



HAL
open science

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

E.A. Djoudi, A. Marie, A. Mangenot, Camille Puech, Stéphanie Aviron, Manuel Plantegenest, J. Pétilon

► **To cite this version:**

E.A. Djoudi, A. Marie, A. Mangenot, Camille Puech, Stéphanie Aviron, et al.. Farming system and landscape characteristics differentially affect two dominant taxa of predatory arthropods. *Agriculture, Ecosystems & Environment*, 2018, 259, pp.98-110. 10.1016/j.agee.2018.02.031 . hal-01783652

HAL Id: hal-01783652

<https://univ-rennes.hal.science/hal-01783652v1>

Submitted on 10 Sep 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

16 **Abstract**

17 Despite the role generalist predators may play in biological regulation, the influence of
18 landscape composition in shaping their assemblages remains little studied, especially when
19 landscape interacts with local factors. In this study, we investigated the effects of farming
20 systems along gradients in landscape elements on the structure and composition of carabid
21 and spider assemblages. Twenty pairs of organic vs. conventional spatially-matched fields
22 were sampled in 2013 along increasing percentage covers of organic farming and semi-natural
23 habitats in the landscape. A total of 24241 spiders and 27767 carabids belonging to 120 and
24 75 species respectively were collected by pitfall traps. Farming systems locally had a strong
25 influence on the community structure (activity-density and species richness) and composition
26 for both spiders and carabids. Structure of spider assemblages was mostly affected by local
27 and landscape factors, whereas that of carabids was more driven by landscape variables and
28 the interaction of the two levels. Spider and carabid community compositions were mostly
29 determined by field farming systems and wood percentage around the field. Our study
30 underlines the importance of landscape context in shaping assemblages of predatory
31 arthropods, and suggests that mechanisms behind the distribution of individual species
32 strongly differ between spiders and carabids.

33

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

35

36

37

38 **1. Introduction**

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

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

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

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

75 This study investigated the relative effects of farming systems and other environmental
76 characteristics perceived to operate at the local (field) and landscape scales on ground-
77 dwelling arthropod predators in agroecosystems. Indeed, these generalist and polyphagous
78 predators strongly contribute to biological regulation (Thies et al., 2011; Cardinale et al.,
79 2012). Among them, spiders and carabid beetles received special attention because i) they are
80 abundant arthropods largely contributing to the local diversity of agroecosystems and ii) they
81 have recognized bio-indicator values in the way they quickly react to changes in habitat
82 structure (for spiders see Bell et al., 2001; for carabid beetles see Luff et al., 1998). We were
83 more specifically interested in assessing the influence of field farming systems at both local
84 and landscape scales (Organic Farming vs. Conventional Farming further abbreviated as OF
85 and CF respectively), habitat and landscape characteristics and their interactions on the
86 structure and species composition of spider and carabid assemblages. We tested the following
87 hypotheses:

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

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

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

108 **2. Material and methods**

109 **2.1. Study site**

110 The study site was located in Brittany, Western France (48° 06' 53'' N, 1° 40' 46'' O). It is
111 characterized by a dense hedgerow network and dominated by mixed crop-livestock farming
112 systems. The landscape is dominated by meadow (~ 40%) followed by corn (30%) and wheat
113 (20%).

114 Forty fields (twenty pairs of organic and conventional fields) cultivated with winter wheat
115 (*Triticum aestivum*) were selected in an area of about 200,000 ha along two landscape
116 gradients: the first was made up by the proportion of OF around the sampled fields (radius of
117 500m; ranging from 3.5 to 30 %) and the second by the proportion of SNH around the
118 sampled fields (from 6.5 to 65.5 %). A Moran's I test showed that the sites and gradients in
119 landscape elements were not spatially auto-correlated (see Puech et al. (2015) for details in
120 sites selection).

121 **2.2. Characterization of local and landscape variables**

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

130 **2.3. Arthropod sampling**

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

138 **2.4. Statistical analyses**

139 **2.4.1. Variable selection**

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

147 **2.4.2. Influence of field farming system and landscape context on community structure**

148 To investigate the relationships between the selected predictor variables (local and landscape
149 variables) and activity-density and species richness of spiders and carabids, General Linear
150 Mixed-effect Models (GLMM) (Zuur et al., 2009), model averaging (Burnham and Anderson,
151 2002) and multi-model inference (Grueber et al., 2011) were used. In each model, a nested
152 spatial random effect was added to account for the spatial dependence between observations:
153 site (landscape around each pair of organic/conventional fields) and field within sites. A

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

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

167 Model selection procedure started with the standardization of all predictor variables (Grueber
168 et al., 2011) using the 'standardize' function of the R package 'arm' (v. 19-3; Gelman and Su,
169 2015). The 'dredge' function of the R package 'MuMin' (v. 1.16.4; Barton, 2016) was then
170 used to fit all possible combinations of models, and their associated Akaike's Information
171 Criteria corrected for small sample sizes were calculated (AICc. A list of the best fitted
172 models with $\Delta AICc < 2$ was generated with the 'get.models' function of the R package
173 'MuMin' and was used for model averaging with the 'model.avg' function in the 'MuMin'
174 package. The final averaged models provided model-averaged coefficients for each retained
175 predictor variable and variable importance (i.e., the sum of the model weights within the set
176 of models that included this variable). Finally, 95% confidence intervals (CI) were calculated
177 for the model-averaged parameter estimates with the 'confint' function in the 'MuMin'
178 package.

179 **2.4.3. Influence of local and landscape variables on community composition**

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

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

189 The choice between redundancy analysis (RDA) and constrained correspondence analysis
190 (CCA) was made according to the first axis length of a detrended correspondence analysis
191 (DCA), (lengths of gradient for the first axis <3.0 and >4 for RDA and CCA respectively:
192 (Ter Braak and Šmilauer, 2002). In analyses, the distance matrix was the response variable
193 and the environmental (landscape and local) variables were the predictors. A stepwise forward
194 selection was used to select variables which best explained variation in the response data.
195 Monte Carlo tests with 999 permutations were carried out to assess the significance of the
196 selected environmental factors and constrained analyses axes, using the R package *vegan* (V
197 2.4-2; Oksanen et al., 2017).

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

203 matrices were used to test differences in species composition between assemblages in OF and
204 CF for both spiders and carabids, using the R package 'vegan' (V 2.4-2; Oksanen et al.,
205 2017).

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

207 **3. Results**

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

211 ***3.1. Influence of field farming system and landscape context on community structure***

212 Field farming system had strong effects on activity-density and species richness of spiders
213 which were significantly higher in OF fields than in CF fields (Fig. 1). Both activity-density
214 and species richness of spiders were influenced by vegetation height (-0.22 ± 0.16 and $-0.08 \pm$
215 0.07 , respectively; Table 2). Spider activity-density was significantly influenced by the
216 interaction between field farming system and the proportion of wood (500 m) (Table 2), the
217 effect being positive in OF fields and negative in CF fields (Fig. 2a). It also decreased with
218 the proportion of meadow in the landscape (-0.25 ± 0.17 ; Table 2, Fig. A.2). It was marginally
219 influenced by the interaction between the percentage of grass strips (500 m) and field farming
220 system (average estimate \pm CI: 0.37 ± 0.33 ; Table 2), the effect being positive in CF fields
221 and non-significant in OF fields (Fig. 2b).

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

226 Table 2; Fig. A.2). On the contrary, the proportion of meadow and wood in interaction with
227 field farming system had negative effects on carabid species richness (-0.09 ± 0.09 and -0.21
228 ± 0.1 , respectively; Table 2, Fig. A.2). The proportion of meadow had a negative impact on
229 carabid species richness in OF fields and no effect in CF fields (Table 2, Fig. 4a), whereas
230 woods had a negative effect (Table 2) in both OF and CF fields (Fig. 4b). In contrast, the
231 proportion of grass strips in the landscape interacted with farming system (Table 2), and had a
232 positive and significant effect on carabid species richness only in CF field (Fig. 4c).
233 Regarding farming systems at the landscape scale, the results showed that the proportion of
234 OF in the landscape had a positive effect on carabid species richness (Table 2; Fig. 5).

235 **3.2. Influence of local and landscape variables on community composition**

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

248 The first three axes of the RDA performed on carabid assemblages were significant ($p=0.001$,
249 $p=0.004$ and $p=0.039$, respectively) and explained 29.83 % of the total variance. As for
250 spiders, the main variables explaining carabid species composition were field farming system

251 and the proportion of wood in the surrounding landscape ($F=4.91$, $p=0.005$ and $F=2.56$,
252 $p=0.01$, respectively) (Fig. 7). The first axis tended to contrast carabid assemblages according
253 to the field farming system. The species *Brachinus sclopeta* and *Poecilus cupreus* were
254 especially abundant in OF fields whereas *Pterosticus melanarius* and *Trechus gr.*
255 *quadristriatus* were especially abundant in fields under CF. On the second axis, landscapes
256 dominated by high proportions of woody SNH in the negative part were associated with high
257 abundances of *Nebria salina*, *Carabus nemoralis* and *Carabus granulatus*.

258 Both in carabids and spiders, the non-metric multidimensional scaling (NMDS) ordination
259 tended to cluster species assemblages observed in fields according to the farming system
260 applied (OF vs. CF) (Figs. A.3 and A.4; ANOSIM tests: spiders: $R^2=0.11$, $p=0.001$ carabids:
261 $R^2=0.12$, $p=0.001$). Results obtained using NMDS analysis were consistent with those
262 obtained using RDA. NMDS also showed more heterogeneity of both spider and carabid
263 assemblages in OF compared to CF.

264 **4. Discussion**

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

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

277 *4.1 Community structure*

278 **4.1.1 Effect of field farming system and local environmental conditions on community** 279 **structure**

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

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

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

299 those of previous studies that have shown that the height of vegetation increases the structural
300 heterogeneity of the habitat, thus offering a greater diversity of niches (Greenstone, 1984;
301 Uetz, 1991; Langellotto and Denno, 2004; Prieto-Benítez and Méndez, 2011). On the other
302 hand, our results are in accordance with the results of few studies (Štokmane and Spunģis,
303 2014, 2016), which can be explained by two main factors. The first one is related to changes
304 in the microclimatic (e.g. temperature, moisture) and structural conditions of habitats
305 modified by vegetation height (Langellotto and Denno, 2004). These changes in habitat
306 directly impact the mobility of individuals, and therefore their catchability, which results in an
307 effect of the sampling method (already mentioned by e.g. Topping and Sunderland, 1992).
308 The second explanation is related to the “nature” of the habitat (i.e. simply structured). Wheat
309 field indeed forms a very homogeneous habitat, in all CF and in some OF fields, with the total
310 or partial absence of other plant species and a reduced spatial heterogeneity. As a result, CF
311 creates a more open habitat with reduced ecological niches, which negatively impacts the
312 structure of spider communities. Overall, most studies were conducted on vegetation-dwelling
313 spiders, which make them hardly comparable to our results on ground-dwelling spiders. It is
314 thus hard to know whether the negative effect of vegetation height on spider abundance and
315 species richness is due to the sampling method or to spatial heterogeneity, but the fact that
316 spiders were caught in higher numbers in OF fields despite they have higher vegetation plaids
317 in favor of the second hypothesis.

318 **4.1.2 Effects of landscape characteristics on community structure**

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

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

328 The proportion of meadow in the landscape had a negative effect on spider activity-density in
329 OF and CF fields. It also interacted with farming system, with a negative effect on carabid
330 species richness in OF fields only. This is partly in contradiction with some previous studies
331 (see Purtauf et al., 2005 for carabids). On the other hand, Caro et al. (2016) suggested that
332 meadows may be poor habitats for carabids. Other studies also reported a negative effect of
333 the percentage of meadow in the landscape on the structure of spider assemblages, as
334 summarized in the review of Prieto-Benítez and Méndez (2011). Meadow exploitation in the
335 last decades, has been found to have drastic effects on both spiders and carabids (see Bell et
336 al., 2001 and Morris, 2000 respectively). Mowing of meadows, especially, leads to a strong
337 destruction of the habitat, which negatively affects arthropod communities (Dennis et al.,
338 2015). Intensive grazing is also generally harmful to biodiversity (Benton et al., 2003; Donald
339 et al., 2006). In our study area, meadows are intensively managed through grazing by cattle
340 and mowing, which may explain the negative impact of percentage of meadow on both spider
341 activity-density and on carabid species richness. The influence of the proportion of meadow
342 in the landscape on carabid species richness differed according to the field farming system,
343 and was significant only in OF fields. Carabid assemblages are modulated by the structure and
344 diversity of vegetation (Lövei and Sunderland, 1996; Rainio and Niemelä, 2003). Carabid
345 assemblages in meadows are then assumed to be more similar to those of CF fields, with both
346 environments disturbed by local practices (e.g. synthetic fertilization, mowing, pesticides),
347 explaining the lack of effect of meadows in CF. Conversely, carabid assemblages in OF fields

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

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

359 The influence of the proportion of wood in the landscape on spider activity-density and
360 carabid species richness depended on the field farming system. For spiders, this resulted in an
361 increasing activity-density with the proportion of wood in the surrounding landscape in OF
362 fields, and in a decreasing activity-density with the proportion of wood in the surrounding
363 landscape in CF fields. OF fields can be considered an attractive environment for spiders (e.g.
364 more food resources and habitat quality). Woods can provide alternative food resources, and
365 shelters for species escaping disturbances from crops, (Tschardt et al., 2005; Bianchi et al.,
366 2006). They constitute sources from which individuals can disperse in the landscape matrix
367 (Chaplin-Kramer et al., 2011). Carabid species richness decreased with the proportion of
368 wood in the surrounding landscape. This can be explained by the fact that dominant species in
369 both farming systems have low dispersal capacities and are mainly species of cultivated and /
370 or open areas. As a result, this negative effect suggests that woods might act as barriers to
371 carabid dispersal (see Lafage et al., 2015b). The fact that CF fields host more small-sized and

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

374 ***4.2. Community composition***

375 **4.2.1 Farming system and community composition**

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

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

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

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

402 **4.2.2 Landscape variables and community composition**

403 Spider and carabid community compositions were also modulated by the surrounding
404 landscape characteristics. The second RDA axes indeed opposed communities of landscapes
405 dominated by cropped elements to communities of landscapes dominated by uncultivated,
406 woody elements. Our results are in agreement with previous studies that showed the
407 importance of landscape in modulating arthropod community composition (e.g. Öberg et al.,
408 2007; Batáry et al., 2008; Schmidt et al., 2008). In landscapes where the cultivated area is
409 dominant, small and medium sized species, with high dispersal abilities, were found (for
410 spiders, see Blandenier, 2009; Simonneau et al., 2016; for carabids, see Luff, 1988; Desender
411 et al., 2008).

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

421 **5. Conclusion**

422 Understanding the interactions between cultivated and uncultivated environments at local and
423 landscape scales can help the design of new agricultural systems (Marshall and Moonen,
424 2002). Our study highlights the importance of distinguishing the various types of semi-natural
425 elements and not considering them as a homogeneous entity, because their effects vary
426 depending on the studied taxa and on the nature of the semi-natural element. Different taxa
427 respond to agricultural practices at different spatial scales and often at multiple spatial scales
428 (Gabriel et al., 2010). This suggests that considering both local and a landscape condition in
429 conservation strategy is required, and that no single indicator group is appropriate to represent
430 biodiversity. Our study indeed shows that spiders and carabids differentially react to changes
431 in local and landscape structure (see also Pétilon et al., 2008; Varet et al., 2013 in other
432 habitat types), and can be considered as complementary ecological models in agroecosystems.

433 **Acknowledgments**

434 E.A.D. PH.D was granted by the “Région Bretagne” (Founding ARED 8960) and the French
435 Foundation Research on Biodiversity (funding the SOLUTION project). This study was
436 partially supported by the FP7-PEOPLE-2013-IRSES fund (project APhiWEB, grant no.
437 611810). We thank the farmers who allowed us access to their farms. Many thanks to Sylvain
438 Poggi and Maxime Hervé for some statistical advices. We thank two anonymous referees for
439 helpful comments, Cyril Courtial for some help in spider identification and Jean-Luc Roger in
440 carabid identification.

441

442

443

444

445

446

447

448

449

450

451

452 **References**

- 453 Barton, K., 2016. MuMIn: Multi-Model Inference. R package version 1.16.4.
- 454 Batáry, P., Báldi, A., Kleijn, D., Tschamntke, T., 2011. Landscape-moderated biodiversity
455 effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B Biol. Sci.*
456 278, 1894 LP-1902.
- 457 Batáry, P., Báldi, A., Samu, F., Szuts, T., Erdos, S., 2008. Are spiders reacting to local or
458 landscape scale effects in Hungarian pastures? *Biol. Conserv.* 141, 2062–2070.
459 doi:10.1016/j.biocon.2008.06.002
- 460 Batáry, P., Orci, K.M., Báldi, A., Kleijn, D., Kisbenedek, T., Erdos, S., 2007. Effects of local
461 and landscape scale and cattle grazing intensity on Orthoptera assemblages of the
462 Hungarian Great Plain. *Basic Appl. Ecol.* 8, 280–290. doi:10.1016/j.baae.2006.03.012
- 463 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models
464 Using **lme4**. *J. Stat. Softw.* 67. doi:10.18637/jss.v067.i01
- 465 Bell, J., Wheater, C., Cullen, W., 2001. The implications of grassland and heathland
466 management for the conservation of spider communities: a review. *J. Zool.* 255, 377–
467 387. doi:10.1017/s0952836901001479
- 468 Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on
469 biodiversity and abundance: A meta-analysis. *J. Appl. Ecol.* 42, 261–269.
470 doi:10.1111/j.1365-2664.2005.01005.x
- 471 Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat
472 heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188. doi:10.1016/S0169-
473 5347(03)00011-9

474 Bianchi, F.J.J., Booij, C.J., Tschardtke, T., 2006. Sustainable pest regulation in agricultural
475 landscapes: a review on landscape composition, biodiversity and natural pest control.
476 Proc. R. Soc. B Biol. Sci. 273, 1715–1727. doi:10.1098/rspb.2006.3530

477 Blandenier, G., 2009. Ballooning of spiders (Araneae) in Switzerland: General Results from
478 an Eleven-Year Survey. Bull. Br. Arachnol. Soc. 14, 308–316.
479 doi:10.13156/ arac.2009.14.7.308

480 Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: Harnessing
481 ecosystem services for food security. Trends Ecol. Evol. 28, 230–238.
482 doi:10.1016/j.tree.2012.10.012

483 Borcard, D., Gillet, F., Legendre, Legendre, P., 2011. Numerical Ecology with R, Springer.
484 doi:10.1017/CBO9781107415324.004

485 Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A
486 Practical Information-Theoretic Approach (2nd ed), Ecological Modelling.
487 doi:10.1016/j.ecolmodel.2003.11.004

488 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani,
489 A., Mace, G.M., Tilman, D., A. Wardle, D., Kinzig, A.P., Daily, G.C., Loreau, M., Grace,
490 J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its
491 impact on humanity. Nature 489, 326–326. doi:10.1038/nature11373

492 Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S., Bretagnolle, V., 2016. Multi-
493 scale effects of agri-environment schemes on carabid beetles in intensive farmland.
494 Agric. Ecosyst. Environ. 229, 48–56. doi:10.1016/j.agee.2016.05.009

495 Castro, A., Wise, D.H., 2009. Influence of fine woody debris on spider diversity and
496 community structure in forest leaf litter. Biodivers. Conserv. 18, 3705–3731.

497 doi:10.1007/s10531-009-9674-7

498 Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of
499 crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932.
500 doi:10.1111/j.1461-0248.2011.01642.x

501 Chavent, M., Kuentz, V., Liqueur, B., Saracco, J., 2013. ClustOfVar: Clustering of variables. R
502 package version 0.8. <https://cran.r-project.org/package=ClustOfVar>.

503 Cole, L.J., McCracken, D.I., Downie, I.S., Dennis, P., Foster, G.N., Waterhouse, T., Murphy,
504 K.J., Griffin, A.L., Kennedy, M.P., 2005. Comparing the effects of farming practices on
505 ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish
506 farmland. *Biodivers. Conserv.* 14, 441–460. doi:10.1007/s10531-004-6404-z

507 Colfer, R.G., Rosenheim, J.A., 2001. Predation on immature parasitoids and its impact on
508 aphid suppression. *Oecologia* 126, 292–304. doi:10.1007/s004420000510

509 Dennis, P., Skartveit, J., Kunaver, A., McCracken, D.I., 2015. The response of spider
510 (Araneae) assemblages to structural heterogeneity and prey abundance in sub-montane
511 vegetation modified by conservation grazing. *Glob. Ecol. Conserv.* 3, 715–728.
512 doi:10.1016/j.gecco.2015.03.007

513 Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and
514 arachnids in relation to structural heterogeneity of grazed , indigenous grasslands. *Ecol.*
515 *Entomol.* 23, 253–264.

516 Desender, K., Dekoninck, W., Maes, D., Crevecoeur, L., Dufrière, M., Jacobs, M.,
517 Lambrechts, J., Pollet, M., Stassen, E., Thys, N., 2008. Een nieuwe verspreidingsatlas
518 van de loopkevers en zandloopkevers (Carabidae) in België. *Inst. voor Natuur- en*
519 *Bosonderzoek* 32.

520 Diekötter, T., Wamser, S., Wolters, V., Birkhofer, K., 2010. Landscape and management
521 effects on structure and function of soil arthropod communities in winter wheat. *Agric.
522 Ecosyst. Environ.* 137, 108–112. doi:10.1016/j.agee.2010.01.008

523 Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of
524 continent-wide impacts of agricultural intensification on European farmland birds, 1990-
525 2000. *Agric. Ecosyst. Environ.* 116, 189–196. doi:10.1016/j.agee.2006.02.007

526 Downie, I.S., Wilson, W.L., Abernethy, V.J., McCracken, D.I., Foster, G.N., Ribera, I.,
527 Murphy, K.J., Waterhouse, A., 1999. The Impact of Different Agricultural Land-uses on
528 Epigeal Spider Diversity in Scotland. *J. Insect Conserv.* 3, 273–286.

529 Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure
530 of ecological distance. *Vegetatio* 69, 57–68.

531 Feber, R.E., Johnson, P.J., Bell, J.R., Chamberlain, D.E., Firbank, L.G., Fuller, R.J., Manley,
532 W., Mathews, F., Norton, L.R., Townsend, M., Macdonald, D.W., 2015. Organic
533 farming: Biodiversity impacts can depend on dispersal characteristics and landscape
534 context. *PLoS One* 10, e0135921. doi:10.1371/journal.pone.0135921

535 Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P.,
536 Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro,
537 V., Inchausti, P., Liira, J., Morales, M.B., Oate, J.J., Part, T., Weisser, W.W.,
538 Winqvist, C., Thies, C., Tschardt, T., 2011. Agricultural intensification and
539 biodiversity partitioning in European landscapes comparing plants, carabids, and birds.
540 *Ecol. Appl.* 21, 1772–1781. doi:10.1890/10-0645.1

541 Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C.,
542 Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald,

543 D.W., Firbank, L.G., 2005. Benefits of organic farming to biodiversity vary among taxa.
544 Biol. Lett. 1, 431–434. doi:10.1098/rsbl.2005.0357

545 Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E., Benton, T.G., 2010. Scale
546 matters: The impact of organic farming on biodiversity at different spatial scales. Ecol.
547 Lett. 13, 858–869. doi:10.1111/j.1461-0248.2010.01481.x

548 Gabriel, D., Sait, S.M., Kunin, W.E., Benton, T.G., 2013. Food production vs. biodiversity:
549 Comparing organic and conventional agriculture. J. Appl. Ecol. 50, 355–364.
550 doi:10.1111/1365-2664.12035

551 Gabriel, D., Tscharntke, T., 2007. Insect pollinated plants benefit from organic farming.
552 Agric. Ecosyst. Environ. 118, 43–48. doi:10.1016/j.agee.2006.04.005

553 Garratt, M.P.D., Wright, D.J., Leather, S.R., 2011. The effects of farming system and
554 fertilisers on pests and natural enemies: A synthesis of current research. Agric. Ecosyst.
555 Environ. 141, 261–270. doi:10.1016/j.agee.2011.03.014

556 Gauffre, B., Mallez, S., Chapuis, M.P., Leblois, R., Litrico, I., Delaunay, S., Badenhausser, I.,
557 2015. Spatial heterogeneity in landscape structure influences dispersal and genetic
558 structure: Empirical evidence from a grasshopper in an agricultural landscape. Mol. Ecol.
559 24, 1713–1728. doi:10.1111/mec.13152

560 Gelman, A., Su, Y.-S., 2015. arm: Data Analysis Using Regression and
561 Multilevel/Hierarchical Models. R package version 1.8-6. [https://CRAN.R-](https://CRAN.R-project.org/package=arm)
562 [project.org/package=arm](https://CRAN.R-project.org/package=arm).

563 Gosme, M., de Villemandy, M., Bazot, M., Jeuffroy, M.H., 2012. Local and neighbourhood
564 effects of organic and conventional wheat management on aphids, weeds, and foliar
565 diseases. Agric. Ecosyst. Environ. 161, 121–129. doi:10.1016/j.agee.2012.07.009

566 Greenstone, M.H., 1984. Determinants of web spider species diversity : Determinants
567 vegetation structural diversity vs . prey availability. *Oecologia* 62, 299–304.

568 Griffin, J.N., Byrnes, J.E.K., Cardinale, B.J., 2013. Effects of predator richness on prey
569 suppression: A meta-analysis. *Ecology* 94, 2180–2187. doi:10.1890/13-0179.1

570 Griffin, M.L., Yeargan, K. V, 2002. Factors potentially affecting oviposition site selection by
571 the lady beetle *Coleomegilla maculata* (Coleoptera : Coccinellidae). *Environ. Entomol.*
572 31, 112–119. doi:10.1603/0046-225x-31.1.112

573 Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in
574 ecology and evolution: Challenges and solutions. *J. Evol. Biol.* 24, 699–711.
575 doi:10.1111/j.1420-9101.2010.02210.x

576 Hänggi, A., Stocklie, E., Nentwig, W., 1995. Habitats of Central European spiders.
577 Characterisation of the habitats of the most abundant spider species of Central Europe
578 and associated species. Centre suisse de cartographie de la faune (CSCF), Neuchâtel.

579 Harvey, P., Nellist, D., Telfer, M., 2002. Provisional Atlas of British spiders (Arachnida,
580 Araneae), Volume 1 & 2. Biological Records Centre, Huntingdon.

581 Hawro, V., Ceryngier, P., Tschardtke, T., Thies, C., Gagic, V., Bengtsson, J., Bommarco, R.,
582 Winqvist, C., Weisser, W.W., Clement, L.W., Japoshvili, G., Ulrich, W., 2015.
583 Landscape complexity is not a major trigger of species richness and food web structure
584 of European cereal aphid parasitoids. *BioControl* 60, 451–461. doi:10.1007/s10526-015-
585 9660-9

586 Henckel, L., Borger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain
587 weed metacommunity dynamics in farmland landscapes. *Proc. R. Soc. B Biol. Sci.* 282,
588 20150002–20150002. doi:10.1098/rspb.2015.0002

589 Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S.,
590 Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J.,
591 Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R., 2007. How landscape
592 structure, land-use intensity and habitat diversity affect components of total arthropod
593 diversity in agricultural landscapes. *J. Appl. Ecol.* 44, 340–351. doi:10.1111/j.1365-
594 2664.2006.01270.x

595 Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P. V., Evans, A.D., 2005.
596 Does organic farming benefit biodiversity? *Biol. Conserv.* 122, 113–130.
597 doi:10.1016/j.biocon.2004.07.018

598 Holland, J.M., Birkett, T., Southway, S., 2009. Contrasting the farm-scale spatio-temporal
599 dynamics of boundary and field overwintering predatory beetles in arable crops.
600 *BioControl* 54, 19–33. doi:10.1007/s10526-008-9152-2

601 Holland, J.M., Luff, M.L., 2000. The effects of agricultural practices on Carabidae in
602 temperate agroecosystems. *Integr. Pest Manag. Rev.* 5, 109–129.
603 doi:10.1023/A:1009619309424

604 Holzschuh, A., Steffan-Dewenter, I., Tschamtko, T., 2009. Grass strip corridors in agricultural
605 landscapes enhance nest-site colonization by solitary wasps. *Ecol. Appl.* 19, 123–132.
606 doi:10.1890/08-0384.1

607 Köhler, H.-R., Triebkorn, R., 2013. Population Level and Beyond? *Wildlife Ecotoxicology*
608 of Pesticides: Can We Track Effects to the Wildlife Ecotoxicology of Pesticides: Can We
609 Track Effects to the Population Level and Beyond? *Sci.* 341 759, 759–765.
610 doi:10.1126/science.1237591

611 Lafage, D., Pétilon, J., 2016. Relative importance of management and natural flooding on

612 spider, carabid and plant assemblages in extensively used grasslands along the Loire.
613 Basic Appl. Ecol. 17, 535–545. doi:10.1016/j.baae.2016.04.002

614 Lafage, D., Sibelle, C., Secondi, J., Canard, A., Pétilion, J., 2015. Short-term resilience of
615 arthropod assemblages after spring flood, with focus on spiders (Arachnida: Araneae)
616 and carabids (Coleoptera: Carabidae). Ecohydrology 8, 1584–1599.
617 doi:10.1002/eco.1606

618 Lambeets, K., Vandegehuchte, M.L., Maelfait, J.P., Bonte, D., 2008. Understanding the
619 impact of flooding on trait-displacements and shifts in assemblage structure of predatory
620 arthropods on river banks. J. Anim. Ecol. 77, 1162–1174. doi:10.1111/j.1365-
621 2656.2008.01443.x

622 Lang, A.G., 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute
623 density estimates of epigeal invertebrate predators in arable land. J. Pest Sci. (2004). 73,
624 99–106. doi:10.1007/bf02956438

625 Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-
626 structured habitats: A meta-analytical synthesis. Oecologia 139, 1–10.
627 doi:10.1007/s00442-004-1497-3

628 Larrivé, M., Buddle, C.M., 2009. Diversity of canopy and understorey spiders in north-
629 temperate hardwood forests. Agric. For. Entomol. 11, 225–237. doi:10.1111/j.1461-
630 9563.2008.00421.x

631 Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier Sci. BV, Amsterdam 24, 870.
632 doi:10.1017/CBO9781107415324.004

633 Lövei, G.L., Sunderland, K.D., 1996. Ecology and Behavior of Ground Beetles (Coleoptera:
634 Carabidae). Annu. Rev. Entomol. 41, 231–256.

- 635 Luff, M.L., 1998. Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain.
636 Biological Records Centre, Huntingdon.
- 637 Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and
638 bioindication. *Agric. Ecosyst. Environ.* 74, 229–273. doi:10.1016/S0167-
639 8809(99)00038-9
- 640 Marini, L., Fontana, P., Scotton, M., Klimek, S., 2008. Vascular plant and Orthoptera
641 diversity in relation to grassland management and landscape composition in the
642 European Alps. *J. Appl. Ecol.* 45, 361–370. doi:10.1111/j.1365-2664.2007.01402.x
- 643 Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: Integrating
644 agricultural, environmental and biodiversity functions. *Agric. Ecosyst. Environ.* 89, 5–
645 21. doi:10.1016/S0167-8809(01)00315-2
- 646 Marshall, E.J.P., West, T.M., Kleijn, D., 2006. Impacts of an agri-environment field margin
647 prescription on the flora and fauna of arable farmland in different landscapes. *Agric.*
648 *Ecosyst. Environ.* 113, 36–44. doi:10.1016/j.agee.2005.08.036
- 649 Martin H. Schmidt, Clough, Y., Schulz, W., Westphalen, A., Tschardtke, T., 2006. Capture
650 Efficiency and Preservation Attributes of Different Fluids in Pitfall Traps. *J. Arachnol.*
651 34, 159–162. doi:10.1636/T04-95.1
- 652 Menalled, F.D., Lee, J.C., Landis, D.A., 1999. Manipulating carabid beetle abundance alters
653 prey removal rates in corn fields. *BioControl* 43, 441–456.
654 doi:10.1023/A:1009946004251
- 655 Mertens, J., Beladjal, L., Janssens, F., Matthys, P., 2007. Pitfall trapping in flooding habitats:
656 A new technique reveals *Archisotoma pulchella* (Collembola: Isotomidae) as new to the
657 Belgian fauna. *Belgian J. Zool.* 137, 177–181.

658 Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses
659 of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10, 178–186.
660 doi:10.1016/j.baae.2008.01.001

661 Morris, M.G., 2000. The effects of structure and its dynamics on the ecology and conservation
662 of arthropods in British grasslands. *Biol. Conserv.* 95, 129–142. doi:10.1016/S0006-
663 3207(00)00028-8

664 Öberg, S., Ekbom, B., Bommarco, R., 2007. Influence of habitat type and surrounding
665 landscape on spider diversity in Swedish agroecosystems. *Agric. Ecosyst. Environ.* 122,
666 211–219. doi:10.1016/j.agee.2006.12.034

667 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson,
668 G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2017. *vegan: Community Ecology*
669 *Package*. R package version 2.4-2.

670 Östman, Ö., Ekbom, B., Bengtsson, J., 2001. Landscape heterogeneity and farming practice
671 influence biological control *Basic and Applied Ecology*. *Basic Appl. Ecol* 2, 365–371.
672 doi:10.1078/1439-1791-00072

673 Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and
674 spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecol.*
675 *Indic.* 6, 780–793. doi:10.1016/j.ecolind.2005.03.005

676 Pétilion, J., Georges, A., Canard, A., Lefeuvre, J.C., Bakker, J.P., Ysnel, F., 2008. Influence
677 of abiotic factors on spider and ground beetle communities in different salt-marsh
678 systems. *Basic Appl. Ecol.* 9, 743–751. doi:10.1016/j.baae.2007.08.007

679 Prieto-Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and
680 richness of spiders (Araneae): A meta-analysis. *Biol. Conserv.* 144, 683–691.

681 doi:10.1016/j.biocon.2010.11.024

682 Puech, C., Baudry, J., Joannon, A., Poggi, S., Aviron, S., 2014. Organic vs. conventional
683 farming dichotomy: Does it make sense for natural enemies? *Agric. Ecosyst. Environ.*
684 194, 48–57. doi:10.1016/j.agee.2014.05.002

685 Puech, C., Poggi, S., Baudry, J., Aviron, S., 2015. Do farming practices affect natural enemies
686 at the landscape scale? *Landsc. Ecol.* 30, 125–140. doi:10.1007/s10980-014-0103-2

687 Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tschardtke, T., Wolters, V., 2005.
688 Landscape context of organic and conventional farms: Influences on carabid beetle
689 diversity. *Agric. Ecosyst. Environ.* 108, 165–174. doi:10.1016/j.agee.2005.01.005

690 R Core Team, 2016. R: A language and environment for statistical computing. R Foundation
691 for Statistical Computing.

692 Rainio, J., Niemelä, J.K., 2003. Ground beetles (Coleoptera : Carabidae) as bioindicators.
693 *Biodivers. Conserv.* 12, 487–506. doi:10.1023/A:1022412617568

694 Riechert, S.E., Lawrence, K., 1997. Test for predation effects of single versus multiple species
695 of generalist predators: Spiders and their insect prey. *Entomol. Exp. Appl.* 84, 147–155.
696 doi:10.1023/A:1003045407626

697 Roubinet, E., Birkhofer, K., Malsher, G., Staudacher, K., Ekbom, B., Traugott, M., Jonsson,
698 M., 2017. Diet of generalist predators reflects effects of cropping period and farming
699 system on extra- and intraguild prey. *Ecol. Appl.* 27, 1167–1177. doi:10.1002/eap.1510

700 Rundlöf, M., Bengtsson, J., Smith, H.G., 2008. Local and landscape effects of organic
701 farming on butterfly species richness and abundance. *J. Appl. Ecol.* 45, 813–820.
702 doi:10.1111/j.1365-2664.2007.01448.x

703 Rundlöf, M., Smith, H.G., 2006. The effect of organic farming on butterfly diversity depends
704 on landscape context. *J. Appl. Ecol.* 43, 1121–1127. doi:10.1111/j.1365-
705 2664.2006.01233.x

706 Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2015. Predator body sizes
707 and habitat preferences predict predation rates in an agroecosystem. *Basic Appl. Ecol.*
708 16, 250–259. doi:10.1016/j.baae.2015.02.003

709 Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2014. Management
710 intensity at field and landscape levels affects the structure of generalist predator
711 communities. *Oecologia* 175, 971–983. doi:10.1007/s00442-014-2949-z

712 Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., Tscharntke, T., 2003. Relative
713 importance of predators and parasitoids for cereal aphid control. *Proc. R. Soc. B Biol.*
714 *Sci.* 270, 1905–1909. doi:10.1098/rspb.2003.2469

715 Schmidt, M.H., Roschewitz, I., Thies, C., Tscharntke, T., 2005. Differential effects of
716 landscape and management on diversity and density of ground-dwelling farmland
717 spiders. *J. Appl. Ecol.* 42, 281–287. doi:10.1111/j.1365-2664.2005.01014.x

718 Schmidt, M.H., Thies, C., Nentwig, W., Tscharntke, T., 2008. Contrasting responses of arable
719 spiders to the landscape matrix at different spatial scales. *J. Biogeogr.* 35, 157–166.
720 doi:10.1111/j.1365-2699.2007.01774.x

721 Schmidt, M.H., Tscharntke, T., 2005. Landscape context of sheetweb spider (Araneae:
722 Linyphiidae) abundance in cereal fields. *J. Biogeogr.* 32, 467–473. doi:10.1111/j.1365-
723 2699.2004.01244.x

724 Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., Balázs,
725 K., Báldi, A., Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Fraser, M.D., Frank, T.,

726 Friedel, J.K., Garchi, S., Geijzendorffer, I.R., Gomiero, T., Gonzalez-Bornay, G., Hector,
727 A., Jerkovich, G., Jongman, R.H.G., Kakudidi, E., Kainz, M., Kovács-Hostyánszki, A.,
728 Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P.,
729 Pulido, F.J., Sarthou, J., Siebrecht, N., Sommaggio, D., Turnbull, L. a, Wolfrum, S.,
730 Herzog, F., 2014. Gains to species diversity in organically farmed fields are not
731 propagated at the farm level. *Nat. Commun.* 5, 4151. doi:10.1038/ncomms5151

732 Simonneau, M., Courtial, C., Pétilion, J., 2016. Phenological and meteorological determinants
733 of spider ballooning in an agricultural landscape. *C. R. Biol.* 339, 408–416.
734 doi:10.1016/j.crv.2016.06.007

735 Stoate, C., Boatman, N., Borralho, R., Carvalho, C.R., Snoo, G.R. d., Eden, P., 2001.
736 Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* 63, 337–365.
737 doi:10.1006/jema.2001.0473

738 Štokmane, M., Spuņģis, V., 2016. The influence of vegetation structure on spider species
739 richness , diversity and community organization in the Apšuciems calcareous fen ,
740 Latvia. *Anim. Biodivers. Conserv.* 32.2, 221–236.

741 Štokmane, M., Spuņģis, V., 2014. Diversity of grass-dwelling spiders (Arachnida: Araneae)
742 in calcareous fens of the Coastal Lowland, Latvia. *J. Insect Conserv.* 18, 757–769.
743 doi:10.1007/s10841-014-9677-x

744 Straub, C.S., Finke, D.L., Snyder, W.E., 2008. Are the conservation of natural enemy
745 biodiversity and biological control compatible goals? *Biol. Control* 45, 225–237.
746 doi:10.1016/j.biocontrol.2007.05.013

747 Straub, C.S., Snyder, W.E., 2006. Species identity dominates the relationship between
748 predator biodiversity and herbivore suppression. *Ecology* 87, 277–282. doi:10.1890/05-

749 0599

750 Ter Braak, C.J., Šmilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows
751 user's guide: software for canonical community ordination (version 4.5). Ithaca, NY,
752 USA.

753 Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier,
754 P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W.W., Winqvist,
755 C., Tschardtke, T., 2011. The relationship between agricultural intensification and
756 biological control: experimental tests across Europe. *Ecol. Appl.* 21, 2187–2196.
757 doi:10.1890/10-0929.1

758 Topping, C.J., Sunderland, K.D., 1992. Limitations to the Use of Pitfall Traps in Ecological
759 Studies Exemplified by a Study of Spiders in a Field of Winter Wheat. *J. Appl. Ecol.* 29,
760 485. doi:10.2307/2404516

761 Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer,
762 J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future
763 of agricultural intensification. *Biol. Conserv.* 151, 53–59.
764 doi:10.1016/j.biocon.2012.01.068

765 Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape
766 perspectives on agricultural intensification and biodiversity - Ecosystem service
767 management. *Ecol. Lett.* 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x

768 Tschardtke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson,
769 J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D.,
770 Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W.,
771 Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der

772 Putten, W.H., Westphal, C., 2012b. Landscape moderation of biodiversity patterns and
773 processes - eight hypotheses. *Biol. Rev.* 87, 661–685. doi:10.1111/j.1469-
774 185X.2011.00216.x

775 Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-
776 use intensity and the effects of organic farming on biodiversity: A hierarchical meta-
777 analysis. *J. Appl. Ecol.* 51, 746–755. doi:10.1111/1365-2664.12219

778 Uetz, G.W., 1991. Habitat Structure and Spider Foraging. Pp. 325–348. In *Habitat Structure;*
779 *the Physical Arrangement of Objects in Space.* (E.D. McCoy, S.A. Bell, H.R.
780 Mushinsky, eds.) London: Chapman and Hall.

781 Uetz, G.W., Unzicker, J.D., Journal, S., May, N., 1976. Pitfall Trapping in *Ecological Studies*
782 *of Wandering Spiders.* *J. Arachnol.* 3, 101–111.

783 Varet, M., Burel, F., Lafage, D., Petillon, J., 2013. Age-dependent colonization of urban
784 habitats: a diachronic approach using carabid beetles and spiders. *Anim. Biol.* 63, 257–
785 269. doi:10.1163/15707563-00002410

786 Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C.,
787 Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tschamntke, T., Weisser, W.W.,
788 Bommarco, R., 2011. Mixed effects of organic farming and landscape complexity on
789 farmland biodiversity and biological control potential across Europe. *J. Appl. Ecol.* 48,
790 570–579. doi:10.1111/j.1365-2664.2010.01950.x

791 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects*
792 *Models and Extensions in Ecology with R.* Springer Science and Business Media.

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	Perennial 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 length	quantitative	m	3692.63- 11134.3	6933.21 (\pm 317)

818

819

820

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>						
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

827

828

829 **Figures**

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

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

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

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

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

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

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

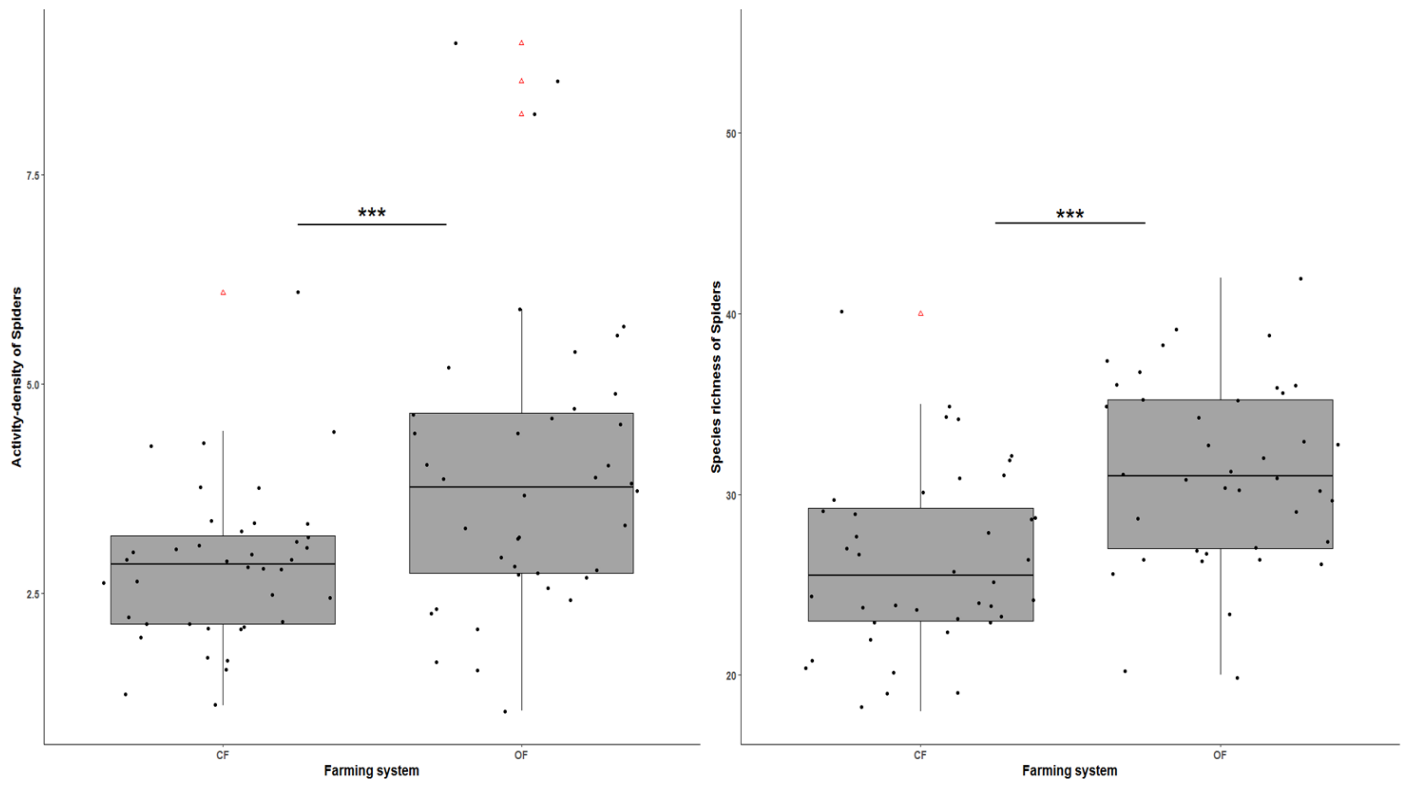
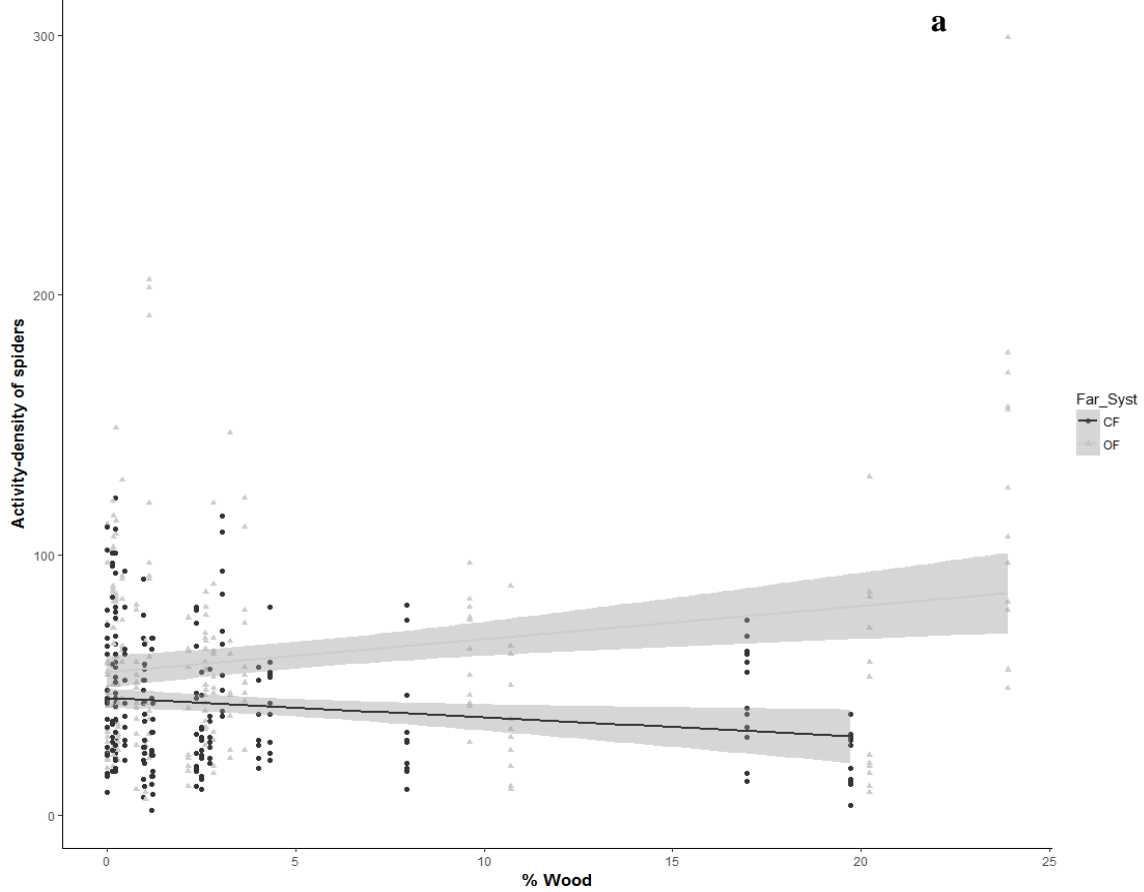


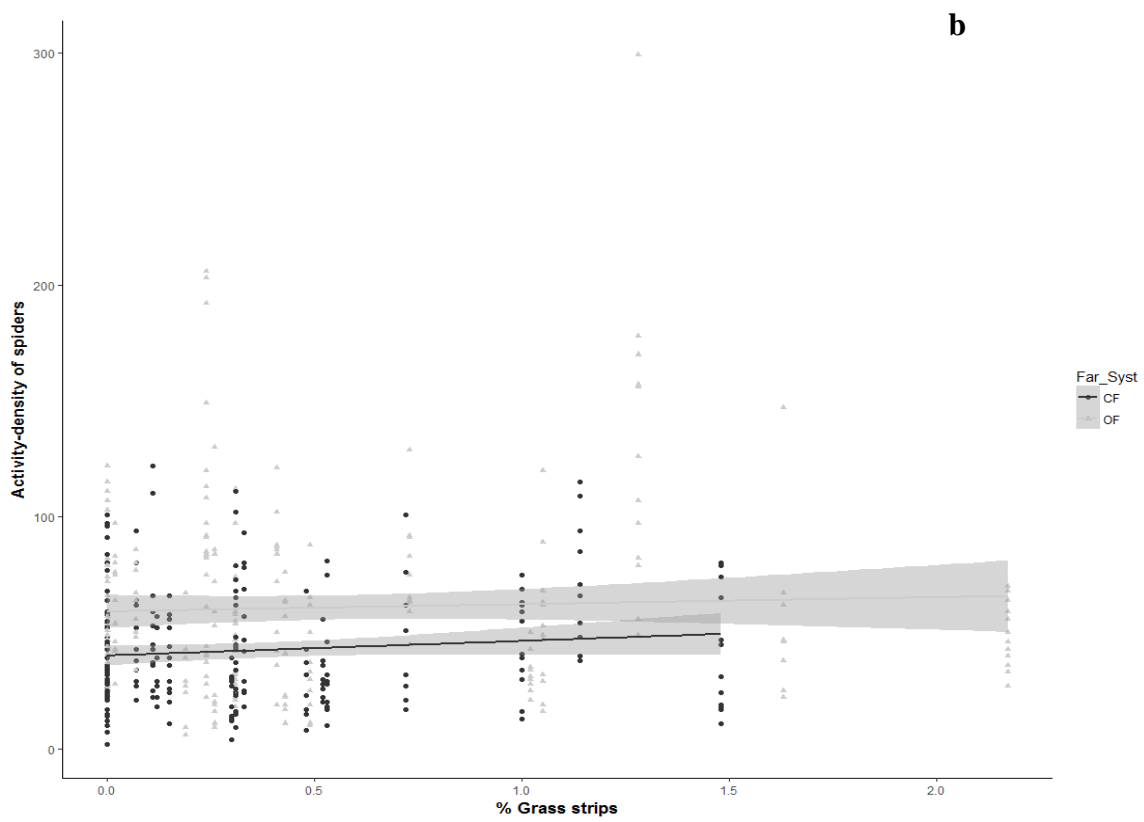
Fig. 1

853

854

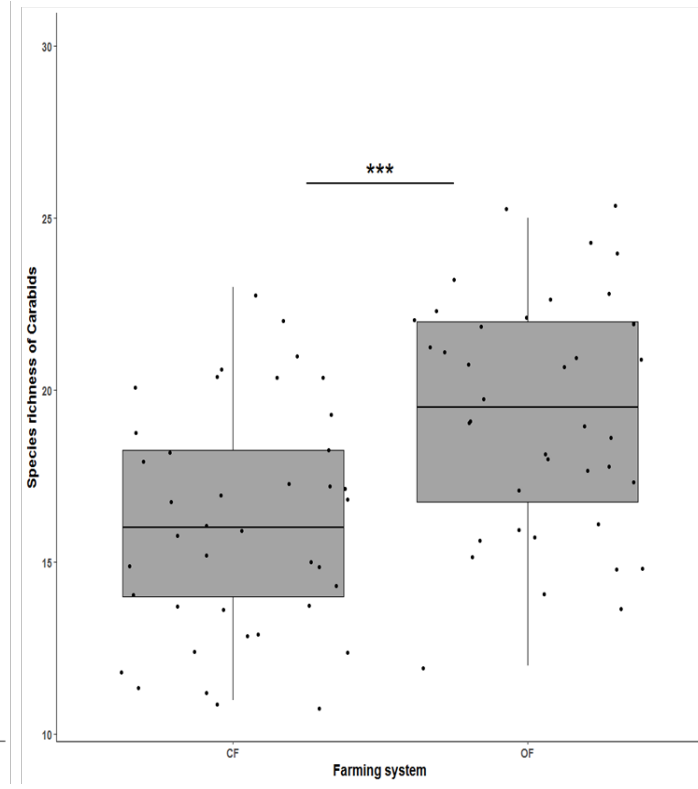
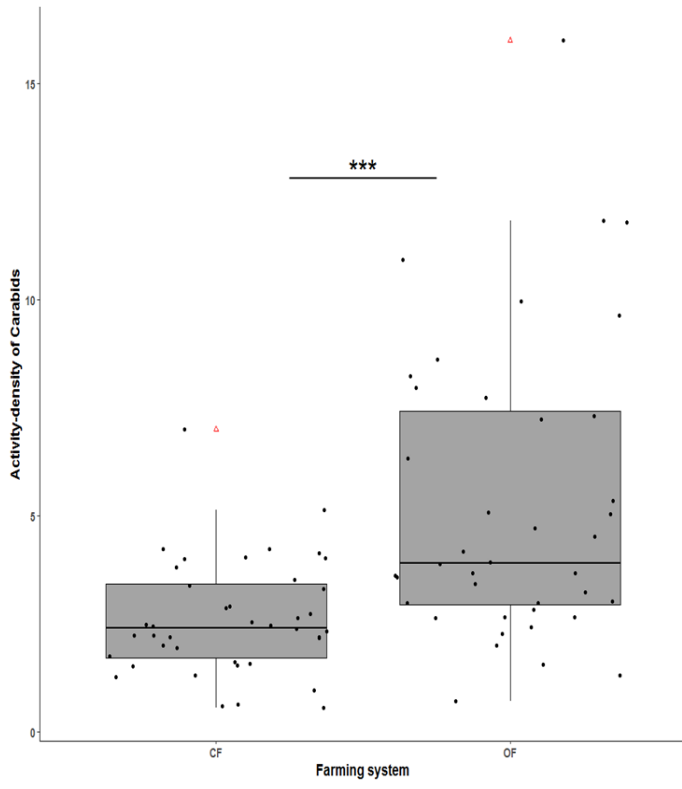


855

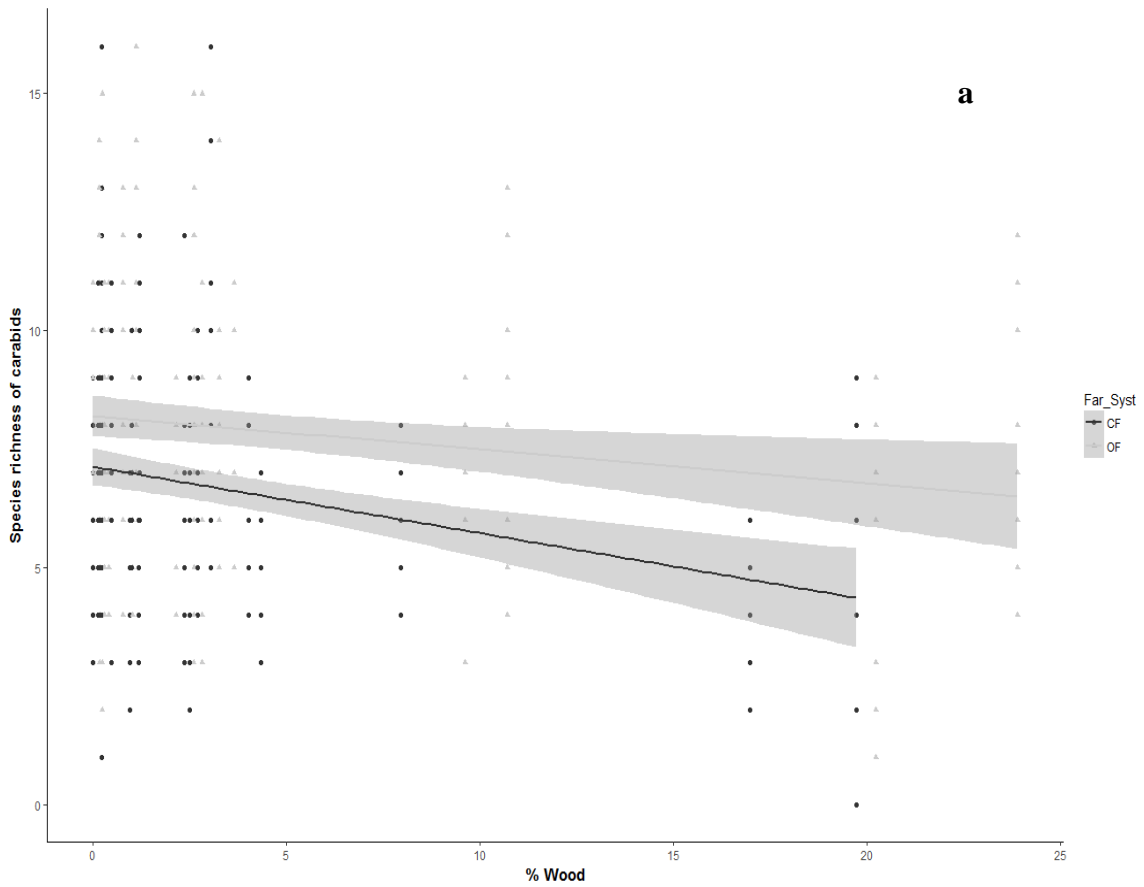


856

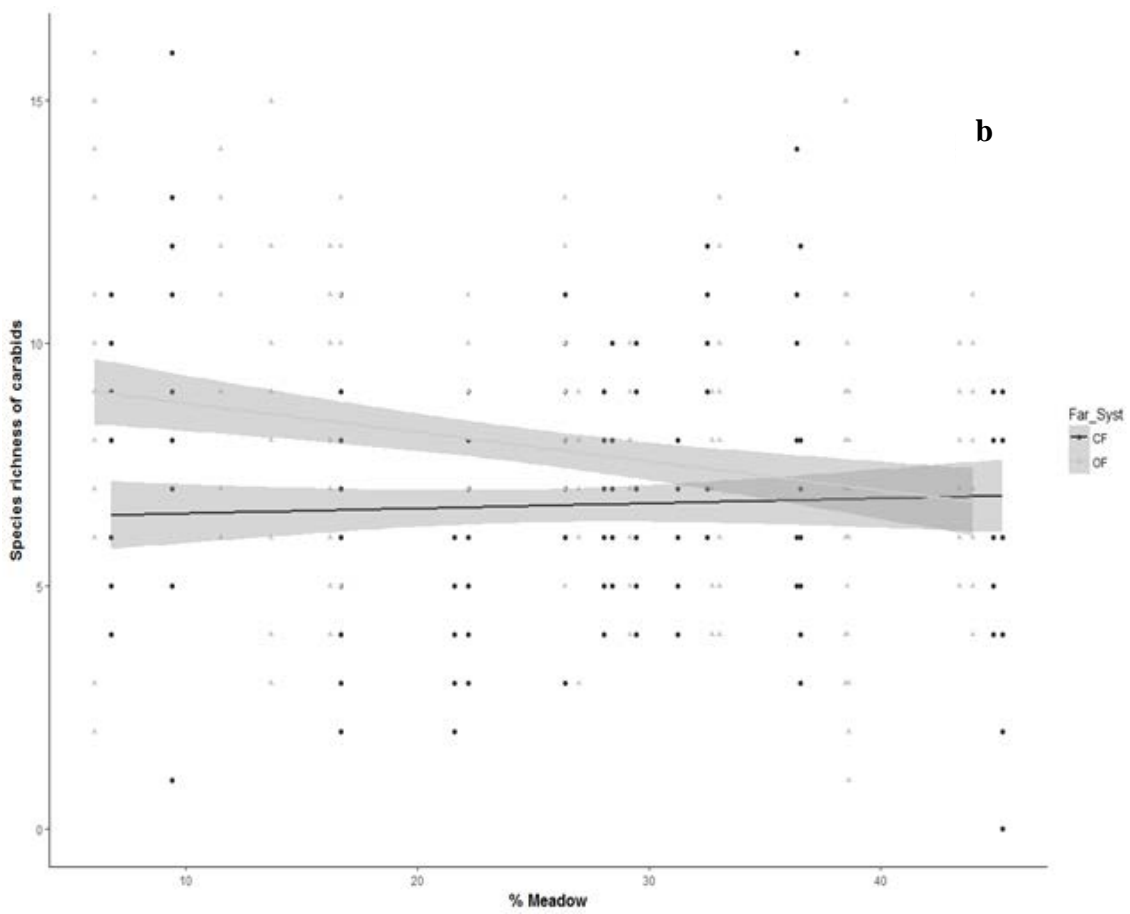
857 **Fig. 2**



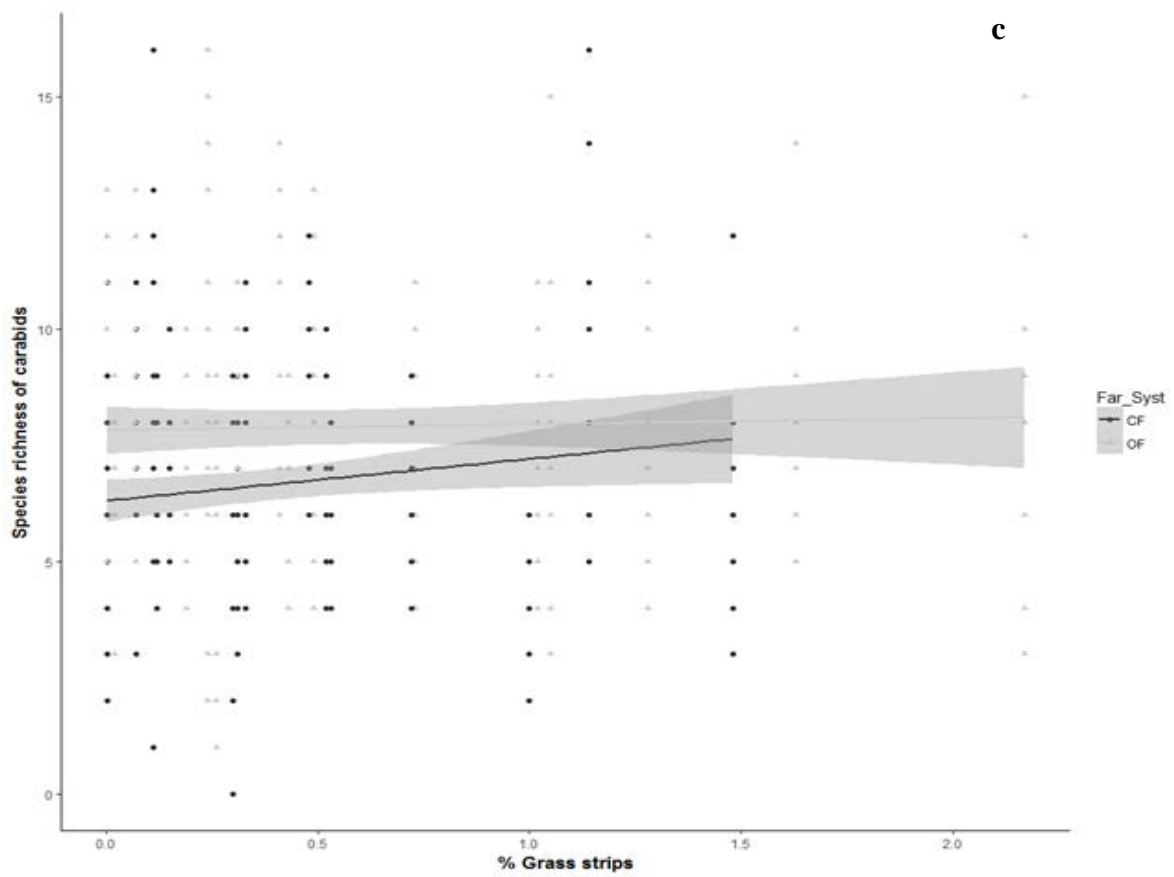
858 **Fig. 3.**



859



860



861

862 **Fig. 4.**

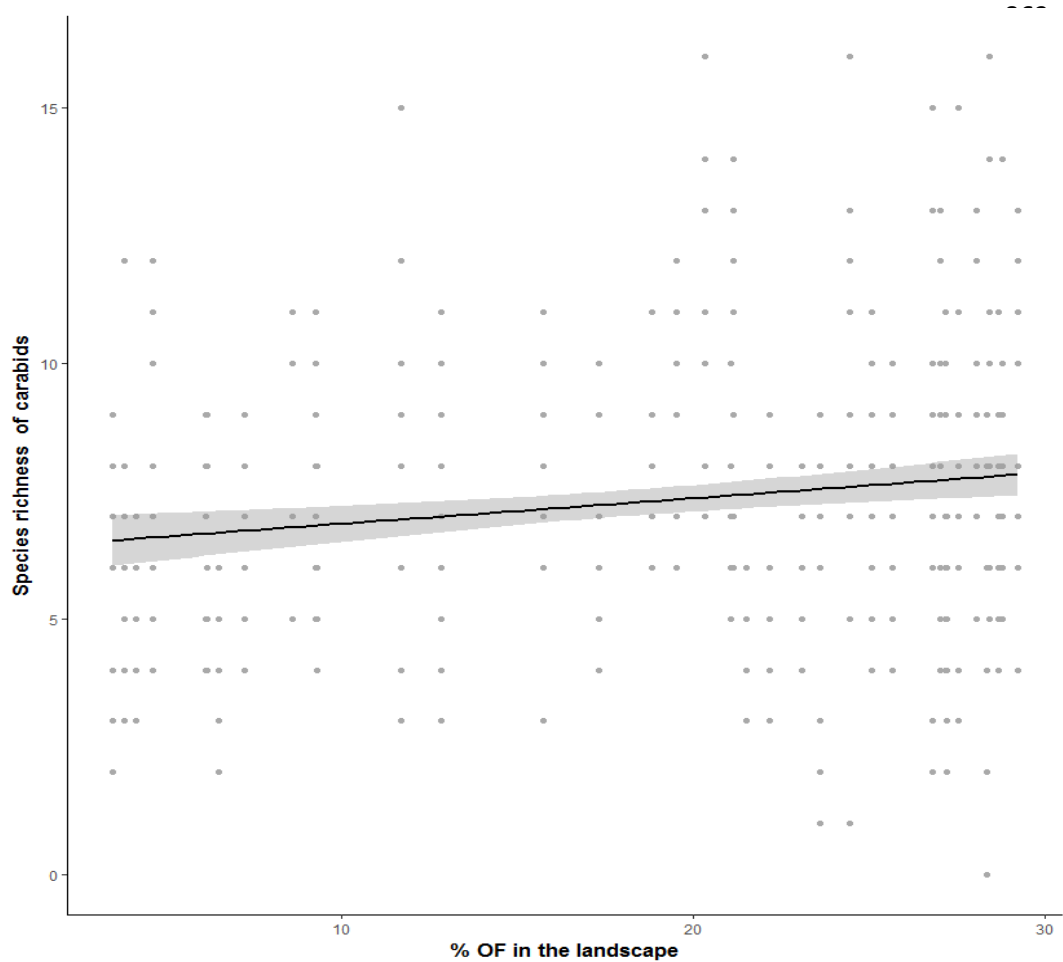


Fig. 5.

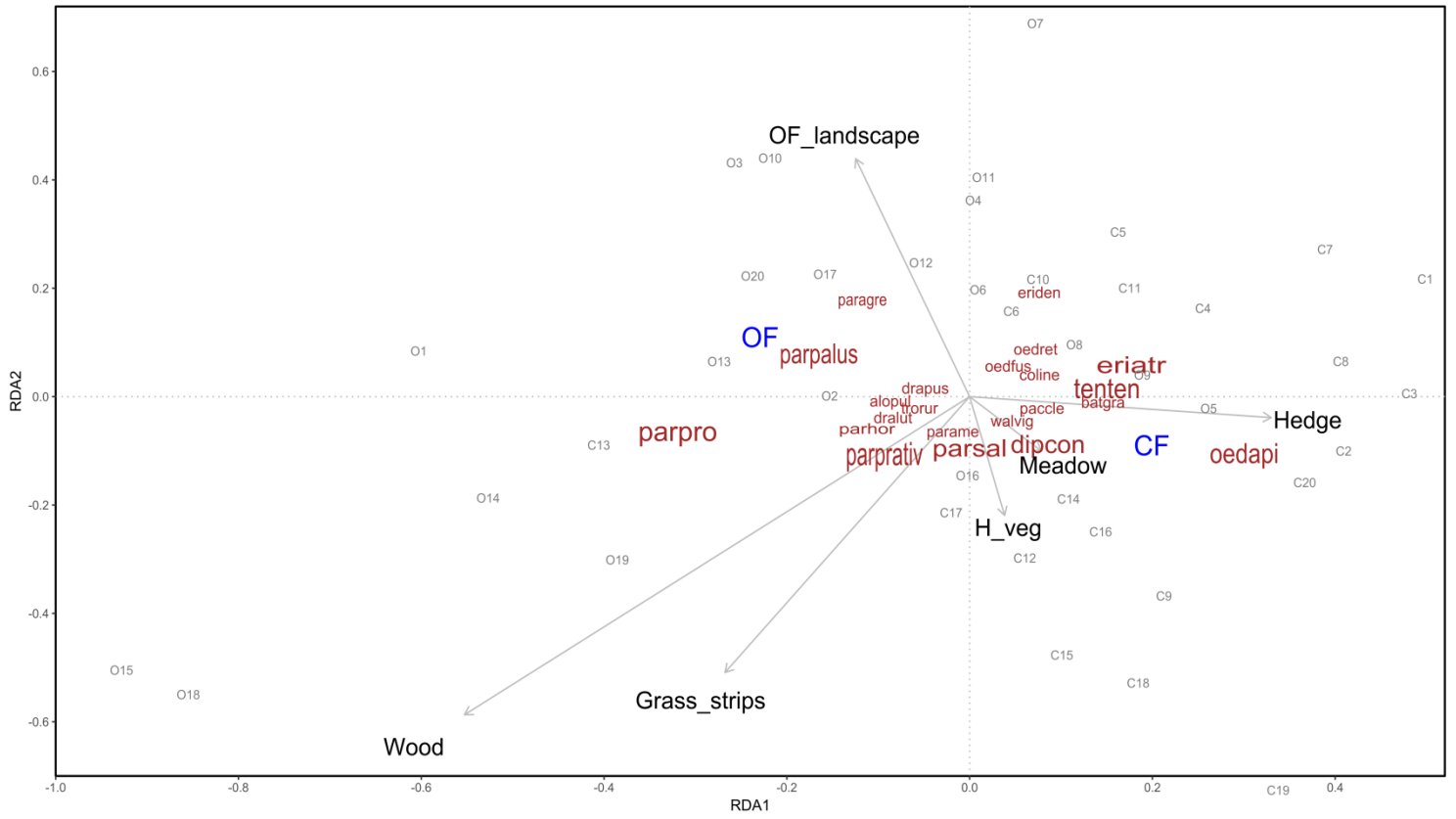


Fig. 6

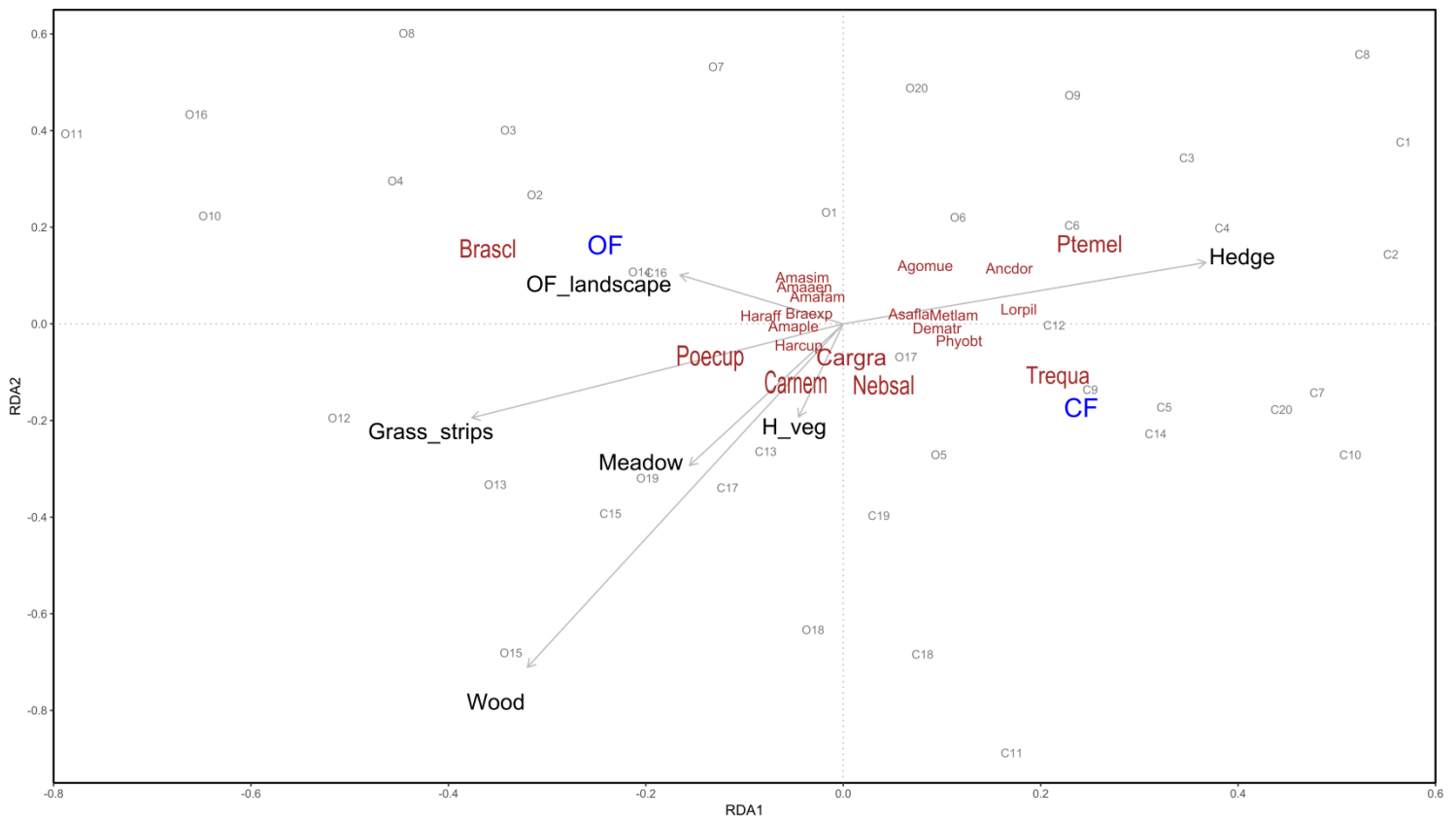


Fig. 7

