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Solitary bee abundance and species richness in dynamic agricultural landscapes

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ABSTRACT

We investigated the influence of the landscape structure on solitary bee abundance and species richness in an agricultural area of western France. We focused on the role of semi-natural habitats, oilseed rape (OSR) and other crops. Our originality was to consider not only the spatial heterogeneity of the crop field mosaic but also its temporal heterogeneity through the crop rotations.

Solitary bees were caught with colored pan traps in 15 margins of OSR fields and 35 margins of non-OSR fields. We found that solitary bee abundance and species richness were higher in margins of OSR fields than in margins of non-OSR fields, showing that early spring-flying species widely use this mass flowering crop. However the high number of rare species in margins of non-OSR fields (21 species recorded exclusively in these margins) highlighted the importance of these margins for the conservation of solitary bee diversity.

The influence of the landscape context on solitary bees showed contrasted results according to the type of margin and the spatial scale. At the finest spatial scale, abundance in margins of OSR fields increased with increasing proportion of non-flowering crops (cereals and temporary grasslands) in the current year. At large spatial scales, solitary bee abundance in margins of non-OSR fields was positively affected by the proportion of long-term grasslands. Moreover, the proportion of fields only sown with cereals during the last 5 years negatively affected abundance and species richness at the large scales whereas the proportion of mixed fields (at least 1 year of grassland in the rotation) had a positive effect on species richness.

We showed that accounting for the cumulative effects of field cover and management through the crop rotations is relevant for studying solitary bee communities. The introduction of less intensive covers, such as temporary grasslands, in cereal rotations positively influences these communities.

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1. Introduction

Pollinators provide a crucial ecosystem service through their role in the sexual reproduction of both wild plants and crops (Klein et al., 2007). Bees (Hymenoptera, Apiformes) are known to be the most important group of pollinators worldwide, and their ongoing decline and its potential ecological and economic consequences are therefore of major concern (Biesmeijer et al., 2006; Gallai et al., 2009; Potts et al., 2010). To maintain their populations in a land-

scape, wild bees require nectar and pollen as food for brood and adults as well as suitable nesting sites (Westrich, 1996). These resources must occur within the foraging range of the species, which ranges from several hundred meters for most solitary bees to a few kilometers for larger species such as bumblebees (*Bombus* spp.) (Gathmann and Tschardt, 2002; Greenleaf et al., 2007).

A recent large-scale study, carried out on five arthropod taxa in seven European countries, showed that bees are among the most sensitive species to agricultural intensification (Hendrickx et al., 2007). Intensive agriculture negatively affects wild bees for several reasons: crop fields replace suitable habitats while being themselves unsuitable (Klemm, 1996) because of (i) disturbance like harvesting and tillage that impede the nesting of most ground-nesting species (Shuler et al., 2005; Morandin et al., 2007), (ii) fertilizers, herbicides and intensive grazing that reduce floral

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resources in fields and in their adjacent elements (such as field margins or roadsides) (De Snoo and Van der Poll, 1999; Kleijn and Verbeek, 2000; Hyvönen et al., 2003), (iii) insecticides and other pesticides that induce direct mortality or sublethal effects (Desneux et al., 2007).

At the field scale, the negative effects of intensive farming practices on bees have been demonstrated mostly by comparing organic and conventional agriculture (Morandin and Winston, 2005; Clough et al., 2007; Holzschuh et al., 2007). At the landscape scale, most studies have dealt with the effects of semi-natural habitat area and fragmentation (Steffan-Dewenter and Westphal, 2008). Bee abundance and diversity are typically fostered as the proportion of semi-natural habitats (grasslands, wooded elements as forests and hedgerows, etc.) increases in a given area (Steffan-Dewenter, 2002; Steffan-Dewenter et al., 2002; Sjödin et al., 2008; Le Féon et al., 2010). In landscape-scale studies, cropland is generally considered as a homogeneous unsuitable area for bees, except entomophilous crops, such as oilseed rape (OSR) *Brassica napus*. OSR provides open flowers so that nectar and pollen are readily available to a wide range of flower-visiting insects. Moreover it flowers in early spring when wild flowers are rare in semi-natural habitats. Westphal et al. (2003, 2009) and Herrmann et al. (2007) demonstrated that this crop positively enhance early colony growth in some bumblebee species. Delbrassine and Rasmont (1988) and Calabuig (2000) showed that many solitary bee species are present in OSR fields but little is known about the influence of OSR on the spatial distribution of solitary bees at the landscape scale.

Recently, the heterogeneity of farming practices in arable land has been studied at the landscape scale: Williams and Kremen (2007) and Holzschuh et al. (2008) have shown that bee diversity, abundance and offspring production are enhanced by the proportion of organic vs. conventional crop fields. These studies referred to the spatial heterogeneity of the crop field mosaic. On the contrary the link between the temporal heterogeneity of the crop field mosaic and bee communities remains mostly undocumented. In particular, the relationship between the past use of fields and their suitability for bees, or for biodiversity in general, has been poorly investigated. Crop rotation is a traditional farming practice that aims at maintaining soil fertility and preventing the magnified impacts of pathogens, pests or weeds that often occur when a single species is cropped repeatedly. Allowed by increasing use of pesticides and fertilizers, the simplification of crop rotations is synonymous with agricultural intensification (Stoate et al., 2001). The diversification of rotations is thus presented as a possible mean of reducing chemical inputs and enhancing biodiversity in agricultural landscapes (McLaughlin and Mineau, 1995). Positive impacts of the diversification of crop rotations on biodiversity may result from: (i) the direct consequences of the global decrease of chemical inputs on the fauna and flora; (ii) the covers introduced in the rotations that may provide additional food resources or better conditions than intensively managed crops. For example, covers like temporary grasslands or fallows provide relatively stable habitats for the maintenance of wildlife in a landscape (Stoate et al., 2001), and legumes, used for their ability to fix atmospheric nitrogen, are mass flowering resources for flower-visiting insects (Köpke and Nemecek, 2010).

So far, the influence of crop rotations on bee communities has been mostly ignored in the literature. Yet, current bee abundance and diversity may be seen as the result of the cumulative effects of landscape composition over the recent years. In this study, our main hypothesis is that accounting for the recent history of field use, through crop rotations, is relevant to better understand the impact of agricultural intensification on bee communities. We investigated whether the composition and structure of the agricultural landscape affect solitary bee

abundance and species richness by testing the following specific hypotheses:

- (1) *Role of mass flowering crops*: OSR locally enhances the presence of solitary bees.
- (2) *Role of the current landscape*: when considering the landscape composition on the year of sampling, semi-natural habitats (wooded elements and long-term grasslands) have positive effects on solitary bee abundance and species richness whereas crop fields have negative effects.
- (3) *Role of crop rotations*: accounting for the recent past use of crop fields allows studying the cumulative effects of field covers on solitary bees. Therefore it provides better or different insights about landscape effects, compared with the standard approach that considers only current land use. Our hypothesis is that rotations with grasslands are associated with greater solitary bee abundance and species richness than cereal-dominated rotations.

In temperate landscapes, authors typically distinguish two groups of wild bees (e.g. Steffan-Dewenter et al., 2002; Winfree et al., 2009): bumblebees (*Bombus* spp.), which are eusocial species, and “solitary bees” (even if different forms of primitive or advanced social behavior exist in some species). We focused on solitary bees for two main reasons: (i) several studies carried out in temperate landscapes have shown that solitary bees are more sensitive to human disturbance than bumblebees because of their more specialized floral or habitat requirements and usually smaller foraging ranges (Steffan-Dewenter et al., 2002; Biesmeijer et al., 2006) and (ii) these species have a low reproductive rate compared to social bees and many other insects (Tepedino and Parker, 1983; Danforth, 1990) so that a small reduction in offspring numbers may have large consequences if it occurs repeatedly over several years.

2. Materials and methods

2.1. Study area

Our study area was a hedgerow network (“bocage”) landscape of 10 km east–west by 15 km north–south, located 60 km north of Rennes, Brittany, France (48°36'N, 1°32'W). This area called “Zone-Atelier de Pleine-Fougères” and mainly devoted to milk production is part of the International Long Term Ecological Research (ILTER) sites and French “Zones Ateliers” networks. Our study area was composed of: (i) semi-natural elements: hedgerows, small woodlots, and long-term grasslands; (ii) cropland (cereals – maize, *Zea mays*, wheat, *Triticum aestivum* and barley, *Hordeum vulgare* – and temporary grasslands) that was examined through two approaches, with and without accounting for their land use history over the recent years; (iii) some OSR fields.

2.2. Bee sampling

Solitary bees were sampled in 2007 on 50 field margins, 15 of which were along OSR fields and the 35 others were randomly located among other fields (grasslands or cereals). OSR was a minor crop and those 15 fields were almost all the OSR fields in the study area in 2007. They ranged in size between 0.4 and 4.9 ha with an average of 2.5 ha. A set of three colored pan traps (one yellow, one white and one blue) was placed linearly in random order 2 m from one another in the middle of each field margin. The traps were made of 500 ml plastic bowls (<http://www.pro-pac.de/>) with the inside sprayed with an UV-reflecting paint. They were mounted on a wooden pole at vegetation height, filled with 400 ml of water with a drop of detergent and then exposed for 24 h following Westphal

et al. (2008). Three samplings were conducted at 5–7 day intervals from mid-April to early May 2007 during the OSR flowering period and under suitable diurnal weather conditions for bee activity (minimum of 15 °C, low wind, no rain, and dry vegetation, Westphal et al., 2008). Specimens were stored in 70% ethanol, then dried, mounted and identified to the species level, except for some individuals that could only be determined to the level of species groups (*Andrena rufula/fulvida* group; *Halictus compressus/simplex* group). Species names follow the ALARM Bee Database held by Stuart P.M. Roberts at the University of Reading (UK) and the reference collection of voucher specimens is held at INRA (Institut National de la Recherche Agronomique) in Avignon (France).

2.3. Characterization of landscape composition and structure

To account for the recent history of land use, a period of 5 years (2003–2007) was considered as it represents the average length of a complete crop rotation in the study area (Thenail et al., 2009). Using ArcGIS 9.3 software (ESRI, Redlands, CA), the whole study area was mapped from aerial photographs (vector map), and land-use was referenced for each field and each year (Nabucet, J., Rantier, Y., Schermann, N., unpublished data). In a second step, we derived two raster maps (resolution of one pixel for 5 m × 5 m) from this geographic information, namely (i) a landscape cover map at the moment of bee sampling (April–May 2007), and (ii) a crop rotation map summarising land-use history over the 2003–2007 period. The latter map was made by distinguishing two classes of crop fields: the fields that were sown only with cereals over the past 5 years (hereafter referred to as “cereal fields in 2003–2007”) and fields where crop rotation included from 1 to 4 years of grassland (referred to as “mixed fields”). Landscape composition was quantified in square windows centred on sampling points using Chloé software (Baudry et al., 2006). We chose three window sizes that cover the range of relevant scales for flight and foraging distances in solitary bees (Gathmann and Tschardt, 2002): 400, 800 and 1200 m in width. For each window size, we determined the proportion of (i) long-term grasslands (≥5 years), (ii) hedgerows and woodlots, (iii) crop fields in 2007 (maize (bare soil at the time of sampling), wheat, barley and temporary grasslands), (iv) oilseed rape fields in 2007, (v) cereal fields in 2003–2007 and (vi) mixed fields. The 50 sampling points can be plotted along gradients of proportions of these different cover types (Appendix A).

Additionally, two variables were used to describe the landscape structure: the total edge length and a metric of landscape grain. First, the total edge length was calculated by pooling all the pixels of road, lane, hedgerow or woodlot that constituted an interface with fields. Second, we used a metric of landscape grain relating to the spatial organization of hedgerows. Landscape grain is often used to characterize structures from fine grain (many small elements) to coarse grain (fewer large elements). Generally speaking, networks with a high density of hedgerows are “fine grain”, i.e. the average mesh of the landscape is small, while “coarse grain” networks have a low density of hedgerows. Our metric was calculated as follows (see also Appendix B for further explanations): the distance of every pixel of the raster map to the closest hedgerow or wood edge was measured. We used three classes of distance: less than 50, 50–100 and more than 100 m, as each has a distinct microclimate (Guyot and Seguin, 1976). Then the number of pixels in the different classes for windows of different sizes (250, 500 and 1000 m in width) was computed for a set of points homogeneously distributed on the whole study site (i.e. a set of pixels, one pixel every 250 m). A matrix “windows × classes of distances” was obtained and then a correspondence analysis was performed to build the gradient (the first axis of the correspondence analysis). This constituted the reference space over the whole studied area. To measure the landscape grain around our sampling points,

they were considered as supplementary elements, and their location in the reference space was calculated using the coordinate of the distance classes in this space.

2.4. Data analyses

We pooled species richness and abundance over the three sampling dates for each of the 50 sampling points. Species richness represented the number of species, and abundance was the total number of individuals. Nearest neighbouring distances among sites ranged from 148.8 to 1211.5 m (mean ± SE = 496.5 ± 30.2 m). These rather short distances make community samples subject to spatial autocorrelation. We investigated this issue using Moran's tests on species richness and abundance values, normalized by a log-transformation, across 300–1800 m distance lags. This distance range was chosen to encompass three times the maximal flight distances usually recorded for most of the solitary bees (Gathmann and Tschardt, 2002). We found no significant autocorrelation at any distances. Therefore, we assumed that possible autocorrelation biases among neighboring samples could be considered as negligible.

Generalized linear models (GLMs) were performed to distinguish the effect of field margin type from that of landscape context. We computed models, including: (i) the type of field margin (OSR or non-OSR field margin) as a categorical variable; (ii) one of the landscape descriptors (landscape composition or structure) as continuous variable and (iii) the interaction of both. Analyses were repeated separately for each landscape descriptor (long-term grassland/wooded elements/crop fields in 2007/OSR in 2007/cereal fields in 2003–2007/mixed fields/metric of landscape grain/total edge length). The probability associated with each landscape variable was assessed using *F* statistic. We initially specified Poisson distribution errors in models, which best accounted for the error distribution in both abundance and species richness. We then compensated for the overdispersion by refitting models using quasi-Poisson rather than Poisson errors (Crawley, 2007). All analyses were performed with R software, version 2.9.2 (R Development Core Team, 2009).

3. Results

3.1. Bee community composition

A total of 600 individuals representing 53 species (or species groups) from nine genera were recorded (Appendix C). The most abundant genera were *Andrena* (73.5% of total abundance, 15 species) and *Lasioglossum* (10.2% of total abundance, 14 species). Two species were particularly abundant and widespread: *Andrena cineraria* (24.2% of total abundance and present on 24 sampling sites) and *Andrena flavipes* (20.8% of total abundance and present on 37 sites). All species were polylectic that is they forage for pollen on a diverse array of plant species, except *Andrena clarkella* that was oligolectic on willow (*Salix* spp.) (Roberts, S.P.M., unpublished data). Most species were short-tongued species. Moreover the community was dominated by ground-nesting species (*Andrena*, *Anthophora*, *Halictus* and *Lasioglossum* spp., 90.5% of total abundance) whereas above-ground nesting species were rare (*Ceratina* and *Osmia* spp., 0.7% of total abundance). Cuckoo bees (*Melecta*, *Nomada* and *Sphecodes* spp.), that parasitise the nests of other bee species, accounted for 8.8% of total abundance.

3.2. Effect of the type of field margin

The OSR vs. non-OSR effect was highly significant for both solitary bee abundance and species richness in all models computed

Table 1
Results of the generalized linear models for the response variables solitary bee abundance and species richness performed at three spatial scales. The type of field margin is margin of oilseed rape field or of non-oilseed rape field. $df = 1$ in all cases. Only the significant P values are listed ($P \leq 0.05$).

Explanatory variables	Response variables											
	400 m				800 m				1200 m			
	Abundance		Species richness		Abundance		Species richness		Abundance		Species richness	
	F	P	F	P	F	P	F	P	F	P	F	P
Permanent elements												
Type of field margin (A)	49.0	<0.001	9.7	0.003	52.0	<0.001	10.5	0.002	52.3	<0.001	11.3	0.002
% of long-term grasslands (B)	1.8	–	1×10^{-05}	–	0.2	–	1.2	–	0.3	–	3.7	–
A \times B	3.0	–	1.5	–	5.3	0.025	1.8	–	4.5	0.039	2.2	–
Type of field margin (A)	47.4	<0.001	10.0	0.003	45.7	<0.001	9.7	0.003	43.2	<0.001	9.6	0.003
% of wooded elements (B)	1.1	–	0.03	–	0.1	–	0.2	–	0.1	–	0.3	–
A \times B	2.7	–	2.8	–	2.0	–	1.7	–	0.2	–	0.5	–
Land use in 2007												
Type of field margin (A)	58.0	<0.001	10.0	0.003	46.6	<0.001	9.5	0.003	44.8	<0.001	10.0	0.003
% of crop fields in 2007 (B)	9.7	0.003	0.9	–	3.1	–	0.1	–	0.3	–	0.6	–
A \times B	4.3	0.043	1.2	–	0.1	–	0.002	–	0.7	–	1.6	–
Type of field margin (A)	43.9	<0.001	9.8	0.003	44.6	<0.001	9.9	0.003	46.8	<0.001	9.9	0.003
% of OSR in 2007 (B)	0.1	–	3×10^{-4}	–	0.4	–	0.9	–	2.4	–	1.4	–
A \times B	0.1	–	0.8	–	0.1	–	0.4	–	0.02	–	1×10^{-4}	–
Crop rotations												
Type of field margin (A)	46.5	<0.001	10.2	0.002	51.8	<0.001	12.1	0.001	53.8	<0.001	12.9	<0.001
% of cereals fields in 2003–2007 (B)	0.5	–	0.7	–	1×10^{-4}	–	2.7	–	0.5	–	4.8	0.033
A \times B	2.3	–	2.2	–	5.3	0.026	5.9	0.019	6.1	0.017	7.0	0.011
Type of field margin (A)	53.6	<0.001	11.2	0.002	52.9	<0.001	13.3	<0.001	50.1	<0.001	12.9	<0.001
% of mixed fields (B)	6.9	0.011	6.0	0.018	5.0	0.030	8.1	0.006	1.6	–	3.5	–
A \times B	1.4	–	5×10^{-4}	–	0.8	–	4.3	0.043	2.5	–	7.0	0.011
Grain												
Type of field margin (A)	49.2	<0.001	10.2	0.003	52.3	<0.001	11.2	0.002	62.7	<0.001	12.3	0.001
Landscape grain (B)	2.3	–	2.4	–	2.1	–	4.2	0.047	0.5	–	5.7	0.021
A \times B	1.7	–	0.04	–	2.8	–	0.7	–	11.7	0.001	1.9	–

at any of the three spatial scales (Table 1). We caught 355 individuals in the 15 margins of OSR fields (mean \pm SE = 23.7 ± 3.4 per margin), but only 245 in the 35 margins of non-OSR fields (7.0 ± 0.9 per margin). The mean species richness was also higher in margins of OSR fields (7.7 ± 0.6 species per margin) than in margins of non-OSR fields (4.8 ± 0.5 species per margin). Among the 53 species, 32 were found in margins of OSR fields. Twenty-one species were found only in non-OSR field margins and six species only in OSR field margins. These 27 species were all rare species in our data set that accounted between one and six individuals in total (Appendix C). The proportion of rare species (number of species with total abundance ≤ 6 /total number of species) was significantly higher in margins of non-OSR fields (0.30 ± 0.04) than in margins of OSR fields (0.18 ± 0.04) ($t = 2.3$, $df = 44.3$, $P = 0.03$).

3.3. Effects of landscape composition

3.3.1. Semi-natural elements

The interaction “type of field margin” \times “proportion of long-term grasslands” was significant for solitary bee abundance at the 800 and 1200 m scales (Table 1). Solitary bee abundance in margins of non-OSR fields increased with increasing proportion of long-term grasslands at these scales whereas it decreased in margins of OSR fields (Fig. 1(a)). There was no significant relationship between the proportion of wooded elements and solitary bee abundance or species richness.

3.3.2. Land use in 2007

The interaction “type of field margin” \times “proportion of crop fields in 2007” was significant at the 400 m scale (Table 1). Solitary bee abundance in margins of OSR fields increased deeply with increasing proportion of crop fields in 2007 at this scale while it remained nearly unchanged in margins of non-OSR fields (Fig. 1(b)).

There was no significant relationship between solitary bee abundance or species richness and the proportion of OSR.

3.3.3. Crop fields with crop rotation component

The interaction “type of field margin” \times “proportion of cereal fields in 2003–2007” was significant for solitary bee abundance and species richness at the 800 and 1200 m scales (Table 1). Solitary bee abundance and species richness in margins of non-OSR fields decreased with increasing proportion of cereal fields at these two spatial scales whereas they increased in margins of OSR fields (Fig. 1(c)).

The proportion of mixed fields had a positive effect on solitary bee abundance at the 400 and 800 m scales and on species richness at the 400 m scale (Table 1). The interaction “type of field margin” \times “proportion of mixed fields” was significant for solitary bee species richness at the 800 and 1200 m scales (Table 1). Solitary bee species richness in margins of non-OSR fields increased with increasing proportion of mixed fields at these two spatial scales whereas it remained nearly unchanged in margins of OSR fields (Fig. 1(d)).

3.4. Effects of landscape structure

There was a significant effect of the landscape grain on solitary bee species richness at the 800 and 1200 m scales (Table 1). When landscape grain became coarser (wooded elements rare and/or clumped), species richness decreased. Moreover, the interaction “type of field margin” \times “landscape grain” was significant at the 1200 m scale for solitary bee abundance (Table 1). When landscape grain became coarser, solitary bee abundance decreased in margins of non-OSR fields but increased in margins of OSR fields. There was no significant relationship between the total edge length and solitary bee species richness or abundance.

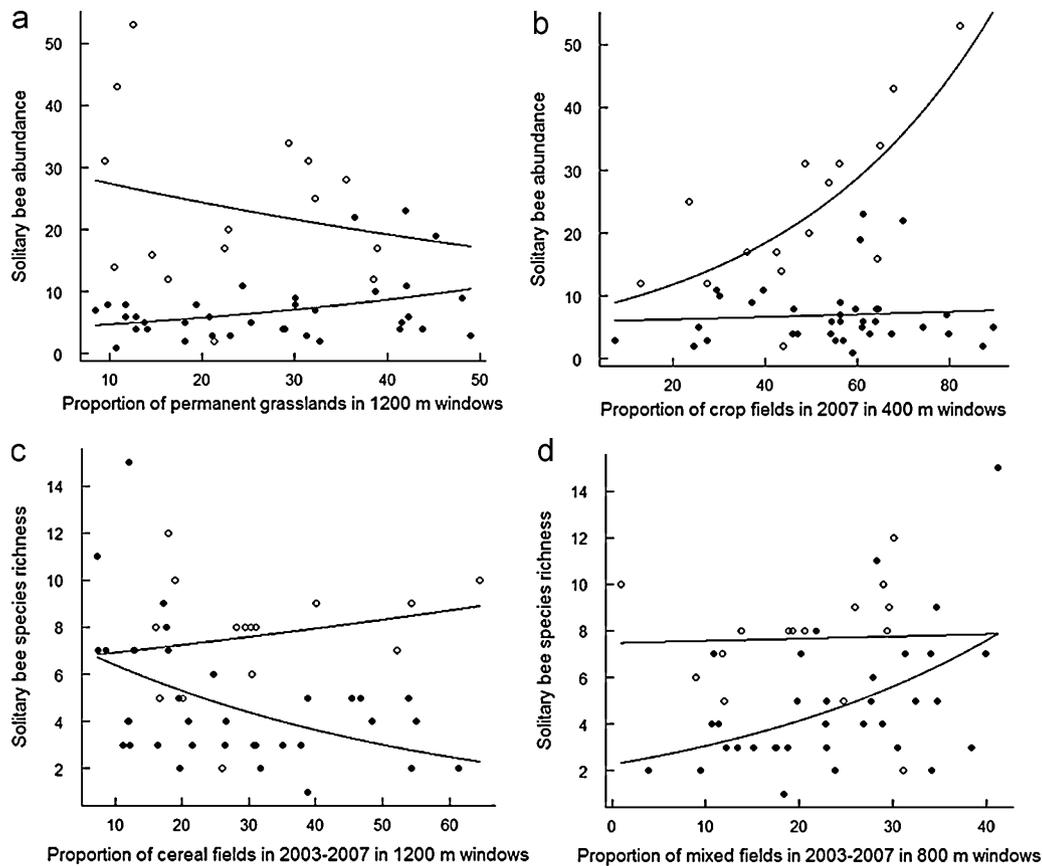


Fig. 1. Relationship between (a) solitary bee abundance and proportion of long-term grasslands in 1200 m × 1200 m windows; (b) solitary bee abundance and proportion of crop fields in 2007 in 400 m × 400 m windows; (c) solitary bee species richness and proportion of cereal fields in 2003–2007 in 1200 m × 1200 m windows; (d) solitary bee species richness and proportion of mixed fields in 2003–2007 in 800 m × 800 m windows. Predictions returned by the Poisson-family models are shown by solid lines: (○) OSR field margins, (●) non-OSR field margins.

4. Discussion

4.1. Influence of oilseed rape on the spatial distribution of bees

Our results provided evidence that OSR fields strongly determine the spatial distribution of solitary bees. The higher number of individuals and species caught in margins of OSR fields compared to randomly located field margins showed that during its blooming period, this mass flowering crop was widely used by solitary bees. OSR flowers are open flowers with nectar and pollen available to a wide range of flower-visiting insects, including short-tongued solitary bees (Delbrassine and Rasmont, 1988; Calabuig, 2000). In our study, bee species were mainly polylectic so that they could use a wide spectrum of floral resources, including Brassicaceae species like OSR. The community was largely dominated by *Andrena* spp. Our results are consistent with those of Calabuig (2000) in Denmark and Delbrassine and Rasmont (1988) in Belgium, who sampled bees in OSR fields and recorded *Andrena* spp. as the dominant genus of solitary bees as well. *Andrena* spp. are typically early spring-flying bees. We can assume that polylectic species like the most abundant *A. cineraria* and *A. flavipes* greatly benefit from the presence of OSR fields. The seasonal pattern of *Nomada* spp., *Andrena*'s cuckoo bees, was synchronised with that of their hosts. But as they do not collect pollen and nectar for their offspring, they require smaller amounts of resources and it is less necessary for them to find rewarding floral patches. Halictidae (*Halictus* and *Lasioglossum* spp.) and their cuckoos *Sphecodes* spp. emerge typically later in the season, which

explains their relatively low abundances in our sampling (Calabuig, 2000).

The positive impact of OSR might be particularly important because it flowers in early spring when wild flowers are still rare. Therefore this crop can play a major role for solitary bees that emerge at this time of the year. Concerning social species, Westphal et al. (2003) and Herrmann et al. (2007) showed that bumblebee abundance and offspring production, respectively, were positively associated with the proportion of OSR in the surrounding landscapes whereas the proportion of semi-natural habitats had no effect. Indeed, for these social species, OSR provided mass resources at the time of colony founding: highly rewarding resources promoted early colony growth, resulting in higher bumblebee abundances later in the season (Westphal et al., 2003). However, the proportion of OSR had no effect on the production of the reproductive units, queens and males (Westphal et al., 2009).

4.2. Influence of the current landscape

When relating solitary bee species richness and abundance with landscape composition and structure, we found contrasted results according to the scale and to the type of field margins (OSR or non-OSR fields). At the finest spatial scale (400 m), solitary bee abundance in margins of OSR fields deeply increased with increasing proportion of crop fields in 2007 while it remained unchanged in margins of non-OSR fields. Results at larger scales confirmed that the attractiveness of OSR fields depends on the quality of the surrounding landscape: the use of OSR by solitary

bees was higher when the surrounding area provided few floral resources (i.e. few long-term grasslands and many cereal fields in 2003–2007). Steffan-Dewenter et al. (2002) found a similar result with honeybees (*Apis mellifera*): this species was more abundant in experimental flower-rich plots when semi-natural habitats were scarce in the landscape.

Concerning margins of non-OSR fields, there was an influence of semi-natural elements on solitary bees at large spatial scales. First, the proportion of long-term grasslands positively influenced their abundance (800 and 1200 m). Second, the proportion of wooded elements had no impact, but their spatial arrangement did, as when landscape grain became coarser, solitary bee abundance decreased in margins of non-OSR fields (1200 m). This result may have several reasons. Few of the recorded species were directly associated with trees either for nesting (wood-nesting species) or for food (species like *Andrena clarkella* specialized on tree flowers). Therefore the role of wooded elements might not be directly linked with trees. Hedgerows and woodlot margins, that represent undisturbed areas, most probably benefit bees with non-woody species floral resources and ground nesting sites (banks, etc.). Moreover high hedgerow density (fine grain) could generate suitable micro-climatic conditions for solitary bees. Indeed, Guyot and Seguin (1976) found that wind speed was reduced by 30–50% and average diurnal temperature increased, for both soil and air, in a landscape with a high density of hedgerows compared to a coarse-grained landscape. These micro-climatic conditions could enhance solitary bee activity as well as offspring survival in soils during hard winters (Szabo and Smith, 1972; Lundberg, 1980).

4.3. Influence of crop rotations

Accounting for the recent history of land use offered greater insights about the influence of crop fields on solitary bee communities at large spatial scales. We found that the proportion of fields only sown with cereals in the last 5 years negatively affected abundance and species richness of solitary bees in the margins of non-OSR fields at the 800 and 1200 m scales. On the contrary, fields where crop rotation included at least 1 year of grassland were associated with greater species richness. The significant interaction (“type of field margin” × “proportion of mixed fields”) at large scales revealed that this landscape variable strongly influenced solitary bee communities in the margins of non-OSR fields whereas it had no or very little effect in margins of OSR fields, supporting the idea that solitary bees in OSR fields are more influenced by landscape context at fine scales. The suitability of temporary grasslands for bees remains to be supported by further data. They are generally sown with Poaceae species only and fertilized, which are practices with questionable impacts regarding bee diversity. Nevertheless our results indicated that including temporary grasslands in crop rotations was beneficial to bees. The introduction of this cover type in cereal rotations could imply a less intensive farming system, potentially beneficial to solitary bees, thanks to (i) reduced pesticides and fertilizer inputs over the whole rotations, (ii) greater floral resources in properly-managed temporary grasslands, (iii) less disturbed soils, better suited for ground-nesting bees (Shuler et al., 2005).

The positive influence of long-term and temporary grasslands vs. the negative influence of fields sown only with cereals can be further modulated by the nature of field margin management. Field margins are managed in relation to adjacent land use (Le Coeur et al., 1997). In our site, the general trend was higher herbicide spraying on crop field margins and more frequent mowing on grassland margins. In reducing floral resources on field margins, herbicides enhanced the negative impact of crops. On the contrary, mowing did not occur before mid or end of May and therefore had no or little impact on early spring-flying species.

The composition of the landscape at the time of sampling had a direct impact on the spatial distribution of solitary bees only at the finest scale (400 m). On the contrary, when considering the landscape use over several years (crop rotations and semi-natural elements), the effects occurred at the larger scales (800 and 1200 m). Therefore, our results are in agreement with the hierarchy theory that predicts that spatial and temporal scales are correlated. Phenomena occurring at large spatial scales are related to slower processes than phenomena occurring at smaller spatial scales (Allen et al., 1987). The maintenance of populations, a slow process, may be due to “large” spatio-temporal patterns, while feeding behavior, a fast process, is related to fine scale patterns (presence of OSR in a given field during the flowering period of this crop).

4.4. Management implications

From a methodological standpoint, our study showed that examining the heterogeneity of the agricultural mosaic over a whole crop rotation cycle was relevant to better understand the effects of agriculture on solitary bee communities. This approach allowed considering the cumulative effects of field cover and management and it demonstrated that introducing less intensive covers, such as temporary grasslands, in cereal rotations positively influence solitary bee communities. Therefore our study suggests that favorable farming systems for bees were mixed farming systems with crop and livestock production. However, in areas specialized in crop production, fallows may play the same role as grasslands (Steffan-Dewenter and Tschardt, 2001).

The introduction of mass flowering crops is also a mean of rotation diversification (Köpke and Nemecek, 2010). Our study highlighted the wide use of OSR by spring-flying solitary bees. But the beneficial effects of OSR on solitary bee communities are likely to depend on the phenology of the species and on their floral and nesting requirements. First, solitary bee species are usually continuously active in this part of Europe from early spring to autumn but each species has a short life span of a few weeks or months. For the species for which the flying period matches that of OSR flowering, OSR could have a high positive impact. We can also mention that, for the early spring-flying species, Brassicaceae species used as winter cover crops could also have a positive impact as they provide flowers before the flowering of OSR. For summer-flying bee species or those with flying periods that extend beyond the end of OSR flowering, it raises the question of the quality of the floral resources provided by the other components of the agricultural landscape, such as semi-natural habitats or other flowering crops (like sunflower *Helianthus annuus*, field bean *Vicia faba* or lacy phacelia *Phacelia tanacetifolia*). Second, OSR is suitable for polylectic or Brassicaceae-specialized species, but other oligolectic species are dependent on alternative food resources. Third, solitary bees also depend on the availability of nesting sites to persist in agricultural landscapes. The idea that OSR is not in all cases beneficial to wild bees is supported by a recent study dealing with social species: Diekötter et al. (2010) showed that an increased amount of mass flowering crops does not necessarily benefit all bumblebee species. The abundance of long-tongued bumblebees decreased with increasing amounts of OSR in landscape. This effect was mediated by the higher abundance of short-tongued bumblebees as competitors in OSR-rich landscapes (Westphal et al., 2003, 2009). Once OSR flowering period finished, short-tongued species spilled over into the landscapes surrounding OSR fields and depleted the flower resources of long-tongued species. The high number of rare species in our margins of non-OSR fields (21 species were recorded exclusively in these margins and the proportion of rare species was higher in these margins than in margins of OSR fields) suggested that the bee community in margins of non-OSR fields is very dis-

tinct from margins of OSR fields, what was supported by the many interactions detected. Therefore margins of OSR fields seem to foster abundance of a wider and more generalized set of species while margins of non-OSR fields might be more valuable for conservation purposes, i.e. supporting rare species.

Many European countries are expected to increase their areas of OSR in the next years to produce biofuels (Van der Velde et al., 2009). In this context, it seems crucial to emphasize that, even if mass flowering crops can foster populations of some solitary bee species, conservation strategies must primarily focus on the preservation of diverse and abundant food and nesting resources through the preservation of semi-natural elements and the development of less intensive farming practices.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2011.06.020.

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