	Continental	Sub-Mediter.	Pannonian
Rainfall (mm)	560	800	680	550
Mean annual temp. (°C)	9.5	8.5	13	10.4
Soil	Deep fertile chernozem	Silt and silt loam	Clay-limestone	Sandy
Production type	Arable crops	Mixed	Arable crops	Mixed
# Arable fields (in # farms)	56 (16)	49 (16)	39 (15)	23 (14)

Table 2

Characteristics of the investigated arable fields: mean ± standard error of numeric variables and levels of the categorical variable crop type in each study region (in order of frequency).

Region		Marchfeld	Southern Bavaria	Gascony	Homokhátság
Agricultural management	Mineral N input (kg/ha)	40 ± 7	52 ± 9	34 ± 8	2 ± 2
	Organic N input (kg/ha)	7 ± 3	56 ± 6	16 ± 5	53 ± 10
	Field operations	6 ± 0.3	12 ± 1	5 ± 0.4	3 ± 0.2
	Pesticide applications	1 ± 0.2	0.8 ± 0.2	0.9 ± 0.2	0
	Crop types	WiC, For, Fab, M/S, Mis, SpC	WiC, For, M/S, Fab, Mis	WiC, S, Fab, For, SpC	For, WiC, M/S
Surrounding landscape	H[a] of surrounding habitats	0.2 ± 0.04	0.9 ± 0.04	0.7 ± 0.05	0.8 ± 0.05
	Arable fields (%)	90.2 ± 2.2	63.7 ± 2.3	74.9 ± 2.6	43.5 ± 3.9
	Non-productive, non-woody habitats (%)	3.9 ± 1.5	6 ± 0.8	2.4 ± 0.8	5.7 ± 2.4

Abbreviations for the crop types: WiC, winter cereals; SpC, spring cereals; For, forage crops; Fab, Fabaceae; M/S, maize/sunflower; Mis, miscellaneous crops.

[a] H = Shannon diversity index

Table 3

Effects of geographic location, agricultural management and surrounding landscape variables on the abundance of plants, earthworms, spiders and bees estimated using negative binomial generalized linear mixed-effects models.

	Plants			Earthworms			Spiders			Bees		
Fixed effects	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*
Winter cereals (Intercept)	2.96	0.48	<0.001	2.25	0.45	<0.001	1.92	0.30	<0.001	5.45	1.41	<0.001
Spring cereals	-0.24	0.26	0.35				-0.05	0.26	0.85	-0.96	0.62	0.12
Fabaceae	0.18	0.23	0.44				-0.33	0.23	0.16	0.34	0.29	0.24
Forage crops	1.39	0.17	<0.001				0.83	0.18	<0.001	0.83	0.24	<0.001
Maize/sunflower	-0.50	0.19	<0.01				-0.31	0.20	0.13	0.23	0.26	0.38
Miscellaneous	-0.55	0.35	0.12				0.21	0.32	0.52	-	-	-
Mineral N input (kg/ha)	-0.007	0.002	<0.001									
Organic N input (kg/ha)	0.02	0.01	<0.01				0.006	0.002	<0.01			
Pesticide applications										-0.67	0.17	<0.001
H[a] of surrounding habitats										-3.21	0.70	<0.001
Arable fields in the surroundings (%)	0.005	0.005	0.29							-0.05	0.01	<0.001
Non-productive, non-woody habitats in the surroundings (%)										-0.08	0.04	<0.05
H[a] of sur. hab. * N-p, n-w. hab.										0.12	0.04	<0.01
Organic N input * arable fields	-0.0002	0.0001	<0.01									
Random effects	SD			SD			SD			SD		
Region (Intercept)	0.60			0.88			0.54			1.29		
Farm	0.35			0.52						0.46		
		SE			SE			SE			SE	
Negative binomial dispersion parameter	2.07	0.30		2.20	0.39		1.65	0.22		24.04	34.48	
Zero-inflation										0.30	0.06	

Bee abundance data were analysed with a model accounting for zero-inflation. *P*-values were calculated from likelihood-ratio tests. Significant fixed effects are marked in bold.

[a] H = Shannon diversity index

Table 4

Effects of geographic location, agricultural management and surrounding landscape variables on species richness of plants, earthworms, spiders and bees estimated using negative binomial generalized linear mixed-effects models.

	Plants			Earthworms			Spiders			Bees		
Fixed effects	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*
Winter cereals (Intercept)	2.48	0.18	<0.001	0.79	0.31	<0.05	1.34	0.28	<0.001	3.61	1.26	<0.01
Spring cereals	0.23	0.15	0.12				-0.04	0.19	0.84	-0.55	0.58	0.34
Fabaceae	-0.23	0.13	0.08				-0.18	0.17	0.30	0.32	0.28	0.26
Forage crops	-0.10	0.11	0.33				0.39	0.13	<0.01	0.63	0.24	<0.01
Maize/sunflower	-0.23	0.12	<0.05				-0.42	0.15	<0.01	0.04	0.27	0.87
Miscellaneous	-0.30	0.26	0.24				0.01	0.24	0.95	-	-	-
Mineral N input (kg/ha)	-0.01	0.00	<0.001							-0.007	0.004	<0.05
Organic N input (kg/ha)							0.005	0.001	<0.001			
Field operations	-0.01	0.01	0.51									
Pesticide applications	-0.16	0.07	<0.05							-0.37	0.17	<0.05
Mineral N input * field op.	0.0006	0.0001	<0.001									
Mineral N input * pesticide appl.	0.002	0.001	<0.05									
H[a] of surrounding habitats	0.30	0.15	<0.05							-1.96	0.63	<0.01
Arable fields in the surroundings (%)										-0.03	0.01	<0.01
Non-productive, non-woody habitats in the surroundings (%)										-0.23	0.10	<0.05
H[a] of sur. hab. * N-p, n-w. hab.										0.16	0.06	<0.01
Arable fields * N-p, n-w. hab.										0.002	0.001	<0.05
Random effects	SD			SD			SD			SD		
Region (Intercept)	0.24			0.60			0.50			0.94		
		SE			SE			SE			SE	
Negative binomial dispersion parameter	8.57	1.98		403.43	0.57		5.88	1.53		403.43	1.97	
Zero-inflation										0.26	0.07	

Species richness of bees was analysed with a model accounting for zero-inflation. *P*-values were calculated from likelihood-ratio tests. Significant fixed effects are marked in bold.

[a] H = Shannon diversity index

Table 5

Range of pairwise Spearman's rank correlations (abundance and species richness) and Procrustes rotation parameter (species composition) between the four taxonomic groups in the four case study regions.

	Abundance		Richness		Composition	
	Spearman's correlation coefficient	Regions where significant	Spearman's correlation coefficient	Regions where significant	Correlation in a symmetric Procrustes rotation	Regions where significant
Plants vs. earthworms	-0.22 – 0.19	-	-0.42 – 0.18	H (-)	0.28 – 0.39	H
Plants vs. spiders	0.14 – 0.51	D (+)	-0.01 – 0.47	F (+)	0.36 – 0.53	A, D
Plants vs. bees	0.19 – 0.55	A, D, F (all +)	0.04 – 0.37	A, D (all +)	0.40 – 0.61	A, F
Earthworms vs. spiders	0.17 – 0.34	A (+)	0.22 – 0.24	-	0.35 – 0.39	A, D
Earthworms vs. bees	-0.06 – 0.17	-	-0.20 – 0.18	-	0.23 – 0.39	-
Spiders vs. bees	-0.10 – 0.43	D, H (all +)	-0.20 – 0.41	D (+)	0.28 – 0.46	-

Regions where coefficients were significant are given as A = Marchfeld, D = Southern Bavaria, F = Gascony, H = Homokhátság.

Figure captions

Fig. 1. Total number of (a) plant, (b) earthworm, (c) spider and (d) bee species in each region. Grey shading indicates the number of species occurring: in all four regions (black), in three regions (dark grey), in two regions (light grey), exclusively in the corresponding region (white).

Fig. 2. Partition of variation in abundance, species richness and species composition of plants, earthworms, spiders and bees explained by geographic location, agricultural management and surrounding landscape derived from partial redundancy analysis. The area of the circles is proportional to the percentage of variation explained by the respective group of explanatory variables. Each box accounts for the total variation (100 %), i.e. the area outside of the circles represents the amount of unexplained variation.

Highlights

- Designing effective measures for biodiversity requires a multi-taxon approach.
- Plants, earthworms, spiders and bees in arable fields across Europe are analysed.
- Patterns in species communities are mainly affected by the study region.
- Abundance, species richness and composition respond differently to drivers.
- Effects of agricultural management are taxon-specific.

Supplementary Material

Table S1

Numbers of investigated arable fields, species richness and abundance in the four study regions. Gamma species richness: The number of species found in all arable fields of the respective study region, in brackets the number of species found exclusively in the respective study region. Alpha species richness: The mean number of species per field ± standard error. Abundance: The mean cover of non-crop plants per field ± standard error and the mean number of animal individuals per field ± standard error, respectively.

Region		Marchfeld	Southern Bavaria	Gascony	Homokhátság
Number of fields		56	49	39	23
Plants	Gamma species richness	88 (35)	107 (40)	138 (68)	105 (52)
	Alpha species richness	5.54 ± 0.55	13.61 ± 1.18	12.82 ± 1.15	13.96 ± 1.01
	Abundance	30.02 ± 5.38	32.67 ± 5.17	79.15 ± 10.45	58.09 ± 8.39
Earth-worms	Gamma species richness	7 (2)	9 (2)	13 (8)	3 (1)
	Alpha species richness	1.84 ± 0.12	3 ± 0.18	4.64 ± 0.24	0.74 ± 0.18
	Abundance	7.91 ± 0.86	12.71 ± 1.4	36.54 ± 4.53	3.22 ± 1.12
Spiders	Gamma species richness	52 (16)	48 (21)	97 (64)	31 (14)
	Alpha species richness	3.8 ± 0.39	7.31 ± 0.54	6.97 ± 0.72	2.44 ± 0.56
	Abundance	8.16 ± 1.4	17.45 ± 1.84	13.28 ± 1.51	5.96 ± 2.09
Bees	Gamma species richness	16 (7)	14 (6)	48 (35)	16 (8)
	Alpha species richness	0.43 ± 0.13	0.49 ± 0.12	3.23 ± 0.57	0.87 ± 0.23
	Abundance	0.54 ± 0.18	0.67 ± 0.18	6.56 ± 1.32	1.04 ± 0.33

Table S2

Plant species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Plant species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Capsella bursa-pastoris	2	9	1	15
Chenopodium album	21	23	16	1
Cirsium arvense	26	1	14	1
Convolvulus arvensis	7	3	18	12
Dactylis glomerata	2	9	5	4
Fallopia convolvulus	1	24	9	3
Galium aparine	12	19	11	2
Lolium perenne	1	14	5	2
Medicago sativa	6	15	5	11
Papaver rhoeas	5	3	4	15
Plantago lanceolata	1	3	7	4
Polygonum aviculare	1	16	1	1
Sinapis arvensis	2	1	3	1
Alopecurus pratensis	1	1		1
Anagallis arvensis		4	15	1
Avena fatua	5	3	23	
Bromus sterilis	4		4	3
Conyza canadensis	2		2	2
Epilobium tetragonum	1	1	3	
Festuca pratensis	1	4	1	
Lactuca serriola	4		8	2
Lolium multiflorum	1	13	9	
Myosotis arvensis		18	5	1
Phleum pratense	1	7	3	

Plantago major		8	1	1
Ranunculus repens		4	3	1
Sonchus asper	1	8	11	
Stellaria media	19	2		8
Taraxacum officinale	5	1		6
Trifolium pratense	3	14	8	
Veronica arvensis		3	3	13
Veronica hederifolia	7	1		3
Veronica persica	4	16	2	
Vicia cracca		3	1	1
Vicia sativa	2	2	1	
Viola arvensis	8	1	1	
Acer campestre		1	1	
Achillea millefolium agg.		1	1	
Alopecurus myosuroides		3	1	
Ambrosia artemisiifolia	1			7
Anthemis arvensis		6		1
Anthemis ruthenica		1		3
Apera spica-venti		17		3
Arctium lappa	1		1	
Arenaria serpyllifolia	1			8
Artemisia vulgaris	1			2
Asperugo procumbens	1			1
Bromus hordeaceus			4	2
Bromus tectorum	3			7
Bryonia dioica	1		1	
Buglossoides arvensis	2			5
Calystegia sepium	3		4	
Carduus nutans			1	3
Centaurea cyanus	2	4		
Cichorium intybus			2	2
Consolida regalis	3			8
Cynodon dactylon			4	2
Daucus carota			2	1
Descurainia sophia	5			8
Echinochloa crus-galli		9	2	
Elymus repens		16		15
Equisetum arvense		25	1	
Eryngium campestre			2	2
Euphorbia helioscopia		3	6	
Geranium dissectum		6	6	
Holcus lanatus		1	3	
Lamium amplexicaule	7			9
Lamium purpureum		5		1
Lapsana communis		8	2	
Lathyrus pratensis	1		4	
Malva neglecta	2		1	
Medicago lupulina		3	7	
Melilotus officinalis		1		1
Mercurialis annua	5		5	
Poa annua		14	1	
Poa pratensis	1	8		
Poa trivialis		5	2	
Polygonum lapathifolium		15	2	
Polygonum persicaria		7	5	

Reseda lutea	1			2
Rumex acetosa		2	2	
Rumex crispus		14	11	
Senecio vernalis	1			6
Senecio vulgaris	1		2	
Setaria pumila			2	1
Sherardia arvensis		9	4	
Silene latifolia		1		9
Solanum nigrum	2	4		
Thlaspi arvense	1	5		
Trifolium campestre		1	3	
Trifolium repens		22	1	
Urtica dioica	1	1		
Valerianella locusta			1	2
Veronica polita			3	1
Vicia hirsuta		6	3	
Vicia sepium		1	1	
Vicia tetrasperma		7	2	
Acer pseudoplatanus		4		
Achillea collina				4
Agrostemma githago				1
Agrostis stolonifera			1	
Allium oleraceum			1	
Allium scorodoprasum				1
Althaea hirsuta			1	
Alyssum alyssoides				2
Amaranthus powellii	6			
Amaranthus retroflexus	5			
Anagallis foemina			7	
Anchusa arvensis	1			
Angelica sylvestris		1		
Anthemis austriaca	13			
Anthemis cotula			11	
Anthriscus caucalis			6	
Aphanes arvensis		8		
Arabidopsis thaliana				1
Arabis hirsuta				1
Arrhenatherum elatius			4	
Atriplex patula			1	
Atriplex prostrata			1	
Avena sterilis	2			
Ballota nigra				1
Bellis perennis		1		
Betula pendula		1		
Brassica nigra			1	
Briza minor			1	
Bromus inermis	1			
Camelina microcarpa				4
Camelina sativa	1			
Cardaria draba				4
Carduus acanthoides	2			
Carex flacca				1
Carex stenophylla				1
Carum carvi		2		
Centaurea scabiosa		1		

Cerastium fontanum		4		
Cerastium glomeratum			2	
Cerastium semidecandrum				6
Chaenorrhinum minus			1	
Chamomilla recutita		19		
Chamomilla suaveolens		4		
Chenopodium ficifolium	4			
Chenopodium hybridum	2			
Chenopodium polyspermum		5		
Chondrilla juncea				1
Chrysopogon gryllus				1
Cirsium canum				1
Cirsium oleraceum		1		
Clematis vitalba	1			
Clover grass	1			
Clover lucerne	1			
Cornus sanguinea		1		
Crepis foetida			1	
Crepis vesicaria			1	
Datura stramonium	2			
Deschampsia cespitosa				1
Digitaria sanguinalis				1
Echium vulgare				1
Elytrigia repens			1	
Equisetum ramosissimum				1
Erodium cicutarium				1
Erophila verna				1
Erysimum diffusum				1
Euphorbia esula				1
Euphorbia exigua			3	
Euphorbia segetalis			1	
Euphorbia virgata				1
Fagopyrum esculentum	6			
Falcaria vulgaris				1
Festuca pseudovina				7
Fraxinus angustifolia			1	
Fraxinus excelsior	2			
Fumaria officinalis			1	
Fumaria vaillantii	1			
Galeopsis angustifolia			4	
Galeopsis speciosa			1	
Galeopsis tetrahit		8		
Galinsoga ciliata		5		
Galinsoga parviflora		1		
Galium spurium	1			
Galium verum				2
Geranium pusillum	1			
Geranium pyrenaicum		1		
Geranium rotundifolium			1	
Glyceria fluitans		1		
Gnaphalium uliginosum		1		
Heracleum sphondylium		1		
Holosteum umbellatum				2
Hordeum murinum				1
Hyoscyamus niger	1			

Juncus bufonius		2		
Kickxia elatine			3	
Kickxia spuria			7	
Koeleria cristata				1
Lactuca saligna			1	
Lamium galeobdolon		1		
Lappula heteracantha				1
Lathyrus hirsutus			1	
Lathyrus nissolia			2	
Lathyrus sativus	1			
Lathyrus tuberosus	2			
Legousia speculum-veneris		1		
Lens culinaris			1	
Leontodon saxatilis			1	
Lepidium perfoliatum				1
Lepidium ruderale				1
Linaria vulgaris			1	
Linum angustifolium			1	
Lotus corniculatus			4	
Malva sp			1	
Matricaria chamomilla	3			
Matricaria inodora				2
Matricaria maritima		14		
Matricaria recutita			1	
Medicago falcata				1
Medicago minima				1
Medicago polymorpha			2	
Medicago sp			1	
Melilotus alba		1		
Melilotus albus				1
Mentha arvensis		1		
Mentha longifolia		1		
Misopates orontium			1	
Myosotis stricta				1
Odontites rubra			1	
Ononis spinosa s. maritima v.				1
Persicaria maculosa	1			
Phalaris paradoxa			1	
Phleum sp		3		
Phragmites australis				2
Picris echioides			18	
Plantago maritima				1
Poa angustifolia				8
Poa bulbosa				1
Polygala amarella				1
Polygonum amphibium		1		
Potentilla anserina		1		
Potentilla reptans			8	
Prunella vulgaris			1	
Prunus spinosa			2	
Pulicaria dysenterica			1	
Quercus humilis			2	
Quercus robur			1	
Ranunculus acris		1		
Ranunculus arvensis			3	

Ranunculus sardous			1	
Ranunculus sp			1	
Raphanus raphanistrum		3		
Rapistrum rugosum s. rugosum			5	
Rhinanthus minor				1
Rorippa palustris		1		
Rubus caesius			11	
Rumex acetosella			3	
Rumex obtusifolius		28		
Salix caprea x aurita		1		
Salix purpurea		1		
Salsola kali				1
Salvia nemorosa	1			
Scleranthus annuus		1		
Scorzonera cana				2
Senecio jacobaea			3	
Serratula tinctoria				1
Silene alba	2			
Silene vulgaris	1			
Sisymbrium loeselii	1			
Sisymbrium orientale				4
Solidago gigantea	1			
Sonchus arvensis			2	
Stachys annua			2	
Stellaria graminea			1	
Stellaria pallida	1			
Symphytum officinale		1		
Tamus communis			1	
Taraxacum sp			1	
Trifolium arvense			1	
Trifolium dubium		2		
Trifolium hybridum			1	
Trifolium incarnatum			1	
Tripleurospermum inodorum	12			
Trisetum flavescens	1			
Valerianellla dentata		1		
Verbena officinalis			8	
Veronica agrestis	2			
Veronica triloba	5			
Veronica triphyllos				1
Vicia bithynica			5	
Vicia faba			2	
Vicia villosa				5
Viola kitaibeliana				3
Viola tricolor	1			
Vulpia bromoides			2	
Vulpia myuros			1	
Xanthium strumarium			2	

Table S3

Earthworm species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Earthworm species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Allolobophora caliginosa	41	44	35	7

Allolobophora rosea	41	29	18	8
Allolobophora chlorotica	8	9	33	
Octolasium lacteum	2	8	4	
Lumbricus castaneus		15	1	
Lumbricus terrestris	8	23		
Octolasium cyaneum		5	4	
Allolobophora cupulifera			1	
Allolobophora georgii				2
Allolobophora muldali			9	
Dendrobaena byblica	2			
Dendrobaena mammalis			4	
Lumbricus festivus	1			
Lumbricus friendi			22	
Lumbricus herculeus			1	
Lumbricus rubellus		13		
Octodrilus transpadanum		1		
Prosellodrilus fragilis			3	
Scheroteca savignyi			19	

Table S4

Spider species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Spider species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Erigone dentipalpis	9	3	7	3
Mangora acalypha	2	6	5	3
Meioneta rurestris	22	35	19	9
Neottiura bimaculata	6	28	8	6
Pachygnatha degeeri	14	34	6	2
Pardosa agrestis	14	4	2	1
Araeoncus humilis	17	17		2
Aulonia albimana	1		2	1
Bathyphantes gracilis	4	5	4	
Diplostyla concolor	1	6	7	
Euophrys frontalis	1		3	1
Mermessus trilobatus	5	15	1	
Microlinyphia pusilla	2	5		2
Oedothorax apicatus	32	36	21	
Pachygnatha clercki	1	2	1	
Pardosa prativaga	3	1	3	
Pelecopsis parallela		1	6	1
Phylloneta impressa	1	13		1
Porrhomma microphthalmum	5	3	3	
Tenuiphantes tenuis	11	19	26	
Xysticus kochi	4	1	3	
Argiope bruennichi		2	2	
Cryptachaea riparia	2	2		
Dicymbium nigrum brevisetosum		3	1	
Drassyllus pusillus	1		1	
Enoplognatha thoracica	3		1	
Erigone atra	7	31		
Ero furcata	1		1	
Gnathonarium dentatum	1	1		
Haplodrassus minor	2			2
Hypsosinga pygmaea	1		1	

Maso sundevalli	2		2	
Meioneta simplicitarsis	1			2
Micrargus herbigradus		1	1	
Micrargus subaequalis	6		2	
Pardosa palustris	2	4		
Phrurolithus festivus			8	1
Pisaura mirabilis			3	1
Robertus arundineti	6		1	
Sibianor aurocinctus			3	1
Tenuiphantes flavipes	1		1	
Tibellus oblongus	1		1	
Trochosa ruricola	1	1		
Acartauchenius scurrilis				1
Aculepeira ceropegia		2		
Agraecina lineata			3	
Araneus diadematus				1
Araniella cucurbitina		1		
Argenna subnigra	2			
Bathyphantes similis				3
Brommella falcigera	1			
Centromerita bicolor		1		
Centromerus sp2			1	
Chalcoscirtus infimus			1	
Cheiracanthium pennyi				1
Clubiona pseudoneglecta			7	
Clubiona reclusa		1		
Clubiona subtilis				1
Cresmatoneta mutinensis			2	
Crustulina guttata			1	
Crustulina sticta			1	
Cyclosa oculata			1	
Dictyna arundinacea				1
Dictyna sp			1	
Diplocephalus cristatus		1		
Diplocephalus graecus			2	
Dismodicus bifrons		1		
Drassyllus lutetianus			1	
Drassyllus praeficus			1	
Drassyllus villicus			1	
Enoplognatha latimana			1	
Enoplognatha mordax			1	
Enoplognatha ovata			1	
Entelecara flavipes		1		
Episinus truncatus			3	
Erigonella hiemalis		2		
Ero aphana			1	
Euophrys gambosa			1	
Gibbaranea bituberculata			1	
Gongylidiellum latebricola		1		
Gongylidiellum murcidum	1			
Hahnia candida			1	
Hahnia nava	1			
Hahnia pusilla		1		
Harpactea hombergi			1	
Heliophanus cupreus			1	

Heliophanus flavipes			1	
Hypsosinga sanguinea	2			
Leptorhoptrum robustum		1		
Linyphia triangularis		1		
Linyphiidae			1	
Liophrurillus flavitarsis			1	
Marpissa nivoyi			1	
Maso gallicus			1	
Meioneta mollis			7	
Meioneta saxatilis	1			
Metopobactrus prominulus			1	
Micrargus apertus			1	
Microlinyphia impigra	1			
Microneta viaria				1
Minyriolus pusillus		1		
Neoscona adianta				1
Neoscona byzanthina			1	
Neriene clathrata			1	
Neriene furtiva			1	
Oedothorax fuscus		7		
Ostearius melanopygius			3	
Ozyptila atomaria			1	
Ozyptila brevipes			1	
Ozyptila simplex			4	
Palliduphantes alutacius			1	
Panamomops sulcifrons			3	
Pardosa hortensis			4	
Pardosa lugubris	1			
Pardosa proxima			11	
Pardosa saltans			1	
Pardosa vittata			5	
Pelecopsis bucephala			1	
Philodromus pulchellus			2	
Phrurolithus minimus			1	
Phrurolithus nigrinus			5	
Pirata latitans		1		
Porrhomma oblitum		3		
Robertus neglectus		4		
Runcinia grammica				2
Silometopus reussi	3			
Singa hamata				1
Sitticus rupicola				1
Steatoda phalerata			1	
Talavera aequipes	1			
Tenuiphantes zimmermanni			1	
Tetragnatha pinicola		5		
Thanatus atratus			2	
Theridion impressum			2	
Theridion nigrovariegatum			1	
Theridion uhligi Martin 1974			1	
Thomisus onustus				1
Tibellus maritimus				1
Tiso vagans		3		
Titanoeca tristis			1	
Tmarus stellio			1	

Trachelas minor			2	
Trichoncoides piscator	1			
Trichoncus hackmani				1
Trichoncus saxicola			1	
Walckenaeria capito			1	
Walckenaeria dysderoides	1			
Walckenaeria nudipalpis		1		
Walckenaeria vigilax		4		
Xerolycosa miniata	1			
Xysticus striatipes	1			
Xysticus ulmi	1			
Zelotes civicus			3	
Zelotes gracilis	1			
Zelotes tenuis			1	
Zora parallela			1	
Zora pardalis			1	
Zora spinimana			1	

Table S5

Bee species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Bee species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Bombus terrestris	3	3	14	1
Andrena labialis	1	1	1	
Bombus lapidarius	3	2	8	
Bombus pascuorum	1	2	6	
Bombus sylvarum		1	2	3
Andrena decipiens			1	1
Andrena dorsata	1			1
Andrena flavipes		2	3	
Andrena ovatula			1	3
Bombus hortorum		1	1	
Bombus ruderatus	1		2	
Eucera nigrescens	3			1
Halictus simplex	2		11	
Lasioglossum pauxillum		2	4	
Megachile leachella			1	1
Rophites canus	2			1
Andrena agilissima			1	
Andrena barbilabris				1
Andrena impunctata			1	
Andrena producta	1			
Andrena sp				1
Andrena variabilis			2	
Andrena wilkella			2	
Anthidium oblongatum			1	
Bombus bohemicus		1		
Bombus confusus			2	
Bombus hypnorum		2		
Bombus vestalis	1			
Coelioxys afra			1	
Colletes similis			1	
Dasypoda altercator			1	
Eucera chrysopyga	1			

Eucera clypeata			3	
Eucera longicornis	1			
Eucera taurica			1	
Halictus eurygnathus				1
Halictus maculatus			2	
Halictus rubicundus	1			
Halictus scabiosae			5	
Halictus seladonius			1	
Halictus sexcinctus				1
Halictus smaragdulus			2	
Halictus tetrazonius gr				1
Halictus tumulorum			3	
Halictus vestitus			1	
Heriades truncorum			1	
Hylaeus gredleri	1			
Lasioglossum calceatum		3		
Lasioglossum corvinum			1	
Lasioglossum discum				1
Lasioglossum fulvicorne		1		
Lasioglossum glabriusculum			5	
Lasioglossum griseolum				1
Lasioglossum interruptum			1	
Lasioglossum lativentre			1	
Lasioglossum leucozonium			2	
Lasioglossum malachurum			9	
Lasioglossum morio			2	
Lasioglossum politum			3	
Lasioglossum punctatissimum			1	
Lasioglossum puncticolle			4	
Lasioglossum sp			2	
Lasioglossum villosulum			4	
Lasioglossum zonulum		2		
Megachile centuncularis			1	
Megachile opacifrons			1	
Megachile rotundata			1	
Melitta leporina		1		
Melitturga clavicornis				1
Rophites algirus	1			
Sphecodes ephippius			1	
Xylocopa violacea			1	