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**Farming system and landscape characteristics differentially affect two
dominant taxa of predatory arthropods**

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Abstract

Despite the role generalist predators may play in biological regulation, the influence of landscape composition in shaping their assemblages remains little studied, especially when landscape interacts with local factors. In this study, we investigated the effects of farming systems along gradients in landscape elements on the structure and composition of carabid and spider assemblages. Twenty pairs of organic vs. conventional spatially-matched fields were sampled in 2013 along increasing percentage covers of organic farming and semi-natural habitats in the landscape. A total of 24241 spiders and 27767 carabids belonging to 120 and 75 species respectively were collected by pitfall traps. Farming systems locally had a strong influence on the community structure (activity-density and species richness) and composition for both spiders and carabids. Structure of spider assemblages was mostly affected by local and landscape factors, whereas that of carabids was more driven by landscape variables and the interaction of the two levels. Spider and carabid community compositions were mostly determined by field farming systems and wood percentage around the field. Our study underlines the importance of landscape context in shaping assemblages of predatory arthropods, and suggests that mechanisms behind the distribution of individual species strongly differ between spiders and carabids.

Key-words: Organic farming, semi-natural habitats, spiders, carabids, Western France.

1. Introduction

During the second half of the 20th century, agriculture experienced widespread industrialization worldwide, resulting in a strong increase in crop yield and in an intensification of farming practices (Stoate et al., 2001). Semi-natural habitats (SNH), such as woodlots, hedgerows covered by perennial vegetation had especially suffered from the mechanization and fields' expansion (Tscharntke et al., 2005). Agricultural practices such as the use of chemical fertilizers and pesticides had devastating effects, both direct and indirect, on not-target animal and plant species (Stoate et al., 2001). Indeed the intensification of farming practices and landscapes simplification have been identified as the main drivers of biodiversity loss in arable lands (Schmidt and Tscharntke, 2005), with strong consequences for agroecosystem functioning (Tscharntke et al., 2005).

Biodiversity provides many ecosystem services crucial for agroecosystem functioning (Tscharntke et al., 2012a), biological regulation of pests by predatory arthropods being one of the most important (Benton et al., 2003; Tscharntke et al., 2005). At the field or farm scale, it has been shown that organic farming positively affects the abundance and species richness of predatory arthropods, but this depends on the studied taxa (Bengtsson et al., 2005; Gabriel et al., 2010). Recent studies have also shown a positive effect of the proportion of organic farming in the landscape for beneficial arthropods (Rundlöf et al., 2008; Gabriel et al., 2010). The landscape heterogeneity, related to the composition and spatial configuration of SNH around the cropland, further influences both the structure (abundance and species richness) and species composition of beneficial arthropods' communities (Batáry et al., 2011). The effect of field farming system might also strongly vary depending on the heterogeneity of surrounding landscapes. Indeed, according to "*the intermediate landscape-complexity hypothesis*" (Tscharntke et al., 2012b), fields in moderately complex landscapes often host higher species diversity compared to homogeneous landscapes where croplands dominate

(Rundlöf and Smith, 2006). However, SNH may also constitute barriers to long-distance dispersal for arthropods (Larrivé and Buddle, 2009; Gauffre et al., 2015). Overall, the effects of interactions between field farming system at local and landscape scales and landscape heterogeneity on beneficial arthropods' communities remain little studied (but see Rundlöf and Smith, 2006; Flohre et al., 2011; Winqvist et al., 2011).

The effects of predator diversity on pest regulation are usually enhanced when they act at different spatiotemporal scales (Schmidt et al., 2003; Straub et al., 2008). The effectiveness of biological control is strongly influenced by the structure and composition of predator communities (Riechert and Lawrence, 1997; Menalled et al., 1999; Griffin et al., 2013; Rusch et al., 2015). In addition, investigating both community structure and species composition allows to better understand agroecosystem functioning (Bommarco et al., 2013), which argues to use these parameters as key response variables.

This study investigated the relative effects of farming systems and other environmental characteristics perceived to operate at the local (field) and landscape scales on ground-dwelling arthropod predators in agroecosystems. Indeed, these generalist and polyphagous predators strongly contribute to biological regulation (Thies et al., 2011; Cardinale et al., 2012). Among them, spiders and carabid beetles received special attention because i) they are abundant arthropods largely contributing to the local diversity of agroecosystems and ii) they have recognized bio-indicator values in the way they quickly react to changes in habitat structure (for spiders see Bell et al., 2001; for carabid beetles see Luff et al., 1998). We were more specifically interested in assessing the influence of field farming systems at both local and landscape scales (Organic Farming vs. Conventional Farming further abbreviated as OF and CF respectively), habitat and landscape characteristics and their interactions on the structure and species composition of spider and carabid assemblages. We tested the following hypotheses:

i) Field farming systems (OF vs. CF) locally drive the structure and composition of arthropod communities. We expect that both abundance and species richness of arthropods are significantly higher in OF fields (Bengtsson et al., 2005), mainly because of less disturbing agricultural practices (e.g. compared to the use of pesticides and chemical inputs in CF). We also expect clear differences in species composition between farming systems for both spiders and carabids. Large species and higher diversity of diets are expected in OF fields and more open habitat and carnivorous species are expected in CF, because of differences in local habitat conditions like vegetation structure and density (including weeds) (Tuck et al., 2014; Henckel et al., 2015) and prey availability (Roubinet et al., 2017).

ii) At the landscape scale, elements surrounding fields modulate the structure and composition of predator communities for both spiders and carabids. We expect a positive effect of the proportion of SNH and organic farming in the landscape on arthropod abundance and species richness (Tscharntke et al., 2012b). We also expect species composition to be influenced by the proportion of SNH only because they provide refuges, habitat for overwintering and alternative food resources (Holland et al., 2009).

iii) There are interacting effects of local, field farming system and landscape elements on the structure and composition of predator communities. We expect the effects of SNH to depend on farming system (Tscharntke et al., 2012b), because a high proportion of SNH can buffer the impact of farming practices (e.g. pesticides in CF) acting as source habitats from which individuals disperse in arable fields (Chaplin-Kramer et al., 2011).

2. Material and methods

2.1. Study site

The study site was located in Brittany, Western France (48° 06' 53'' N, 1° 40' 46'' O). It is characterized by a dense hedgerow network and dominated by mixed crop-livestock farming systems. The landscape is dominated by meadow (~ 40%) followed by corn (30%) and wheat (20%).

Forty fields (twenty pairs of organic and conventional fields) cultivated with winter wheat (*Triticum aestivum*) were selected in an area of about 200,000 ha along two landscape gradients: the first was made up by the proportion of OF around the sampled fields (radius of 500m; ranging from 3.5 to 30 %) and the second by the proportion of SNH around the sampled fields (from 6.5 to 65.5 %). A Moran's I test showed that the sites and gradients in landscape elements were not spatially auto-correlated (see Puech et al. (2015) for details in sites selection).

2.2. Characterization of local and landscape variables

In each field, vegetation height, wheat density, and percentage of wheat and weeds cover (using the Braun-Blanquet index) were measured in four quadrats (1m²) at a 3 m distance from pitfall traps in June 2013. Landscape metrics were computed to characterize the composition and spatial organization of land covers in the surrounding of each focal field. The landscape was characterized in a radius of 500m around each field (Table 1). This distance was chosen because it is relevant to describe landscape for both spiders (Schmidt and Tschardtke, 2005) and carabids (Batáry et al., 2007). In total sixteen variables were calculated, five local variables (field scale) and eleven landscape variables (see Table 1).

2.3. Arthropod sampling

Arthropods were continuously sampled using pitfall traps from May to July 2013. Traps were filled with preservative solution (50 % mono-propylene glycol, 50 % water). In each field, two sampling stations with two pitfall traps each were set up 10 m apart and placed 10 m away from field edges to avoid potential edge effects. Traps were left open continuously and collected every two weeks, for a total of six sampling periods. Catches by pitfall traps are dependent on the activity (mobility) and local density of arthropods, and lead to the calculation of ‘activity-density’.

2.4. Statistical analyses

2.4.1. Variable selection

To avoid multicollinearity between variables, a procedure of variable selection was first applied. A method of ‘Clustering of variables’ that arranges variables into groups of variables strongly related to each other was performed. This method allows handling both quantitative and qualitative variables at the same time. A bootstrap approach was then used to assess the stability of the variable partition and to determine the best number of clusters (R package ‘ClustOfVar’ v.0.8: Chavent, 2013). At the end of this selection seven variables (Fig. A.1) were selected for subsequent analyses (see below).

2.4.2. Influence of field farming system and landscape context on community structure

To investigate the relationships between the selected predictor variables (local and landscape variables) and activity-density and species richness of spiders and carabids, General Linear Mixed-effect Models (GLMM) (Zuur et al., 2009), model averaging (Burnham and Anderson, 2002) and multi-model inference (Grueber et al., 2011) were used. In each model, a nested spatial random effect was added to account for the spatial dependence between observations: site (landscape around each pair of organic/conventional fields) and field within sites. A

temporal random effect, date sampling, was also added to account for a temporal change in assemblages. Full models for spider and carabid activity-density and species richness included the following predictor variables: farming system as fixed effect, height of vegetation, length of hedgerows, proportion of organic farming, wood, meadow and grass strips, as well as the interactions between farming system and all landscape variables.

Full models were first fitted using the 'glmer' function in the R package 'lme4' (v.1.1-12; Bates et al., 2015). To assess the appropriate distribution, statistics on residuals were first calculated with Poisson distribution. When over-dispersion was observed (assessed by comparing the sum of squared Pearson residuals to the residual degrees of freedom), a negative binomial distribution was used. Each model was fitted using the appropriate distribution type and link function. Poisson distribution was selected for spider and carabid species richness. Negative binomial distribution was selected for spider and carabid activity-density.

Model selection procedure started with the standardization of all predictor variables (Grueber et al., 2011) using the 'standardize' function of the R package 'arm' (v. 19-3; Gelman and Su, 2015). The 'dredge' function of the R package 'MuMin' (v. 1.16.4; Barton, 2016) was then used to fit all possible combinations of models, and their associated Akaike's Information Criteria corrected for small sample sizes were calculated (AICc). A list of the best fitted models with $\Delta AICc < 2$ was generated with the 'get.models' function of the R package 'MuMin' and was used for model averaging with the 'model.avg' function in the 'MuMin' package. The final averaged models provided model-averaged coefficients for each retained predictor variable and variable importance (i.e., the sum of the model weights within the set of models that included this variable). Finally, 95% confidence intervals (CI) were calculated for the model-averaged parameter estimates with the 'confint' function in the 'MuMin' package.

2.4.3. Influence of local and landscape variables on community composition

Because of differences in scales (units) the range of values exhibited by predictor variables was high. Predictor variables were then mean-centered and standardized. To avoid the effect of rare species in analyses of community composition, spider and carabid species with less than 5 individuals in the total catches were omitted.

To assess possible relationships between local and landscape variables and arthropod assemblage composition, constrained analyses were used. Following Borcard et al. (2011), species activity-densities were transformed to a Hellinger distance matrix prior to analyses. The Hellinger distance offers a better compromise between linearity and resolution than the chi-square metric and the chi-square distance (Legendre and Legendre, 1998).

The choice between redundancy analysis (RDA) and constrained correspondence analysis (CCA) was made according to the first axis length of a detrended correspondence analysis (DCA), (lengths of gradient for the first axis <3.0 and >4 for RDA and CCA respectively: (Ter Braak and Šmilauer, 2002). In analyses, the distance matrix was the response variable and the environmental (landscape and local) variables were the predictors. A stepwise forward selection was used to select variables which best explained variation in the response data. Monte Carlo tests with 999 permutations were carried out to assess the significance of the selected environmental factors and constrained analyses axes, using the R package *vegan* (V 2.4-2; Oksanen et al., 2017).

To better observe the patterns of community composition between OF and CF, a non-metric multidimensional scaling (NMDS) ordination was performed using the Bray-Curtis similarity index. A two-dimensional solution was selected because it consistently maintained a low stress (<0.2) across multiple runs (Faith et al., 1987). Analyses of similarity (ANOSIM) and Permutational Multivariate Analysis of Variance (PERMANOVA) using Bray-Curtis distance

matrices were used to test differences in species composition between assemblages in OF and CF for both spiders and carabids, using the R package ‘vegan’ (V 2.4-2; Oksanen et al., 2017).

All analyses were conducted using R software (R Core Team 2017).

3. Results

A total of 24241 spiders (OF: 14217, CF: 10024) and 27767 carabids (OF: 18355, CF=9412) belonging to 120 (OF: 104, CF: 95) and 75 (OF: 69, CF: 57) species respectively (Tables A.1 and A.2) were collected.

3.1. Influence of field farming system and landscape context on community structure

Field farming system had strong effects on activity-density and species richness of spiders which were significantly higher in OF fields than in CF fields (Fig. 1). Both activity-density and species richness of spiders were influenced by vegetation height (-0.22 ± 0.16 and -0.08 ± 0.07 , respectively; Table 2). Spider activity-density was significantly influenced by the interaction between field farming system and the proportion of wood (500 m) (Table 2), the effect being positive in OF fields and negative in CF fields (Fig. 2a). It also decreased with the proportion of meadow in the landscape (-0.25 ± 0.17 ; Table 2, Fig. A.2). It was marginally influenced by the interaction between the percentage of grass strips (500 m) and field farming system (average estimate $\pm$ CI: 0.37 ± 0.33 ; Table 2), the effect being positive in CF fields and non-significant in OF fields (Fig. 2b).

As for spiders, field farming system had a strong effect on carabid activity-density and species richness (0.56 ± 0.31 and 0.12 ± 0.09 , respectively; Table 2), that were significantly higher in OF fields (Fig. 3). Carabid activity-density and species richness were positively influenced by the proportion of grass strips in the landscape (0.42 ± 0.37 and 0.15 ± 0.09 , respectively;

Table 2; Fig. A.2). On the contrary, the proportion of meadow and wood in interaction with field farming system had negative effects on carabid species richness (-0.09 ± 0.09 and -0.21 ± 0.1 , respectively; Table 2, Fig. A.2). The proportion of meadow had a negative impact on carabid species richness in OF fields and no effect in CF fields (Table 2, Fig. 4a), whereas woods had a negative effect (Table 2) in both OF and CF fields (Fig. 4b). In contrast, the proportion of grass strips in the landscape interacted with farming system (Table 2), and had a positive and significant effect on carabid species richness only in CF field (Fig. 4c). Regarding farming systems at the landscape scale, the results showed that the proportion of OF in the landscape had a positive effect on carabid species richness (Table 2; Fig. 5).

3.2. Influence of local and landscape variables on community composition

The first two axes of the RDA performed on spider assemblages were significant ($p=0.001$ and $p=0.007$, respectively) and explained 30.2 % of the total variance. The main variables explaining spider species composition were field farming system and the proportion of wood in the landscape ($F=5.03$, $p=0.001$ and $F=3.3$, $p=0.006$, respectively) (Fig. 6). The first axis of the RDA tended to oppose spider assemblages observed in organic fields to spider assemblages observed in conventional fields. Fields under OF were characterized by high abundances of species belonging to the lycosid family (*Pardosa proxima*, *Pardosa palustris*) whereas fields under CF were characterized by high abundances of species belonging to the linyphiid family (*Oedotorax apicatus*, *Erigone atra* and *Tenuiphantes tenuis*). The second axis segregated spider assemblages observed in fields situated in landscapes dominated by high proportions of woody SNH in the negative part of the axis (with high abundances of the lycosids *Pardosa prativaga* and *Pardosa saltans* and of the linyphiid *Diplosyla concolor*).

The first three axes of the RDA performed on carabid assemblages were significant ($p=0.001$, $p=0.004$ and $p=0.039$, respectively) and explained 29.83 % of the total variance. As for spiders, the main variables explaining carabid species composition were field farming system

and the proportion of wood in the surrounding landscape ($F=4.91$, $p=0.005$ and $F=2.56$, $p=0.01$, respectively) (Fig. 7). The first axis tended to contrast carabid assemblages according to the field farming system. The species *Brachinus sclopeta* and *Poecilus cupreus* were especially abundant in OF fields whereas *Pterosticus melanarius* and *Trechus gr. quadristriatus* were especially abundant in fields under CF. On the second axis, landscapes dominated by high proportions of woody SNH in the negative part were associated with high abundances of *Nebria salina*, *Carabus nemoralis* and *Carabus granulatus*.

Both in carabids and spiders, the non-metric multidimensional scaling (NMDS) ordination tended to cluster species assemblages observed in fields according to the farming system applied (OF vs. CF) (Figs. A.3 and A.4; ANOSIM tests: spiders: $R^2=0.11$, $p=0.001$ carabids: $R^2=0.12$, $p=0.001$). Results obtained using NMDS analysis were consistent with those obtained using RDA. NMDS also showed more heterogeneity of both spider and carabid assemblages in OF compared to CF.

4. Discussion

In this study we investigated the relative influence of (i) the farming system applied at local and landscape scales, (ii) the landscape characteristics and (iii) their interaction on spider and carabid assemblages. Confirming our first and our second hypotheses, we found consistent evidence that community structure and composition of both taxa are strongly affected by field farming system, with positive effect of OF for both spiders and carabids. Surrounding landscape characteristics and their interaction with field farming systems were also strong drivers of community structure, which validates our last hypothesis. In this study we highlighted the impact of the interaction between local and landscape variables is shown on community structure for both spiders and carabids, in agreement with very few studies on other taxa (Diekötter et al., 2010; Feber et al., 2015; Flohre et al., 2011; Hawro et al., 2015).

Our results also show that spider and carabid assemblages respond differently to changes in their environment (see also Lafage and Pétilion, 2016), both locally and at landscape scale.

4.1 Community structure

4.1.1 Effect of field farming system and local environmental conditions on community structure

Our results showed a highly significant and positive effect of organic farming at field scale on both the activity-density and the species richness of spiders and carabids. Our results confirm several previous studies (Bengtsson et al., 2005; Hole et al., 2005; Schmidt et al., 2005; Gabriel and Tscharntke, 2007; Rundlöf et al., 2008; Puech et al., 2014; Rusch et al., 2014).

This important effect of field farming system can be mainly explained by two factors. The first factor is related to the practices associated with the two farming systems. Chemicals (e.g. pesticides, synthetic fertilizers) applied in CF fields are indeed recognized for their harmful effects on biodiversity (Köhler and Triebkorn, 2013). Other practices such as organic fertilization, mainly in OF fields, are known to be favorable to arthropod communities (Garratt et al., 2011) by improving soil quality and the availability of potential prey (Schmidt et al., 2005). Secondly, habitat quality differs between the two farming systems. Indeed, the cropping practices applied in OF fields, and especially the lack of herbicides, result in denser vegetation and higher weed diversity (Tuck et al., 2014; Henckel et al., 2015). This is likely to provide particular microclimatic conditions (e.g. temperature, moisture) and a higher spatial stratification, resulting in an increase in abundance and diversity of food resources in OF fields. This can in turn promote the abundance and diversity of spiders and carabid beetles (Lövei and Sunderland, 1996; Langellotto and Denno, 2004).

In our study, the average vegetation height in wheat fields negatively influenced the richness and abundance of spider communities. Our results, on one hand, are in contradiction with

those of previous studies that have shown that the height of vegetation increases the structural heterogeneity of the habitat, thus offering a greater diversity of niches (Greenstone, 1984; Uetz, 1991; Langellotto and Denno, 2004; Prieto-Benítez and Méndez, 2011). On the other hand, our results are in accordance with the results of few studies (Štokmane and Spunģis, 2014, 2016), which can be explained by two main factors. The first one is related to changes in the microclimatic (e.g. temperature, moisture) and structural conditions of habitats modified by vegetation height (Langellotto and Denno, 2004). These changes in habitat directly impact the mobility of individuals, and therefore their catchability, which results in an effect of the sampling method (already mentioned by e.g. Topping and Sunderland, 1992). The second explanation is related to the “nature” of the habitat (i.e. simply structured). Wheat field indeed forms a very homogeneous habitat, in all CF and in some OF fields, with the total or partial absence of other plant species and a reduced spatial heterogeneity. As a result, CF creates a more open habitat with reduced ecological niches, which negatively impacts the structure of spider communities. Overall, most studies were conducted on vegetation-dwelling spiders, which make them hardly comparable to our results on ground-dwelling spiders. It is thus hard to know whether the negative effect of vegetation height on spider abundance and species richness is due to the sampling method or to spatial heterogeneity, but the fact that spiders were caught in higher numbers in OF fields despite they have higher vegetation plaids in favor of the second hypothesis.

4.1.2 Effects of landscape characteristics on community structure

The proportion of grass strips in the landscape had a positive effect on carabid activity-density irrespective of field farming system and on carabid species richness in CF fields only. Grass strips are known to play an important role in the functioning of agroecosystems (Marshall and Moonen, 2002). They can represent an alternative habitat for carabids that use them for food, shelter and refuges, but also for overwintering (Holland et al., 2009). Grass strips may also

favor the dispersal of arthropods in the landscape matrix (Holzschuh et al., 2009). The influence of grass strips in the landscape on carabid species richness was significantly lower in OF fields than in CF fields. This may result from OF fields being more similar to grass strips in their plant structure and diversity than CF fields.

The proportion of meadow in the landscape had a negative effect on spider activity-density in OF and CF fields. It also interacted with farming system, with a negative effect on carabid species richness in OF fields only. This is partly in contradiction with some previous studies (see Purtauf et al., 2005 for carabids). On the other hand, Caro et al. (2016) suggested that meadows may be poor habitats for carabids. Other studies also reported a negative effect of the percentage of meadow in the landscape on the structure of spider assemblages, as summarized in the review of Prieto-Benítez and Méndez (2011). Meadow exploitation in the last decades, has been found to have drastic effects on both spiders and carabids (see Bell et al., 2001 and Morris, 2000 respectively). Mowing of meadows, especially, leads to a strong destruction of the habitat, which negatively affects arthropod communities (Dennis et al., 2015). Intensive grazing is also generally harmful to biodiversity (Benton et al., 2003; Donald et al., 2006). In our study area, meadows are intensively managed through grazing by cattle and mowing, which may explain the negative impact of percentage of meadow on both spider activity-density and on carabid species richness. The influence of the proportion of meadow in the landscape on carabid species richness differed according to the field farming system, and was significant only in OF fields. Carabid assemblages are modulated by the structure and diversity of vegetation (Lövei and Sunderland, 1996; Rainio and Niemelä, 2003). Carabid assemblages in meadows are then assumed to be more similar to those of CF fields, with both environments disturbed by local practices (e.g. synthetic fertilization, mowing, pesticides), explaining the lack of effect of meadows in CF. Conversely, carabid assemblages in OF fields

differed from those in meadows mainly because of the relative stability of OF fields and their higher floristic diversity.

The proportion of OF in the landscape positively impacted carabid species richness irrespective of the field farming system. Our results are consistent with the few studies that addressed this issue (Rundlöf et al., 2008; Gabriel et al., 2010), which found an overall positive effect of the proportion of OF at landscape scale on the diversity of several taxa (e.g. butterflies, birds, plants). Gabriel et al. (2010) found positive effects of OF at the landscape scale, but not for all the studied taxa, whereas Gosme et al. (2012) found a negative effect of the proportion of OF at the landscape scale on crop pests (aphids) and diseases (leaf blotch). Our result suggest that OF fields could act as sources and favor carabid species richness by spreading individuals into the landscape matrix (Meyer et al., 2009).

The influence of the proportion of wood in the landscape on spider activity-density and carabid species richness depended on the field farming system. For spiders, this resulted in an increasing activity-density with the proportion of wood in the surrounding landscape in OF fields, and in a decreasing activity-density with the proportion of wood in the surrounding landscape in CF fields. OF fields can be considered an attractive environment for spiders (e.g. more food resources and habitat quality). Woods can provide alternative food resources, and shelters for species escaping disturbances from crops, (Tscharntke et al., 2005; Bianchi et al., 2006). They constitute sources from which individuals can disperse in the landscape matrix (Chaplin-Kramer et al., 2011). Carabid species richness decreased with the proportion of wood in the surrounding landscape. This can be explained by the fact that dominant species in both farming systems have low dispersal capacities and are mainly species of cultivated and / or open areas. As a result, this negative effect suggests that woods might act as barriers to carabid dispersal (see Lafage et al., 2015b). The fact that CF fields host more small-sized and

mobile species could explain the reason why the negative effect of woods is stronger under CF fields.

4.2. Community composition

4.2.1 Farming system and community composition

Although spiders and carabids have different community drivers, we found a major difference in species composition according to the farming systems probably resulting from differences in habitat structure and quality between the two farming systems.

CF fields provide a more homogeneous and simplified habitat structure, regularly disturbed by practices harmful for arthropods (e.g. pesticides, synthetic fertilizers: Köhler and Triebkorn, 2013). Assemblages are consequently primarily determined by species' ability to resist disturbances (Hendrickx et al., 2007) and prey availability (Roubinet et al., 2017). This results in spider assemblages dominated by small and highly dispersive species (mainly Linyphiidae) in CF fields (Downie et al., 1999; Cole et al., 2005; Feber et al., 2015). For carabids, assemblages were dominated in CF fields by predatory species, as a consequence of little diversity of food resources and therefore greater direct and / or indirect competition (Niemelä 1993), and mostly nocturnal species, a strategy to escape from (other) predators in these open environments (Erikstad et al., 1989).

In contrast, OF fields provide more favorable environments with no synthetic inputs, higher spatial heterogeneity and stratification, thicker litter layer, and a greater diversity of cultivated plants and weeds (Tuck et al., 2014; Henckel et al., 2015). These conditions increase ecological niches diversity and result in higher food resources and lowered competition, which could explain spider assemblages dominated by larger species of lycosids, species known to hunt on the ground and finding refuges in the litter (Harvey et al., 2002). Habitat in OF fields may provide protection against other predators (Uetz 1991; Castro and Wise, 2009).

Carabid assemblages were characterized by medium to large species, feeding on a larger diversity of diets and including both diurnal and nocturnal species, mainly due to an enhanced diversity of cultivated vegetation and weeds. It must finally be stressed that a large part of the variance in species assemblages remains unexplained for both spiders and carabids, suggesting that variables other than those mentioned above (either not measured or not retained for the statistical analysis) play an important role in shaping arthropod communities.

4.2.2 Landscape variables and community composition

Spider and carabid community compositions were also modulated by the surrounding landscape characteristics. The second RDA axes indeed opposed communities of landscapes dominated by cropped elements to communities of landscapes dominated by uncultivated, woody elements. Our results are in agreement with previous studies that showed the importance of landscape in modulating arthropod community composition (e.g. Öberg et al., 2007; Batáry et al., 2008; Schmidt et al., 2008). In landscapes where the cultivated area is dominant, small and medium sized species, with high dispersal abilities, were found (for spiders, see Blandenier, 2009; Simonneau et al., 2016; for carabids, see Luff, 1988; Desender et al., 2008).

In landscapes dominated by woods, we found medium and large sized species, mostly forest-specialist species. Woody areas can actually constitute sources from which individuals will disperse in the landscape (Chaplin-Kramer et al., 2011). This is reflected for spiders by the abundance of the following species: the lycosids *Pardosa prativaga* and *Pardosa saltans*, and the linyphiid *Diplosyla concolor*. All are forest species, except for *P. prativaga* usually found in permanent meadows (Harvey et al., 2002), but known to be very mobile. For carabids, characteristic species were *Carabus nemoralis*, *Carabus granulatus* and *Nebria salina*, all medium to large species, occurring in forests and having low dispersal capacities (Desender et al., 2008; Luff, 1998).

5. Conclusion

Understanding the interactions between cultivated and uncultivated environments at local and landscape scales can help the design of new agricultural systems (Marshall and Moonen, 2002). Our study highlights the importance of distinguishing the various types of semi-natural elements and not considering them as a homogeneous entity, because their effects vary depending on the studied taxa and on the nature of the semi-natural element. Different taxa respond to agricultural practices at different spatial scales and often at multiple spatial scales (Gabriel et al., 2010). This suggests that considering both local and a landscape condition in conservation strategy is required, and that no single indicator group is appropriate to represent biodiversity. Our study indeed shows that spiders and carabids differentially react to changes in local and landscape structure (see also Pétilion et al., 2008; Varet et al., 2013 in other habitat types), and can be considered as complementary ecological models in agroecosystems.

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793

794 **Supplementary materials**

795 **Table A.1**

796 Taxonomic list of spider species, and their abbreviation.

797 **Table A.2**

798 Taxonomic list of carabid species, and their abbreviation.

799 **Fig. A.1.** Clustering method on all the qualitative and quantitative, local and landscape
800 variables (see Table 1 for details).

801 **Fig. A.2.** Model-averaged coefficients (Estimates) $\pm$ 95% confidence intervals (whiskers) for
802 activity-density of (a) spiders, (b) carabids and species richness of (c) spiders, (d) carabids.
803 Points to the left of the median line are negative relationships, to the right positive. Black
804 points and whiskers indicate variables with statistically significant effect, gray are those with
805 no significant effect. The effect was considered statistically significant if the 95% CI did not
806 overlap zero.

807 **Fig. A.3.** Non-metric multi-dimensional scaling ordination (NMDS) based on Bray-Curtis
808 dissimilarities in spider activity-density within the farming system (OF vs. CF). Fields in OF
809 are green coloured, while the fields in CF are red coloured.

810 **Fig. A.4.** Non-metric multi-dimensional scaling ordination (NMDS) based on Bray-Curtis
811 dissimilarities in carabid activity-density within the farming system (OF vs. CF). Fields in OF
812 are green coloured, while the fields in CF are red coloured.

813

814 **Tables**

815 **Table 1**

816 Complete list of local and landscape variables measured in the study, with their type
 817 (qualitative vs. quantitative), unit, min-max and mean (together with the standard error).

Scale	Variable Name	Description	Variable type	Unit/class	Min-Max	Mean ($\pm$ SE)
<i>Field scale</i>						
	Far_Syst	Field farming system (organic vs conventional)	qualitative	OF vs CF	- 1-3	- 2.28 ($\pm$ 0.11)
	Moy_ble	Ground covered by wheat	qualitative	Braun-Blanquet index	1-5	1.94 ($\pm$ 0.19)
	Moy_adv	Ground covered by weeds	qualitative	Braun-Blanquet index	63.75-142.5	88.1 ($\pm$ 2.5)
	AH_veg	Average vegetation height	quantitative	cm	6.75-33	19.3 ($\pm$ 0.92)
	Moy_nbplt	Wheat density	quantitative	number of stems per m ²		
<i>Landscape scale (500m radius)</i>						
	OF_landscape	Proportion of organic farming	quantitative	% of cover	3.49-29.22	18.22 ($\pm$ 1.4)
	CF_landscape	Proportion of conventional farming	quantitative	% of cover	42.48-86.5	66.24 ($\pm$ 1.7)
	NR	Proportion of missing data regarding farming type	quantitative	% of cover	5.64-31.47	15.53 ($\pm$ 1.1)
	Farm_anl	Annual crops	quantitative	% of cover	25.53-84.05	56.5 ($\pm$ 2)
	Farm_inter	Perinnial crops	quantitative	% of cover	6.27-45.57	28.5 ($\pm$ 1.7)
	Wood	Proportion of Wood	quantitative	% of cover	0.001-23.89	3.9 ($\pm$ 0.96)
	Grass_strips	Proportion of Grass strips	quantitative	% of cover	0.001-2.17	0.5 ($\pm$ 0.08)
	Meadow	Proportion of Meadow	quantitative	% of cover	6.03-45.27	28 ($\pm$ 1.7)
	Road_Frame	Proportion of built areas	quantitative	% of cover	2.36-20.35	9.3 ($\pm$ 0.73)
	Water	Proportion of water elements	quantitative	% of cover	0.001-4.31	0.7 ($\pm$ 0.16)
	Hedge	Hedgerow lengh	quantitative	m	3692.63- 11134.3	6933.21 ($\pm$ 317)

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821 **Table 2**

822 Model-averaged coefficients estimates from the averaged best-fitting models predicting spider
 823 and carabid activity-density and species richness in relation to local and landscape variables
 824 and their 95% confidence interval (CI). Non-significant results are shown only if they were
 825 retained in the model; significant results are shown in bold and marked with asterisks (*:
 826 $0.05 < p \leq 0.01$, **: $0.01 < p \leq 0.001$ and ***: $p < 0.001$).

Full average	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	CI
<i>(a) Spider Activity density</i>						
Far_Syst	-0.355765	0.069666	0.069846	5.094	<0.001 ***	0.13689526
AH_veg	-0.217088	0.083084	0.0833	2.606	0.009 **	0.16326494
Grass_strips	0.133842	0.102286	0.102507	1.306	0.191	0.20571637
Meadow	-0.25457	0.087261	0.087498	2.909	0.003 **	0.17149204
Wood	0.030623	0.098039	0.098295	0.312	0.755	0.19265434
Far_Syst:Grass_strips	0.372817	0.190153	0.190432	1.958	0.050 .	0.33419057
Far_Syst:Wood	-0.574069	0.144602	0.144977	3.96	<0.001 ***	0.28415074
Far_Syst:Meadow	0.083383	0.129895	0.130037	0.641	0.521	0.37447995
OF_landscape	0.030174	0.066225	0.066321	0.455	0.649	0.23933703
Hedge	0.007198	0.035587	0.035653	0.202	0.840	0.23121912
<i>(b) Carabid Activity density</i>						
Far_Syst	0.561786	0.161937	0.162357	3.46	<0.001 ***	0.06247381
Grass_strips	0.42724	0.19173	0.192201	2.223	0.026 *	0.07830962
Wood	-0.075344	0.147521	0.14771	0.51	0.609	0.06927828
Far_Syst:Grass_strips	0.181845	0.304353	0.30474	0.597	0.550	0.10416957
OF_landscape	0.098848	0.164958	0.165188	0.598	0.549	0.06462907
Hedge	-0.006525	0.058333	0.058469	0.112	0.911	0.1011686
Far_Syst:Hedge	-0.040712	0.167294	0.167429	0.243	0.807	
Meadow	-0.035828	0.106245	0.10639	0.337	0.736	0.31821331
<i>(c) Spider Species richness</i>						0.37670913
Far_Syst	-0.187147	0.031789	0.031875	5.871	<0.001 ***	0.49953749
AH_veg	-0.083503	0.03985	0.039955	2.09	0.036 *	0.91717591
Meadow	-0.060389	0.049242	0.049324	1.224	0.220	0.22672361
Grass_strips	0.00479	0.019641	0.019679	0.243	0.807	0.45806267
Hedge	-0.002454	0.016324	0.016362	0.15	0.880	0.1548897
Wood	0.002429	0.017275	0.017316	0.14	0.888	0.49580823
<i>(d) Carabid Species richness</i>						
Far_Syst	0.12681	0.04692	0.04705	2.696	0.007 **	0.09220482
Grass_strips	0.1498	0.04949	0.04963	3.019	0.002 **	0.09726138
Meadow	-0.0962	0.04631	0.04644	2.071	0.038 *	0.09101474
OF_landscape	0.15166	0.05042	0.05056	3	0.002 **	0.09910058
Wood	-0.21627	0.05179	0.05193	4.165	<0.001 ***	0.10178075

Far_Syst:Grass_strips	0.28175	0.10361	0.1039	2.712	0.006**	0.20363693
Far_Syst:Meadow	-0.20307	0.09127	0.09152	2.219	0.026 *	0.17938587
Far_Syst:Wood	-0.2105	0.09666	0.09692	2.172	0.029 *	0.18996042
AH_veg	-0.01416	0.03384	0.03389	0.418	0.676	0.12846965
Far_Syst:OF_landscape	-0.01844	0.05922	0.05933	0.311	0.756	0.26189057

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Figures

Fig. 1. Comparison of activity-densities and species richness of spiders between organic and conventional farming. ***: significant effect identified in GLMM. Outliers are represented by red triangle.

Fig. 2. Activity-density of spiders depending on the percentage of wood (a) and grass strip (b).

Fig. 3. Comparison of activity-densities and species richness of carabids between organic and conventional farming. ***: significant effect identified in GLMM. Outliers are represented by red triangle.

Fig. 4. Activity-density of carabids depending on the percentage of wood (a), meadow (b) and grass strip (c).

Fig. 5. Species richness of carabids depending on the percentage of the organic farming in the landscape.

Fig. 6. Redundancy analysis ordinations (RDA) diagram representing the effects of local and landscape variables on spider assemblages. The ordination shows the significant continuous variable “wood” and the factorial variable “Farming system”. Variables and species are represented by their abbreviations (see Tables 1 and A.1, respectively). Fields under organic farming are represented by the letter “O” and those under conventional ones by the letter “C”.

Fig. 7. Redundancy analysis ordinations (RDA) diagram representing the effects of local and landscape variables on carabid assemblages. The ordination shows the significant continuous variable “wood” and the factorial variable “Farming system”. Variables and species are represented by their abbreviations (see Tables 1 and A.2, respectively). Fields under organic farming are represented by the letter “O” and those under conventional ones by the letter “C”.

Fig. 1

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Fig. 2

858 **Fig. 3.**

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862 **Fig. 4.**

Fig. 5.