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1 Different components of landscape complexity are necessary to preserve multiple taxonomic  
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3

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## 18 Abstract

19 Increase in pesticide use and landscape homogenization are two key drivers of the decline in  
20 farmland biodiversity. The effects of these two drivers are often complex, interactive and vary  
21 among taxonomic groups. Our study tested the hypothesis that pesticide use influences the  
22 effect of different components of landscape complexity on different taxonomic groups. We  
23 sampled 32 rice paddy landscapes of 1\*1 km in the Camargue (south of France), a wetland  
24 internationally recognized as an exceptional biodiversity hotspot. We assessed the abundance  
25 and diversity of 7 taxa (plants, bees, butterflies, hoverflies, carabids, spiders and birds) in 3 or  
26 4 crop fields per landscape. For each landscape, we measured the length of different field  
27 margins (ditch, grass strip, hedgerow), the proportion of semi-natural areas and crop diversity.  
28 For each field, we measured management intensity by the treatment frequency index (TFI) of  
29 pesticides. We then tested our hypothesis across 118 fields. Our results show that different  
30 components of landscape complexity influence different taxonomic groups: crop diversity and  
31 the length of ditches influence bee abundance and species richness, the proportion of semi-  
32 natural areas influence spider abundance and species richness, and the length of grass strips  
33 influences bird abundance. Moreover, we show that local pesticide use modulates these  
34 effects, with more positive effects of landscape complexity in intensively-managed fields.  
35 However, we found no interactive effect between landscape complexity and field  
36 management for plants, butterflies, hoverflies and carabids. Our study therefore suggests that  
37 different components of landscape complexity need to be maintained in order to preserve  
38 multiple taxonomic groups. Moreover, it suggests that increasing landscape complexity is  
39 particularly relevant to restore biodiversity in intensively-managed fields. Agricultural  
40 policies should therefore support the simultaneous increase in semi-natural areas, field  
41 margins length and crop diversity to conserve a wide range of taxonomic groups in  
42 intensively-managed rice paddy landscapes.

43

44 **Keywords:** Agriculture, Biodiversity, Camargue, Landscape, Pesticides, Rice farming

## 45 1 Introduction

46 Agricultural intensification has led to a worldwide decrease in farmland biodiversity (Kleijn  
47 et al., 2011; Rosenberg et al., 2019). Pesticides have been increasingly used to fight crop bio-  
48 aggressors, with widespread deleterious effects on non-target species. A large body of  
49 literature has shown a negative impact of pesticides on species through direct (contamination)  
50 or indirect actions (e.g. by trophic disruption; e.g. Bengtsson et al., 2005; Hole et al., 2005).  
51 Concomitantly, agricultural landscapes have become more homogeneous, with fewer patches  
52 of semi-natural cover, larger fields, fewer field margins and a lower crop diversity (Krebs et  
53 al., 1999; Tschamntke et al., 2005). This decrease in agricultural landscape complexity has  
54 been identified as a key driver of farmland biodiversity loss (Benton et al., 2003).

55 The effects of pesticides and landscape complexity on biodiversity have however been  
56 shown to vary greatly between studies, depending on the context or the taxonomic groups  
57 considered (e.g. Karp et al., 2018; Put et al., 2018). For instance, an extensive meta-analysis  
58 highlighted that organic farming had a positive effect on biodiversity in 68% of studies  
59 whereas it had mixed, non-significant or negative effects in 32 % of studies (Tuomisto et al.,  
60 2012). Several studies found that landscape complexity had a stronger influence on the  
61 species richness of wild bees in intensively rather than in extensively-managed fields (Carrié  
62 et al., 2017; Tuck et al., 2014). Another meta-analysis showed that landscape complexity had  
63 a significant effect on bees and spiders but no effect on parasitoids and predatory beetles  
64 (Shackelford et al., 2013).

65 Several hypotheses have been formulated to explain the variability in the effects of  
66 pesticide use and landscape complexity on biodiversity. First, species or taxonomic groups  
67 associated with distinct traits (e.g. mobility, diet, or breeding site preferences) may be  
68 influenced by different components of landscape complexity (Fahrig et al., 2011; Martin et  
69 al., 2019). For instance, a high proportion of semi-natural areas may provide nesting sites,

70 foraging resources or shelter for some species (Woltz et al., 2012) whereas a diversity of crop  
71 types may provide continuous and complementary resources throughout the season for other  
72 species (Smith et al., 2014). A second hypothesis arises from the fact that pesticides and  
73 landscape complexity may have interactive effects on biodiversity (Batáry et al., 2011). For  
74 instance, the value of semi-natural areas as a refuge may be particularly high for species  
75 facing a high level of pesticide within crops (Klaus et al., 2021; Ricci et al., 2019; Smith et  
76 al., 2020). Conversely, extensively-managed fields may provide sufficient resources for a  
77 wide range of farmland species, which may therefore be little affected by an increase in the  
78 amount of semi-natural areas (Carrié et al., 2017). For some species, extensively-managed  
79 crop fields might even provide more abundant food resources than semi-natural areas  
80 (Banaszak, 1992; Shaw et al., 2020), which could potentially lead to a negative effect of an  
81 increase in semi-natural areas.

82         Interactive effects of pesticide use and landscape complexity on biodiversity have  
83 mostly been evaluated by studies focusing on a single indicator of landscape complexity, the  
84 percentage of semi-natural areas, and a limited number of taxa (e.g. Park et al., 2015;  
85 Nicholson et al., 2017). Moreover, they have mostly been studied in dry agricultural systems  
86 (e.g. Diekötter et al., 2010; Djoudi et al., 2018). Yet, rice crops represent 22.8 % of the world  
87 cereal surface area (FAO, 2018). It is a flooded crop and is therefore one of the main crops in  
88 wetland agricultural areas (Singh et al., 2001). Paddy landscapes are characterized by a high  
89 density of irrigation and drainage ditches surrounding rice fields. As a result, ditches are the  
90 predominant type of field margin in these landscapes, before grass strips and hedgerows,  
91 which are usually dominant in other agricultural landscapes (Marshall and Moonen, 2002).  
92 Despite the significant proportion of field margins in paddy landscapes, there is a lack of  
93 knowledge on how pesticide use may affect their benefits on biodiversity.

94           In this paper, we evaluate the interactive effects of pesticide use and landscape  
95 complexity on different taxonomic groups in the rice paddy landscapes of the Camargue. The  
96 Camargue (Rhône delta) is internationally recognized as a biodiversity hotspot, listed in the  
97 Ramsar Convention and classified as a Biosphere Reserve by UNESCO (Blondel et al., 2019).  
98 While several studies have highlighted the negative effect of pesticides use on paddy  
99 biodiversity in this area (Mesléard et al., 2005; Tourenq et al., 2003), it remains unclear how  
100 landscape complexity resulting from the paddy structure intertwined with semi-natural areas  
101 influences biodiversity, and whether pesticide use modulates these effects. We studied a wide  
102 range of taxa (plants, bees, butterflies, hoverflies, carabids, spiders and birds). Following  
103 studies conducted in a whole range of agricultural landscapes and synthesized above, we  
104 predicted that pesticide use would have a negative effect on biodiversity, and that landscape  
105 complexity would have a neutral effect on biodiversity in extensively-managed fields and a  
106 positive effect in intensively-managed fields. Moreover, we hypothesized that distinct taxa  
107 may respond to different components of landscape complexity, namely, the proportion of  
108 semi-natural areas, the length of semi-natural linear elements (ditches, grass strips and  
109 hedgerows) and crop diversity, depending on their traits. More specifically, we predicted that  
110 mobile taxa (birds, pollinators) would be impacted by resources availability at large spatial-  
111 level (semi-natural areas and crop diversity; Tschardt et al., 2012) while low-mobility taxa  
112 (plants, carabids, spiders) would be impacted by local management (pesticides and field  
113 margins; Smith et al., 2014).

114

## 115 2 Material and methods

### 116 2.1 Study area

117 Our study was conducted in the Regional Natural Park of the Camargue, located in the Rhone  
118 delta (Southern France), where 56 000 ha of semi-natural habitats (mostly wetlands) are in  
119 direct contact with 23 000 ha of farmland (PNRC, 2016). The Camargue is subject to a  
120 Mediterranean climate with warm summers (average monthly temperature between May and  
121 October above 15°C), as well as strong intra- and inter-annual variation in rainfall (from 240  
122 to more than 1 200 during the last 40 years, average: 600 mm/year; Blondel et al., 2019). The  
123 average altitude is 4 m, with the southern part of the delta being below sea level. These  
124 physical characteristics result in a salinity gradient from north to south, cultivation being  
125 possible in the less salty parts thanks to the supply of fresh water from the Rhône used to  
126 flood rice fields. Rice is therefore the dominant crop, cultivated either in monoculture or in  
127 rotation with wheat or alfalfa (Mouret, 2018). Ditches used to flood rice fields result in a  
128 strong connectivity among rice fields, as well as between agricultural and semi-natural areas,  
129 since semi-natural areas partly depend on the water drained from rice fields in the context of  
130 river containment and rainfall reduction (Drobinski et al., 2020).

131

### 132 2.2 Landscape and site selection

133 We revisited data collected during the FarmLand project ([http://www.farmland-](http://www.farmland-biodiversity.org/)  
134 [biodiversity.org/](http://www.farmland-biodiversity.org/); Sirami et al., 2019). We used land cover maps derived from the 2011 land  
135 cover map of the Regional Natural Park of the Camargue (scale 1:5000). First, we selected all  
136 1x1 km agricultural landscapes, i.e. those covered by at least 60 % of agricultural land  
137 (including all crops and grasslands), but less than 90 % (in order to avoid extremely  
138 simplified landscapes). Second, following the protocol developed by Pasher et al. (2013), we  
139 selected a sample of 32 landscapes along uncorrelated gradients of crop diversity, assessed by



140 the Shannon diversity index of the crop covers types, and total length of field margins  
141 (Alignier et al., 2020; Fig. 1).

142 Four sampling sites were selected in distinct crop fields within each landscape. A total of  
143 eleven different crops types were sampled (rice, wheat, alfalfa, chickpeas, corn, grassland,  
144 millet, mustard, rape, sorghum and tomatoes). Sampling sites were at least 200 m from each  
145 other, at least 50 m from the border of the landscape, and at least 50 m from patches of non-  
146 agricultural cover types such as forests and built infrastructures. As a result, we selected a  
147 total of 128 crop fields.

148

### 149 2.3 Multi-taxa sampling

150 We sampled seven taxa distributed over a large spectrum of the farmland food web: plants,  
151 bees, butterflies, hoverflies, carabids, spiders and birds (Appendix A). Sampling took place in  
152 2013, in April and May in dry crop types, i.e. all crop types but rice, and between the end of  
153 June and early August in rice fields, so that biodiversity surveys were conducted at a similar  
154 stage of crop development. All taxa were recorded in three sampling sites within each  
155 landscape, except birds, which were recorded in four sampling sites. Plants were recorded  
156 along two 50-m long and 1-m large transects, one located along the field border and the other  
157 in the field center, once in April for wheat and once in August for rice. Bees and hoverflies  
158 were captured using pan traps, six along borders and six at the center, installed during four  
159 days. The sampling was carried out twice during the growing season in all crop types (April –  
160 July). During the same periods, pitfall traps were used to capture carabids and spiders only in  
161 dry crops types. Butterflies were sampled along two 50-m long and 5-m large transects,  
162 respectively located along the border and in the center of the field. Two repetitions were  
163 realized in dry crop fields (April – May) and one in rice fields (July; including in the center of  
164 flooded rice fields). Birds were sampled during 10-minutes point counts. Two point counts

165 were realized in April and May in dry crop fields and one in June for rice fields. Bird  
166 individuals contacted beyond 100 meters and those observed in flight were removed from the  
167 analyses to avoid including birds only in transit between two areas located outside the  
168 sampling sites. For the specific sampling protocol of each taxa, please refer to the supporting  
169 information SI 3 of Sirami et al. (2019). For all taxa, we considered species richness and  
170 abundance per field as proxies of biodiversity (Gotelli and Colwell, 2001). We selected the  
171 maximum abundance per species between the two visits for each field. We calculated the  
172 coverage of our sampling, which is defined as the proportion of the total number of  
173 individuals in an assemblage that belong to the species present in the sample (Chao & Jost  
174 2012). All taxa but one (carabids) were associated with a sampling coverage above 78%  
175 (Appendix B). However, for all taxa, coverage index was not correlated with any explanatory  
176 variable (Pearson coefficient < 0.4). Although this analysis suggests that results for carabids  
177 should be treated with caution, it confirms that this under-sampling does not represent a  
178 potential bias in our study.

179

## 180 2.4 Landscape and field variables

181 We conducted extensive ground-truthing surveys during the 2013 field season to map all  
182 fields, linear elements between adjacent fields, and semi-natural covers. We then measured  
183 the length of the three types of field margins: (1) hedgerows, which correspond to tree lines  
184 composed by tamarisk *Tamarix gallica* and other deciduous shrubs; (2) grass strips, which are  
185 herbaceous plants in the field margin including grassy vehicle tracks used for agricultural  
186 purposes; (3) ditches, which are colonized by common reed *Phragmites australis* and often  
187 covered by the invasive primrose-willow *Ludwigia peploides*. Complex field margins, i.e.  
188 those including more than one the above listed field margin type, were affected to the  
189 dominant type of semi-natural linear element. We measured the proportion of semi-natural

190 areas (*Nat\_Cover*), composed of wetlands, extensive grasslands, woodland and field margins.  
191 We measured the Shannon diversity index of crops ( $Crop\_SHDI = - \sum_{i=1}^n p_i \ln p_i$ , where  $p_i$   
192 corresponds to the proportion of crop cover type  $i$  in the landscape).

193 For each of the 128 fields, we collected information on the use of fertilizers and  
194 chemical pesticides by interviewing farmers. This information could not be obtained for 10 of  
195 the 128 fields. We thus calculated a treatment frequency index (TFI) of pesticide use for 118  
196 fields (74 rice, 33 wheat and 11 other dry crops) as follows:  $TFI = (\sum_{i=1}^n (Applied\ dose\ i *  
197 Treated\ area)) / (Advised\ dose * Total\ field\ surface)$  where *Applied dose i* is the used  
198 dose of pesticide  $i$  relative to the *advised dose* reported on the E-phy portal  
199 (<https://ephy.anses.fr>) of the French agency for food, environmental and occupational health  
200 and safety (Anses). We added one additional point of TFI when seeds were coated. TFI is a  
201 standard index to synthesize the pesticide treatment intensity of a field, and to compare land-  
202 use intensity among fields (Brunet et al., 2008). Organic fields have a TFI equal to zero, as in  
203 the Camargue they do not receive any pesticides, either chemical or non-chemical. We  
204 controlled the correlation between TFI and fertilizers to avoid confounding effects (Pearson  
205 coefficient < 0.64; Appendix C).

206

## 207 2.5 Data analysis

208 We used linear mixed-effects models to assess how landscape complexity modulates the  
209 effect of pesticide on our two response variables: abundance and species richness of each taxa  
210 measured at the field level. Fixed effects were the length of hedgerows, grass strips and  
211 ditches (respectively *Hedgerow*, *Grass\_strip* and *Ditch*), the percentage of semi-natural areas  
212 (*Nat\_Cover*), crop diversity (*Crop\_SHDI*) and pesticide use (*TFI*) as well as interaction terms  
213 between TFI and landscape variables. To further explore the nature of these interactions, we  
214 used the Johnson-Neyman technique which identifies the region of significance (Bauer and

215 Curran, 2005). All explanatory variables were centered and scaled. We took into account the  
216 potential impact of crop type, spatial autocorrelation, and the partially nested structure (due to  
217 several fields being sampled in the same landscape) by including crop type and landscape id  
218 as random effects in the model.

219 We ran models with all combinations of effects which could be derived from this general  
220 model using the dredge function in R (Barton, 2020), and we ranked models using the Akaike  
221 information criterion (AIC<sub>c</sub>; Burnham & Anderson, 2002). Then, we averaged parameters of  
222 models with a delta AIC<sub>c</sub> smaller than two. We discussed the effect of variables when the  
223 confidence intervals of their estimate did not include 0. The same modeling procedure was  
224 used for abundance and species richness as response variables. Birds, hoverflies, bee and  
225 spider species richness variables were square root transformed to fit a normal distribution.  
226 Species richness was modelled with a Gaussian or a Poisson distribution for butterflies. Initial  
227 models for abundance assumed a Poisson error distribution with a log link function. When  
228 residuals data showed overdispersion, models were refitted with a negative binomial error  
229 distribution and a logit link (Appendix D). Statistical analyses were run using lme4 (Bates et  
230 al., 2015), MuMin (Barton, 2020), entropart (Marcon and Hérault, 2015) and interaction  
231 packages (Long, 2019) in R 3.5.3 (R Core Team, 2017).

232

### 233 3 Results

234 The dominant type of field margins was ditches (median = 5 659 m per km<sup>2</sup>;  
235 range: [2 404; 10 851]), followed by grass strips (median = 2 806 m; range: [1 160; 7 513])  
236 and hedgerows (median = 435 m; range: [0; 5 473]). Semi-natural areas covered on average  
237 21.0 ± 0.69 % of landscapes (median = 20 %; range: [11; 39]). Crop diversity was on average  
238 0.74 ± 0.04 (median = 0.69; range: [0; 1.5]). Organic farming (TFI = 0) represented 25.6 % of  
239 sampled fields. Average TFI in conventional crop fields was 3.4 ± 0.15. Herbicides were the

240 main treatment type used in conventional crop fields and represented 64.7 % of the total TFI,  
241 whereas fungicides and insecticides represented respectively 13.5 % and 3.4 %. Coated seeds  
242 were used in nearly half of sampled conventional fields and represented 18.4 % of the total  
243 TFI. There was no strong correlation among explanatory variables since all Pearson  
244 correlation coefficients were under 0.5 (Appendix C). Due to protocol constraints, the number  
245 of sampled sites varied among taxa, ranging from 28 sites for carabid and spiders, to 118 sites  
246 for birds (Appendix E). We recorded a total of 506 species for a total number of 18 374  
247 individuals belonging to the seven considered taxa (Appendix E).

248 TFI was selected in 12 of the 15 models, with either a negative or a non-significant  
249 effect on response variables (Table 1). Landscape variables were selected in all models but  
250 one. Different taxa were influenced by different components of landscape complexity, with  
251 either positive, negative or non-significant effects.

252 Interactive terms between TFI and landscape variables were selected in 7 of the 15  
253 models, with either positive or non-significant interactive effects. Crop diversity had a  
254 negative effect on bee abundance when TFI was low and no effect when TFI was high (Fig. 2  
255 A; Appendix F; Fig. F.1). The length of ditches had a negative effect on bee species richness  
256 when TFI was low and a positive effect when TFI was high (Fig. 2 B; Appendix F; Fig. F.2).  
257 The proportion of semi-natural areas had no effect on spider abundance and richness when  
258 TFI was low and a positive effect when TFI was high (spider abundance Fig. 2 C, and spider  
259 richness Fig. 2 D; Appendix F; Fig. F.3 and F.4). The length of grass strips had no effect on  
260 bird abundance when TFI was low and a positive effect when TFI was high (Fig. 2 E; Table 1;  
261 Appendix F; Fig. F.5).

262 We did not detect any interaction effect between TFI and landscape complexity for  
263 carabids, hoverflies and plants. However, we detected a significant effect of several landscape  
264 variables or TFI on all these taxa, except plants. The length of hedgerows had a negative

265 effect on hoverfly species richness ( $\beta = -0.10, \pm 0.04$ ; Table 1). The proportion of semi-  
266 natural areas had a negative effect on carabid abundance and species richness ( $\beta = -0.36, \pm$   
267  $0.15$  and  $\beta = -1.27, \pm 0.54$ ; Table 1). Crop diversity had a negative effect on carabid  
268 abundance ( $\beta = -0.34, \pm 0.16$ ; Table 1).

269

## 270 4 Discussion

271 Our study shows that the effect of landscape complexity varies depending on local  
272 management and different taxa respond to different components of landscape complexity.  
273 Moreover, we show that, for bees, birds and spiders, pesticide use modulates the effects of  
274 landscape complexity, with positive or neutral effects in intensively-managed fields, and  
275 neutral or negative effects in extensively-managed fields. However, differences in the level of  
276 mobility of the different taxa did not explain differences in the way they responded to  
277 landscape complexity and local management.

278 Our results are in agreement with previous studies that highlighted an interactive effect  
279 between pesticide use and landscape complexity, measured as the proportion of semi-natural  
280 areas, for birds (Batáry et al., 2010; Dänhardt et al., 2010; Smith et al., 2010), bees  
281 (Nicholson et al., 2017; Park et al., 2015; Rundlöf et al., 2008), spiders (Djoudi et al., 2018;  
282 Schmidt et al., 2005) and other farmland taxa (e.g. plants: Rader et al., 2014; butterfly:  
283 Rundlöf and Smith, 2006; small mammals: Fischer et al., 2011a). However, we show that the  
284 proportion of semi-natural areas is not necessarily the component of landscape complexity  
285 that contributes to interactive effects between pesticide use and landscape complexity.

286 In intensively-managed fields, we found that spider abundance and species richness  
287 are favored by the proportion of semi-natural areas and that bird abundance and bee species  
288 richness increase with the length of semi-natural linear elements, grass strips and ditches  
289 respectively. However, in extensively-managed fields, these same elements have no effect on

290 these taxa or even have a negative effect (for bee species richness). The positive interactive  
291 effect between pesticide use and semi-natural patches or linear elements is consistent with the  
292 fact that they provide easily accessible resources and undisturbed environment favorable to a  
293 large panel of species occurring in intensively-managed fields (Alignier et al., 2020; Duru et  
294 al., 2015). Semi-natural patches and linear elements play thus a stronger role as a source or  
295 refuge for species facing a high level of pesticide use within crops (Klaus et al., 2021; Ricci et  
296 al., 2019; Smith et al., 2020). Similarly, our observations in extensively-managed fields are in  
297 line with the hypothesis that these fields provide sufficient resources for a wide range of  
298 farmland species, and an increase in the amount of semi-natural areas may have little effect, if  
299 any, in this context (Carrié et al., 2017). The negative effect of ditch length on bee species  
300 richness could be due to the lower water consumption of organic farming compared to  
301 conventional farming, with therefore less available wet material for solitary bee nest building  
302 (Krunić et al., 2005; Westrich, 1996). We also found a significant interaction between crop  
303 diversity and pesticide use, with a negative effect of crop diversity on bee abundance in  
304 extensively-managed fields and no effect in intensively-managed fields. This result is  
305 consistent with the ‘minimum total habitat area requirement’ hypothesis, which states that  
306 biodiversity decreases with crop diversity if most species require large amounts of a single  
307 crop type (Sirami et al., 2019). Moreover, it suggests that this mechanism only applies when  
308 pesticide use is low enough.

309 Our prediction that land-use intensity would have a negative effect on biodiversity was  
310 only partially validated. Indeed, we observed a higher spider abundance and species richness  
311 in intensively-managed fields than in extensively-managed ones. Possible explanations for  
312 this result include the fact that most spider species are relatively tolerant to pesticides (Pekár  
313 & Beneš, 2008; Pekár, 2012; Wang et al., 2006) and that feeding resources for spiders may be  
314 higher in conventional fields than in organic fields, as was show for the Chironomidae

315 biomass, which is higher in conventional fields than in organic rice fields (Suhling et al.,  
316 2000). Other studies have observed a positive effect of land use intensity on species richness,  
317 including the recent meta-analysis on 6 taxa conducted by Millard et al. (2021). As this  
318 positive effect is particularly strong for Dipteran, the authors hypothesize that it may be due to  
319 the positive effect of fertilizer on this taxa (Millard et al., 2021). Variations in species  
320 richness and abundance of different taxonomic groups in response to landscape complexity  
321 and field management intensity are likely to result in variations in ecosystem services  
322 (support, regulation, cultural, Dainese et al., 2019; Tschardt et al., 2021).

323         Our results also provide a new possible explanation for the lack of interactive effect  
324 between local management and landscape complexity observed in some studies (e.g. Brittain  
325 et al., 2010; Winqvist et al., 2011). A reason often proposed for the lack of interactive effect is  
326 that studies did not consider landscape gradients large enough to include the threshold at  
327 which interactions between local management and landscape complexity may appear.  
328 However, most studies on the interactive effects between local management and landscape  
329 complexity consider only a limited set of taxa and use the proportion of semi-natural areas in  
330 the landscape as the sole indicator of landscape complexity (e.g. Clough et al., 2005; Fischer  
331 et al., 2011b; Winqvist et al., 2011). By showing that different components of landscape  
332 complexity influence different taxa and that interactive effects between pesticide use and  
333 landscape complexity differ depending on these distinct components, our study suggests that  
334 the inability of some studies (including the present one) to observe interactive effects between  
335 local management and landscape complexity may derive from the fact that they focused on  
336 inadequate landscape variables.

337         In the present study, we did not detect any interactive effect between pesticide use and  
338 landscape complexity on plants, hoverflies, butterflies, and carabids. As suggested above, this  
339 could be due to the absence of relevant explanatory variables such as the amount of flowering



340 resources for butterflies or hoverflies (Goulson et al., 2015; Uhl and Brühl, 2019) or the  
341 amount of fertilization for plants (Wang et al., 2019). Our results contrast with studies that  
342 found interactions between pesticide use and the proportion of semi-natural cover for some of  
343 the taxa we studied (e.g. plants Rader et al., 2014; butterfly: Rundlöf and Smith, 2006). In  
344 these studies, semi-natural areas are composed of forests and grasslands, whereas Camargue  
345 is characterized by the presence of atypical semi-natural cover types such as wetlands or  
346 sansouïres (i.e. salted grasslands of *Salicornia sp.*), which host a very specific biodiversity.  
347 The effect of these atypical semi-natural cover types on biodiversity observed in crop fields  
348 may therefore be very different from the effect of forests and grasslands. This could explain  
349 why we did not observe interactive effects found in other regions. Our inability to detect  
350 interactive effects could also be due to the fact that some landscape variables were not  
351 associated with a gradient large enough to detect significant effects. This could for instance be  
352 the case for the three field margins because we selected landscapes along a gradient based on  
353 the total length of all semi-natural linear elements and later split these semi-natural elements  
354 into three. To explore whether this impeded our ability to detect significant interactions  
355 between pesticide use and landscape complexity, we performed an additional analysis, using  
356 the total length of all field margins as an explanatory variable instead of the three variables  
357 corresponding to the three types of field margins. However, this complementary analysis did  
358 not show more robust interaction effects between landscape complexity and pesticide use  
359 (Appendix H).

360

## 361 5 Conclusion, and conservation implications and future directions for 362 cultivation in wetland areas

363 Our results show that increasing the length of grass strips and ditches, the proportion of semi-  
364 natural areas, as well as crop diversity, is necessary to maintain multiple taxonomic groups in

365 intensively-managed rice paddy landscapes. Here, we focused on the role of three main types  
366 of field margins (hedgerows, grass strips and ditches). It is however important to note that  
367 field margins in paddy landscapes are often wide and complex. They are wide because of the  
368 presence of irrigation ditches, which must be separated from the cultivated zone to avoid  
369 damaging them. Several types of vegetation can therefore co-occur on the same field margin.  
370 For the sake of simplicity, we categorized field margins as hedgerows or grass trips depending  
371 on the dominant type of vegetation found along the margins or as ditches when vegetation  
372 was mostly absent. Since different types of vegetation are likely to play a key role for  
373 different taxa, further studies should investigate in more details the role of such complex field  
374 margins to improve recommendations for their management. In particular, this could help to  
375 propose specific agri-environmental schemes for rice producers. Indeed, current field margin  
376 management often aims at simplifying them by burning and crushing the vegetation along the  
377 ditches.

378         In rice paddy landscapes, drainage ditches connect rice fields to adjacent wetlands. As  
379 a result, high concentrations of pesticides used for rice cultivation are likely to be found in  
380 adjacent natural wetlands, as this was the case few years ago in the study area (S.N.P.N.,  
381 2013). The negative effect of pesticides on biodiversity are therefore coherent with the call  
382 from managers of the Camargue Regional Natural Park to encourage ecological alternatives to  
383 the use of pesticides. One possible avenue is to explore landscape management that promotes  
384 ecosystem services that could limit the need for pesticide use (e.g. weed control by birds;  
385 Pernollet et al., 2015, pest control by insects; Mesléard et al., 2005).

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Figure 1. Location of the thirty-two 1x1 km rice paddy landscapes selected to sample biodiversity in the Camargue croplands, Rhône delta in 2013.



Figure 2: Biodiversity as a function of landscape complexity depending on high and low values of TFI for which a significant interaction was retained. Dashed line corresponds to the model prediction for the minimum value of TFI for **A** bee abundance, **B** bee species richness, **C** spider abundance, **D** spider species richness and **E** bird abundance. Solid line corresponds to the model prediction for the third quartile value of TFI. Grey zones delimit the confidence intervals at 95%. Crosses are observed data below the landscape component median and points are data over the median.



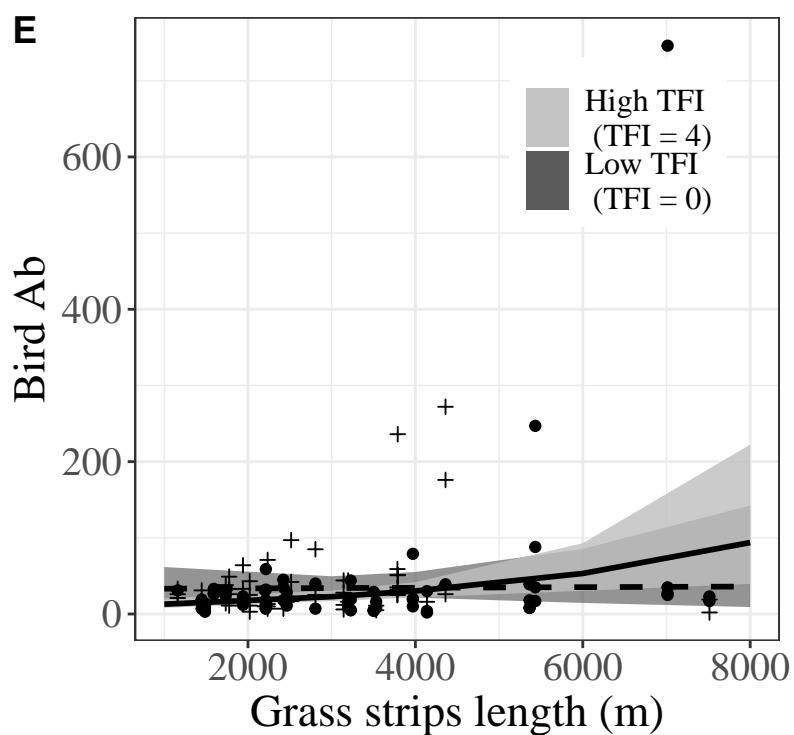
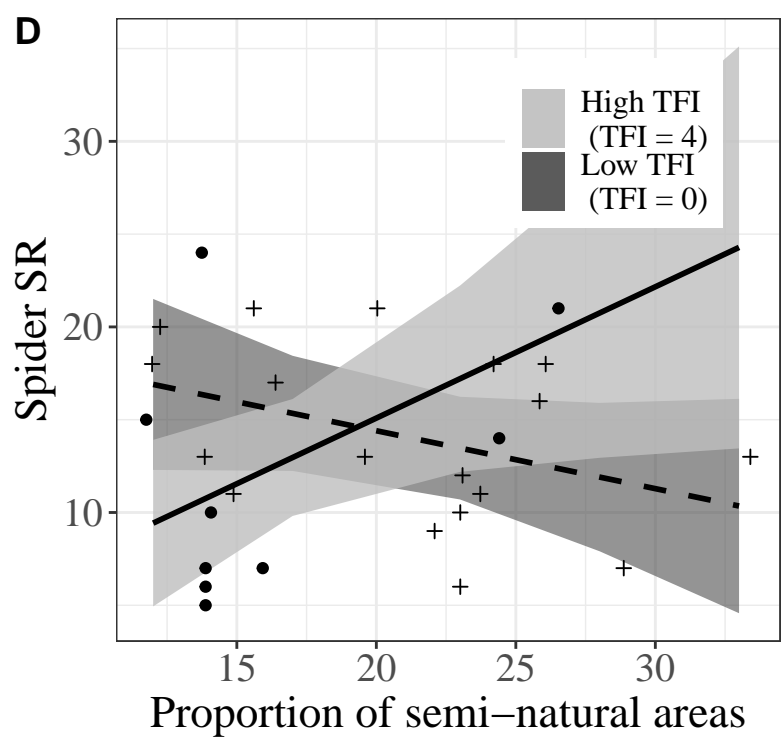
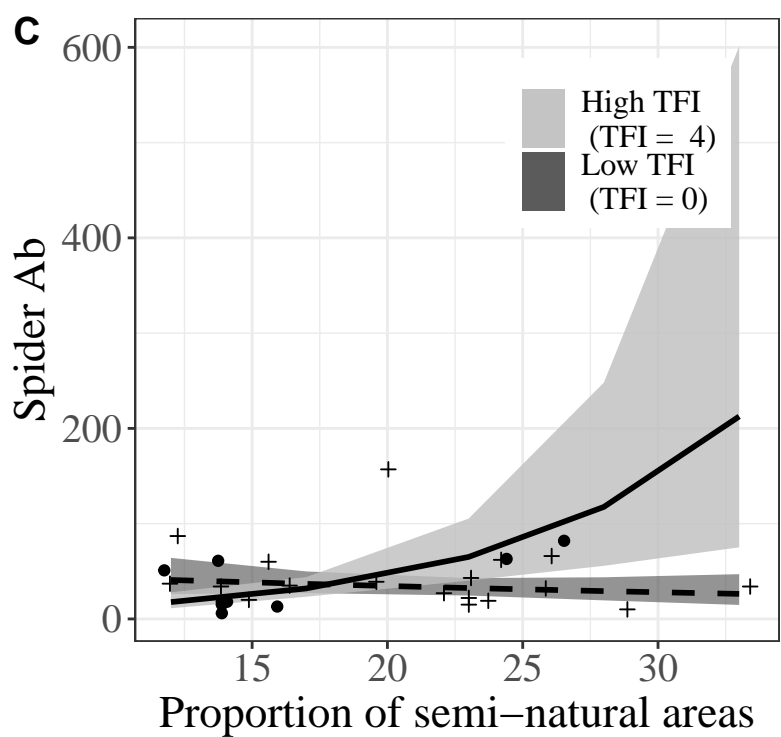
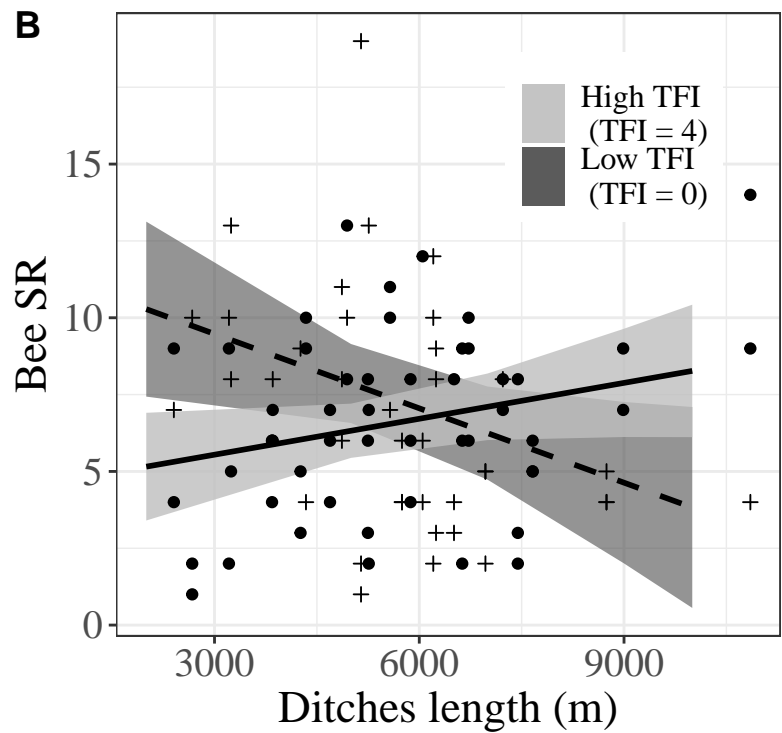
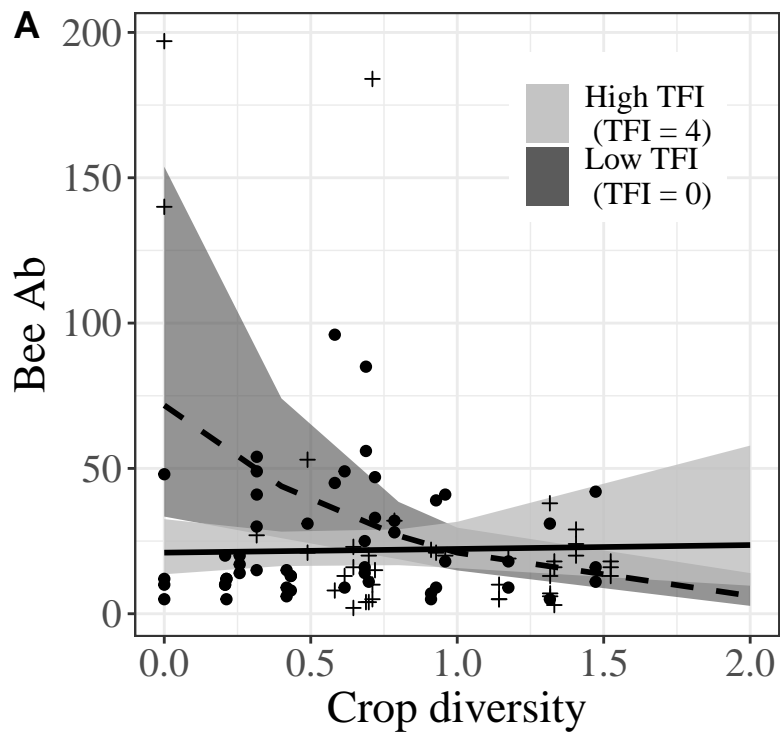


Table 1: Effect of variables retained after model selection and averaging, for species richness (SR) and abundance (Ab) of each taxon. The symbol  $\circ$  indicates that the 95 % confidence interval of the estimate contains zero, + indicates a significant positive effect, - indicates a significant negative effect and no symbol if the variable is not retained in the model. Estimates  $\pm$  SE of the effects are given in Appendix G.

	Bee SR	Bee Ab	Bird SR	Bird Ab	Butterfly SR	Butterfly Ab	Carabid SR	Carabid Ab	Plant SR	Spider SR	Spider Ab	Hoverfly SR	Hoverfly Ab
Hedgerow			○	○						○	○	-	
Grass strip	○	○		+					○	+	+	○	○
Ditch	○											○	○
Crop diversity		○	○			○	○	-		○		○	○
Semi-natural		○					-	-		○	+		○
TFI	○	○	○				○	○	○	○	○	○	○
Hedgerow * TFI				○								○	
Grass strip * TFI	○			+									
Ditch * TFI	+												
Crop diversity * TFI		+											
Semi-natural * TFI										+	+		

Increasing landscape complexity had a more positive effect on biodiversity in intensively-managed rice paddy landscapes.