Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems

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A B S T R A C T

Biological diversity is influenced by many environmental factors, which can act either at a local scale (e.g. quality and quantity of feeding and nesting resources, habitat type) or at a landscape scale (e.g. habitat fragmentation, composition and configuration of landscape features). To effectively manage or promote biodiversity in heterogeneous environments such as intensive agrosystems, a thorough knowledge of the spatial and temporal scale of ecological factor effects is required. This study investigates the effects of ecological correlates on local wild bee diversity in semi-natural farmland habitats, and predicts changes in species richness according to local-scale and landscape-scale correlates to further guide bee conservation practices. Local floral richness, the proportion of semi-natural habitats in the landscape (1000 m radius) and the type of semi-natural habitats influenced bee richness at a field scale. However, the magnitude of the effect varied seasonally and according to local bee abundance. Model predictions showed that increasing floral richness on farms had a greater effect on bee richness than increasing the proportion of semi-natural habitats. While increasing the number of semi-natural habitats would be a more effective strategy for promoting bee diversity at the landscape scale, it may not be feasible in intensive farming systems.

1. Introduction

Diversity and composition of animal communities depend on biotic and abiotic environmental factors, which can interact at different temporal and spatial scales (Holyoak et al., 2005; Moritz et al., 2013). In particular, ecological correlates of diversity for a given biological group may be perceived at the landscape scale (e.g. habitat type, landscape configuration and composition) or the local scale (e.g. predation, competition, feeding and nesting resources). In human-dominated systems such as farmlands, habitat management or agricultural practices may severely affect animal and plant communities through the modification of landscape and local characteristics (Bretagnolle and Gaba, 2015; Gaba et al., 2013). For example, many invertebrates have multiple habitat requirements, such as bees and butterflies that use complementary habitats for nesting and feeding (Holzschuh et al., 2006; Klein et al., 2003; Ouin et al., 2004). Highly biodiverse

agroecosystems are usually associated with heterogeneous landscapes that have a large diversity of habitats arranged in complex spatial configurations (Fahrig et al., 2011; Hass et al., 2018; Senapathi et al., 2016). Yet, the ongoing intensification of agriculture has led to a decrease in landscape heterogeneity and quality (Benton et al., 2003) due to the reduction of the quantity and diversity of semi-natural habitat remnants, crop homogenisation and the increase in field sizes (Robinson and Sutherland, 2002). A decline in habitat quality can also be observed at the local scale with significant modification and loss of the diversity of plants due to the use of external inputs (e.g. herbicides, fertilizers) (Baessler and Klotz, 2006; Rollin et al., 2016; Storkey et al., 2009; Sutcliffe and Kay, 2000). As a consequence, animal and plant diversity have strongly declined in agro-ecosystems (Bretagnolle and Gaba, 2015; Chamberlain et al., 2000; Donald et al., 2001; Sotherton, 1998; Wilson et al., 1999).

To reverse these negative trends, alternative management

approaches, such as agro-environmental schemes, have been developed during the last few decades for promoting biodiversity, especially bee diversity, and the ecosystem services they deliver (Decourtye et al., 2010; Grass et al., 2016; Senapathi et al., 2016; Sprague et al., 2016). However, the efficiency of these practices is still unclear. Kleijn et al. (2006), for example, have shown that only half of the agro-environmental schemes promoted at the European level had a significant positive effect on biodiversity. The effectiveness can varies according to the type of measure, the focus taxonomic group or the environmental context and spatial scale considered (Batáry et al., 2011; Grass et al., 2016; Henry et al., 2012; Kleijn et al., 2011; Senapathi et al., 2016; Tscharntke et al., 2005). We therefore need more studies that evaluate the efficiency and trade-offs between practices developed at the farm and landscape scales and aimed to enhance animal-delivered services (Garibaldi et al., 2017).

In intensive agricultural systems, semi-natural vegetation surrounding fields is the habitat most frequently used by bees and promotes a higher local bee diversity than any other source of flowers such as flowering crops (Rollin et al., 2015, 2013). Therefore, conservation of semi-natural habitats at a landscape scale is one of the most promising strategies for preserving wild bee populations (Kleijn and Sutherland, 2003; Knop et al., 2006). However, depending on the context, there might be a minimum threshold of flower cover needed for an herbaceous habitat-oriented management strategy to be more profitable to wild bees than a local, floral-specific resource-oriented management strategy (Rollin et al., 2013). There may be an optimum threshold of wild flower cover, depending on the varying wild bee families, that could result in the best compromise between these two management strategies. Moreover, Rollin et al. (2015) have shown an intermittent turnover of bee species according to the focal spatial scales, with a maximal turnover within 50 km2 areas (7 km in diameter) and thus suggest to concentrate conservation efforts within such medium-scale areas, e.g. by maximizing the density of allocated semi-natural habitats. In this context, to develop more effective management practices, it is necessary to consider the effect of landscape composition and structure on the occurrence and spatial organisation of the species or ecologically related species. We need to better understand how ecological correlates shape the diversity of targeted biological groups, and at which optimal spatial scale, in order to conceive efficient conservation and management practices for maintaining or restoring diversity at local and landscape scales.

Here we focused on wild bees as an example of a species rich community in an intensive agricultural system in western France, in the buffer area recommended by Rollin et al. (2015). In order to guide conservation efforts, we aimed to understand the relative importance of the floral context at the local scale and the quantity of surrounding semi-natural habitats at the landscape scale that promote wild bee diversity in farmlands.

2. Material and method

2.1. Sampling design

Field data is from Rollin et al. (2015, 2013), with a specific focus on those sampling sites surrounded by *semi-natural herbaceous* habitats. This survey was carried out in the springs and summers of 2010, 2011 and 2012 in the LTSER *Zone Atelier Plaine & Val de Sèvre*, a 450 km^2 intensive agricultural territory in western France, that comprises over 16,000 fields (Fig. 1; Bretagnolle et al., 2018). This study area consists mostly of intensive arable land, with annual crops accounted on average for 80% of total land cover (40% for cereals, 9% for oilseed rape, 12% for sunflower and 9% for maize). Temporary and permanent grasslands, as well as small but numerous remnant patches of forest, covered only between 3% and 7% of the total land but permit to provide highly heterogeneous landscapes in some areas. A spatially extensive sampling strategy was therefore favoured to best cover the

variety of ecological contexts throughout the study area. Sampling sites were located in 30 grid cells (ten cells sampled per year) randomly drawn without replacement from a 3.3 x 3.3 km spacing grid covering the whole study area (see Rollin et al., 2015, 2013) (Fig. 1). Local bee diversity was sampled using capture surveys of flower-visiting bees in a total of 702 sites in semi-natural herbaceous habitats (permanent grasslands, external field margins and spontaneous weed plants in crops or stubble fields) over the three years, including three relevant periods in the bee activity season: (i) the rapeseed (*Brassica napus*) flowering period in April-May, (ii) the food restriction period, with no mass-flowering crop available, in late spring or early summer and (iii) the sunflower (*Helianthus annuus*) flowering period in July-August. Surveys, for each sampling period during a given year, were conducted for 12–15 consecutive days. Sampling sites were surveyed once by capturing flower-visiting bees with a net along walking transects of 50 m long and 2 m wide, in only one direction (i.e. without back and forth), during 15 min sampling sessions. Sites were sampled between 10:00 and 19:00, and only during good weather (Hoehn et al., 2010; Westphal et al., 2008). We consider here the local (α) wild bee diversity, which was measured as the bee species richness, i.e. the number of distinct wild bee species, observed at a given sampling site (walking transects). We then applied generalized linear mixed models (GLMMs) to explore how α diversity is affected by a suite of *a priori* relevant ecological correlates, as well as by some potentially confounding variables (mainly due to sampling design).

2.2. Local and landscape scale ecological determinants of bee richness

The main local-scale variable liable to affect bee diversity was the floral species richness at the sampling site. The main landscape-scale variable considered in this study was the percentage of semi-natural habitats within a given radius around sampling sites. We chose a series of 10 radii, ranging from 200 to 3000 m so as to cover the distance range with the steepest spatial accumulation of bee species (Rollin et al., Unpublished. Data, see Supplementary material). This range also roughly covers the range of wild bee maximum foraging distances reported in the literature (reviewed by Zurbuchen et al., 2010b). Herbaceous and woody semi-natural habitat areas were computed for each site and radius, based on land use maps made available on a Geographic Information System (ArcView® V.9.0.) and up-dated twice a year (see, e.g. Marrec et al., 2014; Rollin et al., 2013). Fallows, permanent and temporary grassland surfaces were recorded throughout the study area and were summed to estimate semi-natural herbaceous habitat areas. Field and road margins were assigned to thin 2 m wide strips on both sides of the road and trail networks, and subsequently handled as an approximation of interstitial semi-natural herbaceous habitats. Likewise, the assignment of linear landscape elements (hedgerows and forest edges) to the confines of ligneous semi-natural habitats followed the procedure in Henry et al. (2012). Regardless of the chosen radius, we combined herbaceous and ligneous semi-natural areas (e.g. hedgerows) under the general denomination of *semi-natural habitat*.

In addition to floral species richness we distinguished between two types of sampling sites, namely grassland sampling sites (permanent and temporal grasslands, fallows) vs. marginal sampling sites (external field margins, road margins) at the local scale. We were also concerned that bee diversity at a given sampling site would be partly influenced by two important sampling features, the total number of captured bees and/or the density of floral units (i.e. all open flowers and inflorescences that could be visited by bees; Potts et al., 2003) found along the sampling transect. To assess floral density, all the distinct flower species found along sampling transects were recorded and an abundance score of 1, 10 or 100 was assigned to each of them according to a visually estimated minimal number of floral units. Species scores were then summed within each site (walking transect).

Bee foraging activity is also strongly dependent on certain temporal drivers that need be controlled for, particularly temperature variations
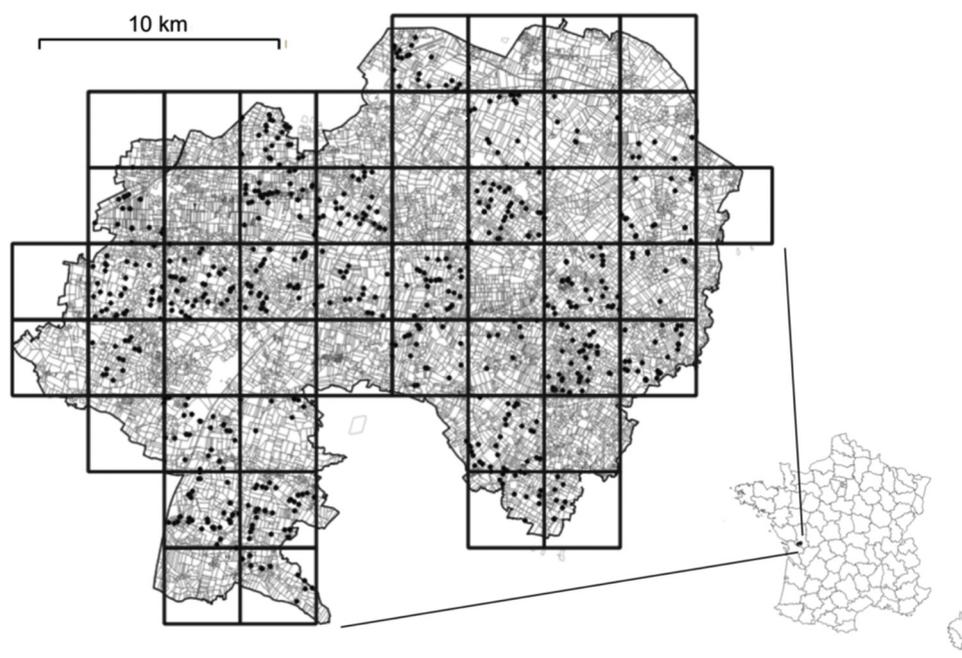
on a daily scale (Corbet et al., 1993; Kelber et al., 2006; Kwon and Saeed, 2003) and phenological variations across seasons (Michener, 2007; Tylianakis et al., 2005; Westrich, 1989). Both temperature at the time of capture and period of the season were introduced into the analysis as additional explanatory variables. Temperature was coded as a quadratic function because its effect on bee foraging activity has been showed to be non-linear (Rollin et al., 2013). The *Period* of the season refers to the three study periods within a year (i.e. rapeseed in spring, sunflower in early summer, and the food restriction period in-between), and was further tested in statistical interaction with the other ecological correlates assuming that the importance of ecological correlates might not be stationary over time.

Finally, special attention was paid to account for inter-annual variation and spatial autocorrelation among neighbouring sampling sites, which are typical sources of random statistical noise, and were taken into account by specifying appropriate random grouping structures within the frame of generalized mixed models (Rollin et al., 2013). Spatially neighbouring sites were grouped by grid cell identity, which were then nested within years (see also below).

2.3. Statistical analysis

To evaluate the influence of the local and landscape context on bee diversity we used generalized linear mixed model (GLMM) with a zero-inflated negative binomial distribution of errors. This type of model was chosen because no bees were caught in 31.7% of the sampled sites (223 out of a total of 702 sites). Bee richness was used as the response variable. Fixed effects included local- and landscape-scale variables, climatic conditions and season. Local variables were represented by (i) *habitat type* (grasslands vs field margins), (ii) *floral richness*, (iii) *floral density* and (iv) interactions between *habitat type* and *floral richness*. Indeed, Öckinger and Smith (2007) have shown that the quality of floral resources can change according to the type of semi-natural habitat (grasslands vs. field margins) and significantly affects bee species richness and density of other insect pollinators. Landscape variables included the *proportion of semi-natural habitats* that we computed at different landscape scales (see above).

Possible confounding factors or other sources of significant statistical noise were investigated in our dataset. The possible biases were (i) distribution gradients at the scale of the study area (i.e. non-stationary),

(ii) inter-annual variation, (iii) seasonal variation, (iv) temperature-dependent variation in bee foraging activity at the daily time scale and (v) the local abundance of bees. Possible bias due to a large-scale distribution gradient was systematically accounted for by including the grid cell identity as a random factor within the frame of a mixed model structure, i.e. generalized linear mixed models (GLMMs) (Rollin et al., 2013). Likewise, inter- annual variations were considered by including the year as a higher-level random variable, within which grid cells were nested (Rollin et al., 2013). The observed number of species recorded in a sample (or a set of samples) is very sensitive to the number of individuals (Gotelli and Colwell, 2001). For this reason, we added as co-variable the *number of bees* at each sampling site. Seasonal variations were accounted for by including the period as a factor. Moreover, bee foraging activity is affected by temperature but its effect on bee occurrence frequency or bee abundance might not be linear (Corbet et al., 1993; Kelber et al., 2006; Kwon and Saeed, 2003). Thus, temperature dependent variations were considered by introducing standardized and squared temperature data (∘C) as a fixed variable into the model (Saveliev et al., 2009).

Based on AIC values, we determined that 1000 m was the scale at which the proportion of semi-natural habitat returned the best model fit. Accordingly, results and predictions in this study were presented at this landscape scale. All analyses were computed using the R software, version 3.4.2 (R Development Core Team, 2017).

3. Result

3.1. Effect of ecological correlates on bee diversity at local and landscape-scales

Ecological correlates that explained α diversity were floral richness, proportion of semi-natural habitats in the landscape and type of semi-natural habitats, as well as the period (three levels) and total number of bees per sampling site (Table 1, Fig. 2). Floral richness at the local scale ($Z = 3.61$; $p < 0.01$; Fig. 2A) as well as the proportion of semi-natural habitats at a radius of 1000 m ($Z = 1.892$; $p = 0.05$; Fig. 2B) were positively related to bee richness. Bee richness was higher in grasslands than in field margins ($Z = -2.689$; $p < 0.01$; Fig. 2C). In addition, bee richness was significantly higher during the sunflower flowering period (Fig. 2D) than in both the rapeseed ($Z = -4.643$; $p < 0.01$) and the food

Table 1

Ecological correlates associated with the local (α) bee richness, based on GLMMs and log-likelihood ratio tests. The "×" denote statistical interactions. Ecological correlates with p-value < 0.050 are strictly significant.

Type of effect	Estimate	Std.Error	Z value	p-value
Floral diversity	0.067	0.019	3.610	< **0.010**
Floral density	0.001	0.001	0.266	0.790
Period 1 vs 2	0.010	0.090	0.113	0.993
Period 1 vs 3	−0.438	0.094	−4.643	< **0.010**
Period 2 vs 3	−0.448	0.084	−5.342	< **0.010**
Type of SN habitat	−0.346	0.129	−2.689	< **0.010**
Quantity of SN habitat (1000 m radius)	0.811	0.429	1.892	**0.050**
Type of SNh x Floral diversity	0.023	0.022	1.055	0.290
Number of bees	0.048	0.002	18.186	< **0.010**
Temperature	−0.049	0.061	−0.812	0.420

restriction periods ($Z = -5.342$; $p < 0.01$). Finally, bee richness was positively correlated with total bee abundance ($Z = 18.186$; $p < 0.01$).

3.2. Effect of equilibrium between local and regional ecological correlates on bee diversity

Bee richness was positively related to richness of flowering plants. Moreover, the magnitude of this effect (represented by the difference between upper and lower limits of the shared area in Fig. 3) was overall higher than that predicted for a change in availability of semi-natural habitats within a 1000 m radius, at least for the upper range of semi-natural habitat proportions (20–30%).

Furthermore, the magnitude of the effect of the floral species richness was higher during the sunflower flowering period than during the two other periods. Predictions of bee diversity for periods 1 and 3 (respectively during the flowerings of rapeseed and sunflower) were more similar to each other than to those of period 2 (food restriction period), despite overall similarity response pattern between all three periods, which included increasing bee richness with higher floral richness, higher bee abundance and higher proportion of semi-natural habitats. During the sunflower flowering period (July-August), local bee diversity was higher than during other periods. The lowest measure of bee richness would be expected during the food restriction period
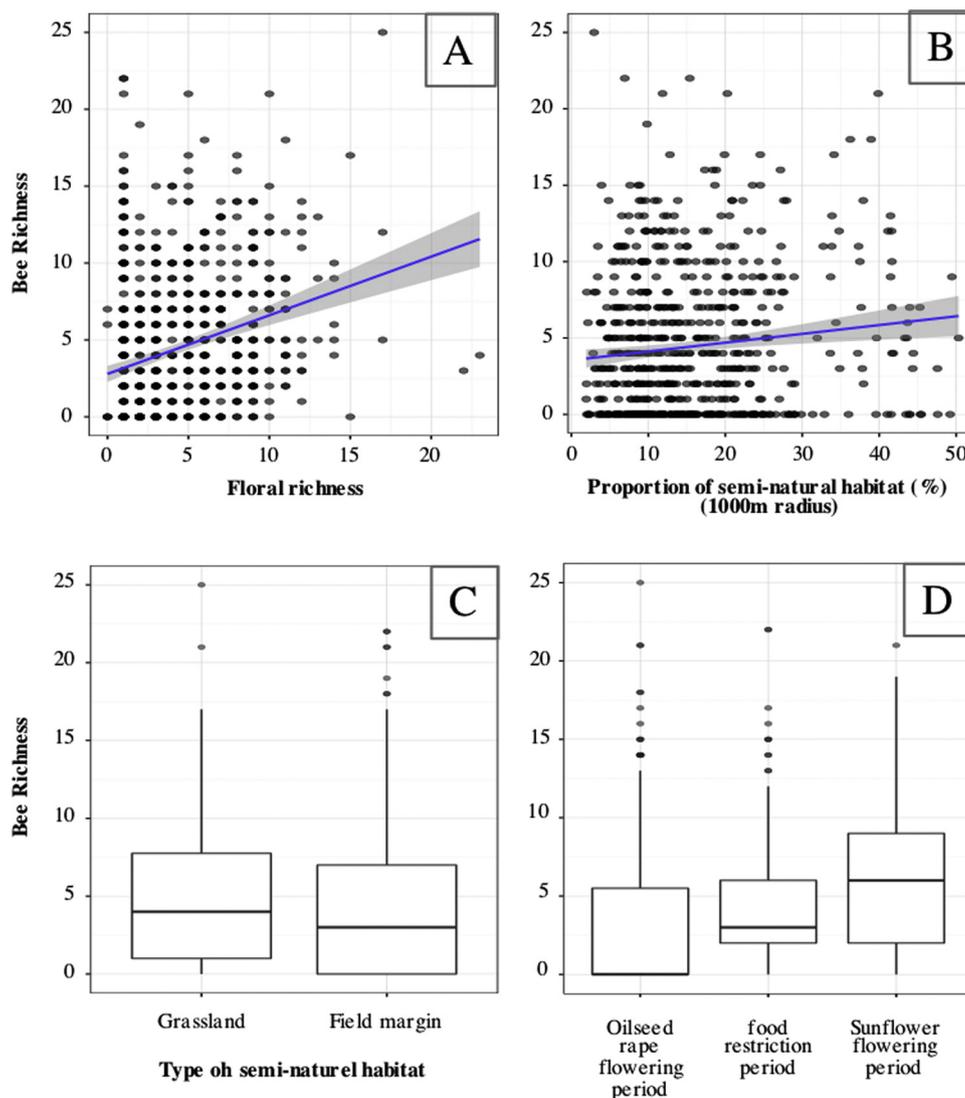

Fig. 2. Variation in bee richness according to local floral richness (A), proportion of semi-natural habitat in the landscape (buffer of 1000 m radius; B), semi-natural habitat type (C) and flowering periods (D). Shaded areas (A, B) stand for the confidence interval (95%).
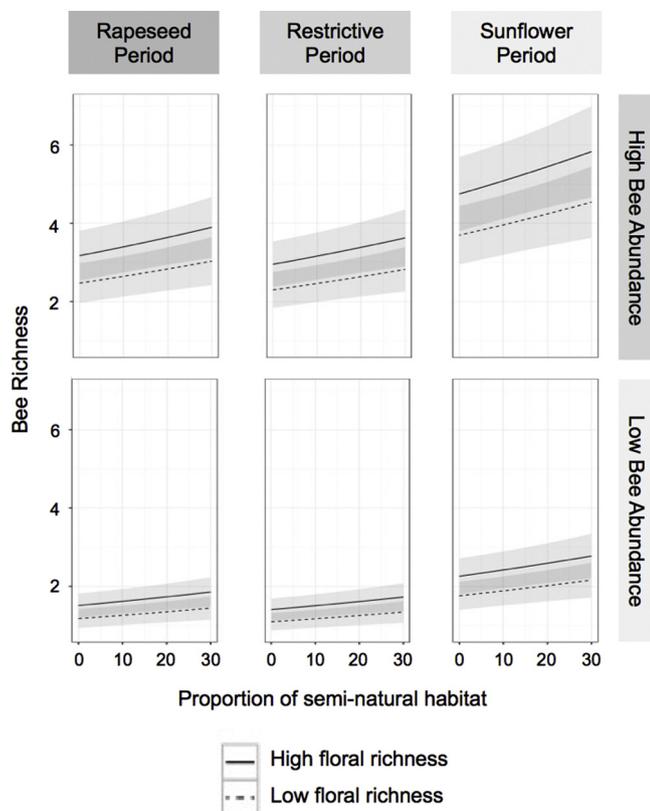
Fig. 3. Model predictions of the bee richness variation according to (i) local bee abundance (high: top row; third quartile = 23 bees / and low: bottom row; first quartile = 5 bees), (ii) local floral richness (high: black curves; third quartile = 8 species / and low: dashed curves; first quartile = 2 species), (iii) proportion of semi-natural habitats in the landscape (from 1 to 30% of the 1000 m radius), for (iv) each period (Column 1: rapeseed flowering period; Column 2: food restriction period; Column 3: sunflower flowering period). Shaded areas stand for the confidence interval (95%).

(June).

4. Discussion

4.1. Effect of ecological correlates at the local scale

Previous studies have suggested that habitat type and quality are important factors in explaining the diversity of wild bees as they are usually related to the floral richness of resources for pollinators (Biesmeijer et al., 2006; Carvell et al., 2006; Öckinger and Smith, 2007). Accordingly, we found that bee diversity increased with increasing richness of floral resources. Moreover, Williams et al. (2012) have shown that an increase in the quantity of flowers in the vicinity of bumble bee colonies had a positive effect on their growth. Increased floral richness promotes higher bee diversity most likely due to the pollen and nectar specialisations of bees. Behavioural and structural adaptations of bee species (e.g. density and localisation of the mass of stiff hairs for collecting pollen grains) can determine the type of pollen collected (Michener, 2007; Thorp, 1979). Likewise, nectar selection is strongly determined by morphological constraints in bee species (e.g. tongue length, body size) and by quality and quantity of nectar rewards delivered by floral resources (Potts et al., 2003; Roubik and Buchmann, 1984).

Secondly, we found that grasslands supported higher bee diversity than field margins. Grasslands usually have larger areas than field margins; therefore, they are expected to provide more diverse and greater amounts of floral resources. This is supported by our results that

show that floral richness and floral density is greater in grasslands during two of the three studied periods (Rollin et al., Unpublished. Data). In addition, in our study system vegetation of field margins is frequently scythed/mown for security (along the road) or for reducing the risk of propagating pathogens or crop predators (pers. obs.), which may explain the lower bee diversity detected when compared to grasslands. Moreover, field margins can receive various pesticides as drift that come from the neighbouring crops (Botías et al., 2015). Our results are consistent with those found by previous studies that show increased richness of insect pollinators in grasslands with high local floral abundance with relation to field margins (e.g. Öckinger and Smith, 2007).

4.2. Importance of the quantity of semi-natural areas and the interaction with local bee population size

As expected we found a strong effect of the proportion of semi-natural vegetation on wild bee diversity (e.g., Goulson et al., 2008; Le Féon et al., 2010; Senapathi et al., 2016). Semi-natural habitats are the most favourable habitat types for wild bees, providing feeding and nesting resources and therefore acting as population refuges (Goulson et al., 2010; Öckinger and Smith, 2007). They contain the most abundant and diversified wild bee communities (Rollin et al., 2015, 2013) and increasing their proportion in agricultural landscapes may promote bee species diversity (Duelli and Obrist, 2003; Le Féon et al., 2010; Senapathi et al., 2016). Similarly, landscape-scale ecological correlates also affect bee diversity: the loss of natural and semi-natural habitats or the transformation of permanent grasslands into annual crops both have negative effects on wild bee species (Breeze et al., 2012; Goulson et al., 2008; Le Féon et al., 2010; Senapathi et al., 2016).

However, the magnitude of the effect of semi-natural habitat proportion on bee richness was higher at high bee abundance than at low bee abundance. This could be explained by the dual function of semi-natural habitats, as a source of both feeding resources and nesting sites (Goulson et al., 2010; Öckinger and Smith, 2007)

4.3. Seasonal effect on the magnitude of the ecological correlates

Although predictions of bee diversity trends were similar between periods (bee diversity increasing with floral richness, proportion of semi-natural surrounding sampling sites and bee abundance), we detected a highly significant seasonal effect on bee diversity. Bee diversity during the rapeseed and sunflower flowering periods was higher than during the food restriction period (Fig. 3), while the regional bee diversity γ was higher overall during the food restriction period (Rollin et al., 2015). Competition with the honey bee *Apis mellifera* could explain these results. During mass flowering crop periods, honey bees foraged preferentially in rapeseed and sunflower fields and were found much less frequently and in lower abundance in wild floral resources of herbaceous semi-natural habitats (Rollin et al., 2013). In the absence of mass-flowering crops, however, honey bees foraged more frequently in semi-natural herbaceous resources, a shift in floral resource exploitation that may lead to greater competition for floral resources between wild bees and the honey bee. Despite many studies seeking evidence for competition between honey bees and wild bees and possibly, a negative effect of the honey bee on wild bee communities, current evidence is scarce (Goulson and Sparrow, 2008; Gross, 2001; Henry and Rodet, 2018; Hudewenz and Klein, 2013; Roubik, 1978; Shavit et al., 2009; Thomson, 2006, 2004). Yet Magrach et al. (2017) recently showed that honey bee spillover from crops into semi-natural habitats leads to a reassembly of plant–pollinator interactions through increased competition with other pollinator species.

In addition, in our study area, it should be noted that the global diversity in semi-natural herbaceous habitats (regional bee diversity; γ) during the food restriction period was similar to that of the sunflower period and even significantly higher than that of the rapeseed period,

while local diversity (α) showed the opposite trend (Rollin et al., 2015). This suggests that the among-community diversity changes or the spatial turnover (Crist et al., 2003) was higher at an intermediate period than earlier or later in the season (Rollin et al., 2015). In other words, at the second period, wild bee diversity might be spatially re-organised, with lower local diversity and higher spatial turnover. Interestingly, this scenario would be compatible with the hypothesis that honey bees exclude wild bees by local competition in between the two mass-flowering periods, a period of reduced food availability (Requier et al., 2015). An effect of local competitive exclusion is plausible (Henry and Rodet, 2018) given that foraging honey bees may occur locally at very high abundances owing to their ability to communicate the location of floral resources (Dyer, 2002).

4.4. Spatial scale and potential species bias

Our results and prediction focus on a 1000 m buffer landscape scale, as this was the resolution that better explained the distribution of our data (AIC model selection). This scale is consistent with results found in similar studies (e.g. Connelly et al., 2015; Zurbuchen et al., 2010b) and probably reflects foraging range of most bee species. Recent evidences suggest that maximum foraging range of wild bee species, especially small-size bees, has been underestimated in various previous studies (Zurbuchen et al., 2010b). For example, Castilla et al (2017) found that all bee species sampled in this study (n = 10), even very small-sized bees, such as several Halictidae spp. or *Trigonisca buyssony* (Apidae) amongst others, exhibited foraging movements that exceeded the 1000 m. However, evidences found in Europe suggest that only a few bee species are able to exceed this distance (Greenleaf et al., 2007). The majority of wild bee species do not move farther than 500 m away from their nests due to the associated energetic costs (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010a). Given the spatial scale considered (1000 m buffer) in this study, our results might thus underestimate species richness and might be biased towards large-sized species.

4.5. Implications for conservation and farmland management

The results of our study suggest that promoting local diversity of floral resources may be more efficient in increasing wild bee richness than conserving or restoring adjacent natural/semi-natural habitats (Fig. 2). Yet both strategies provided positive effects in increasing bee diversity and are expected to be complementary. On one hand, semi-natural habitats at the landscape scale are fundamental for providing nesting resources to wild bee populations, which are usually scarce in farm fields and surrounding field margins. On the other hand, increasing the proportion of semi-natural vegetation would indirectly promote total floral richness found within these habitats, and accentuate their positive effect on bee diversity. This positive effect could be mitigated by floral abundance in these habitats. In our study, semi-natural patches frequently provided scarce floral resources as measured by floral abundance (pers. observation; Rollin et al., 2013). In our model-prediction approach (Fig. 3), the greatest landscape effect was predicted beyond a 20–25% threshold for herbaceous semi-natural habitats (within a 1000 m radius). However, it might be unrealistic to increase the area of semi-natural habitats in these proportions. In fact, this value far exceeds the land cover farmers may actually sustain at the farm scale. Indeed, areas of ecological interest in arable lands (trees, hedges, fallow land, grass strips, buffer strips at the edge of fields, woods and forests) must be at least 3% of the Useful Agricultural Area (target of 7% of UAA by 2020) (Heidsieck and Allier, 2013). Thus, promoting this type of habitat appears to be a very promising measure for increasing bee diversity, but increasing semi-natural habitats to 25% of the land cover or more would be difficult to implement and its feasibility could vary widely depending on crop type and the initial landscape context. Moreover it is necessary to diversify the types of

semi-natural habitat, in order to promote a variety of floral resources and nesting sites, the latter being indispensable in allowing permanent wild bee populations to settle in the landscape (Carrié et al., 2018; Goulson et al., 2010; Senapathi et al., 2016). Therefore, in highly intensive farmland landscapes, a mixed strategy involving improved semi-natural elements as well as promoting floral resources in crops (through, e.g. herbicide reduction) is likely the most promising scenario, whereas in less intensive agricultural contexts, protecting or restoring the diversity of semi-natural herbaceous habitats would be favoured.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.01.012.

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