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Title:

8 **Increasing amount and quality of green infrastructures at different scales promotes**

9 **biological control in agricultural landscapes**

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29 **ABSTRACT**

30 Green infrastructures are key elements for the delivery of ecosystem services in agricultural
31 landscapes. However, how to combine quality and quantity of green infrastructures at
32 multiple spatial scales to optimize the delivery of ecosystem services remains largely
33 unknown. In this study, we investigated how hedgerow amount in the landscape modulated
34 the local effect of grassland quality (plant species richness) on the spillover of biological pest
35 control services in adjacent sunflower fields. We quantified biological pest control and
36 predator communities in 23 adjacent sunflower-grassland field couples selected along two
37 uncorrelated gradients: a gradient of plant species richness in grassland and a gradient of
38 hedge length in the landscape. Our study shows that increasing the amount or the quality of
39 green infrastructures can enhance biological pest control in adjacent crops but that the effects
40 depend on the pest considered. We found that weed seed predation depends only on hedge
41 length in the large scale landscape, while aphid predation depends on plant species richness in
42 the adjacent grassland and on the hedge length in the immediate landscape. Also, the
43 abundance of spiders affects aphid predation suggesting a key role of this functional group for
44 controlling aphids in sunflower fields. This study suggests that management options based on
45 increasing local plant species richness should be prioritized in landscapes with low amount of
46 hedgerows, and confirms the fact that increasing hedgerow networks should promote pest
47 control services.

48

49 **KEY WORDS**

50 Grasslands; Hedgerows; Landscape context; Pest regulation; Natural enemies

51

52

53 1. Introduction

54 Biological control of crop pests is a key regulating service delivered by natural enemies
55 that can significantly increase crop production while contributing to the reduction of pesticide
56 use (Naranjo et al., 2015). Biological control by predatory arthropods depends on multiple
57 factors operating at different spatial scales from the plant and the field, up to the whole
58 landscape level (Tscharntke et al., 2007; Rusch et al., 2010). Green infrastructures, such as
59 grasslands or hedgerows, can increase the abundance and the diversity of natural enemies
60 which may in turn increase local pest regulation (Rand et al., 2006; Chaplin-Kramer et al.
61 2011). The effects of green infrastructures on biological control have been either examined at
62 the local or landscape scales, e.g. by testing the effect of an adjacent green infrastructure, such
63 as flower strips or fallows (Albrecht et al., 2010; Tschumi et al., 2015), or by quantifying the
64 effect of large-scale proportion of green infrastructures, such as grasslands or hedgerows in
65 the landscape (Chaplin-Kramer et al., 2011; Rusch et al., 2016). However, a limited number
66 of studies have investigated how broad-scale landscape context modulates the effect of local
67 green infrastructure on biological pest control and have yielded contrasting results (Werling
68 and Gratton, 2010; Tschumi et al., 2015). For instance, it has been hypothesized that
69 landscape complexity may modulate the local effect of green infrastructure on biodiversity
70 and ecosystem services (Tscharntke et al., 2012). Minimal effect of local green infrastructure
71 is predicted in extremely simplified landscapes or in complex landscapes with a high
72 proportion of non-crop habitat (> 20 %) whereas maximal effect is predicted in simple or
73 intermediate landscapes. The reason is that extremely simplified landscapes do not provide
74 sufficient resources to maintain efficient natural enemy communities whereas complex
75 landscapes already support abundant and diverse communities already providing high level of
76 biological pest control. Producing operational knowledge about multi-scale effects of green

77 infrastructures on biodiversity and ecosystem services is urgently needed to promote farming
78 systems less dependent on agrochemical inputs.

79 Beside the importance of landscape context potentially shaping biological pest control
80 services in agricultural landscapes, the quality of green infrastructures is expected to affect
81 population dynamics, spillover of beneficial organisms as well as the function they provide
82 (Riolo et al., 2015). An important parameter of green infrastructure quality is the diversity of
83 organisms they host. For instance, plant species richness – used as a surrogate of quality – can
84 enhance diversity (Hertzog et al, 2017) as well as organism abundance (Scherber et al., 2010;
85 Garrat et al., 2017) at multiple trophic levels, and increase the level of ecosystem functioning
86 such as primary productivity, soil fertility, biological pest control or pollination (Scherber et
87 al., 2010; Garrat et al., 2017; Isbell et al., 2017). In addition, we do not know how green
88 infrastructure quality may interact with the landscape context. Indeed most studies conducted
89 at the landscape scale usually assume similar levels of quality across green infrastructures
90 while investigating landscape composition or configuration (e.g. Aviron et al. 2005; Olimpi
91 and Phipott, 2018). Considering explicitly the quality of green infrastructure may provide
92 major insights into how landscape context influences predator-prey interactions and pest
93 regulation service (Sarhou et al., 2014; Garrat et al., 2017; Bengtsson et al., 2019).

94 Grasslands are key green infrastructures for biodiversity conservation and provision of
95 multiple ecological functions in agricultural landscapes (Werling et al., 2014; Newbold et al.,
96 2015). The level of contribution of grasslands to the maintenance of such ecological functions
97 depends on habitat characteristics related to plant communities, management intensity as well
98 as the surrounding landscapes (Joern and Laws, 2013). Enhancing grassland plant species
99 richness may be a way to improve the potential contribution of grassland towards pest control
100 in agricultural landscapes. To develop this management opportunity, it is important to
101 evaluate its effectiveness within landscapes which provide contrasted amounts of green

102 infrastructures, i.e. resources for natural enemies. Among green infrastructures, hedgerows
103 may be particularly appropriate to maintain biodiversity and ecosystem services in intensive
104 agricultural landscapes that are generally poor in grasslands and other semi-natural habitats
105 (Dainese et al., 2017). Hedgerows are shown to benefit many invertebrate natural enemies,
106 such as carabid beetles or spiders (Pywell et al., 2005), and vertebrate natural enemies, such
107 as birds (Vickery et al., 2009) or rodents (Michel et al., 2007).

108 In this study, we examined the role of local grassland quality and hedge length at
109 different scales in the landscape in shaping pest control in sunflower fields. We tested 1)
110 whether higher plant species richness of focal grassland (a local factor) increases weed and
111 aphid predation in adjacent sunflower field; 2) whether higher amount of hedgerows at
112 different spatial scales (a landscape factor) enhances weed and aphid predation in sunflower
113 field; and, 3) how local and landscape variable interactions affect natural pest control services.
114 We hypothesized that an increase in plant species richness has a global positive effect on
115 diversity and abundance of predatory arthropods in the focal grassland, which in turn should
116 lead to higher predation rates of weeds and aphids in sunflower field due to natural enemy
117 spillover. We hypothesized that the amount of hedges has also a positive effect on pest
118 predation rates in sunflower field. Lastly, we expected that hedge amount in the landscape
119 modulates the positive effect of local grassland plant diversity on biological pest control.

120

121 **2. Material and methods**

122 *2.1. Study area and experimental design*

123 The study was conducted in 2015 in the French Long-Term Socio-Ecological Research
124 site (LTSER) “Zone Atelier Plaine et Val de Sèvre” located in western France (46.11°N,
125 0.28°W) (Fig. 1) (Bretagnolle et al., 2018). The study area covered 450 km² of an intensively
126 managed agricultural plain, mostly dedicated to cereal production. Historically, it was a

127 typical rural area characterized by the presence of mixed crop-livestock systems, grassland
128 being the dominant land-use fifty years ago (> 60 % of the total area) (Bretagnolle et al.,
129 2018). Since that time, the conversion from grazing livestock to annual crop production has
130 resulted in a strong decline in grassland cover which represented in 2015 about 10 % of the
131 total surface. Other permanent green infrastructures in the study area were mainly composed
132 of hedgerows and in a lesser extent of forest fragments (3 % of the area) (Bretagnolle et al.,
133 2018). Since 1994, land use has been monitored yearly at the field scale (15 000 fields
134 approximately) and mapped onto a Geographical Information System (QUANTUMGIS 2.18)
135 (QGIS Development Team, 2017). Around 34 categories of crop types were recorded as well
136 as roads, paths, forests, towns and hedgerows.

137 The study design consisted in the selection of 23 sunflower fields, each of them being
138 adjacent to a grassland field. The 23 pairs of fields were located along two uncorrelated
139 gradients ($r = 0.38$) (Appendix A in supplementary material, Fig. A.1): one gradient of plant
140 species richness in the adjacent grassland and one gradient of hedgerow length within a 1 km
141 radius around each pair of fields (Table 1). The gradient of hedge length was calculated at this
142 scale as it falls within the range of the most explaining scales for invertebrate diversity and
143 abundance (Chaplin-Kramer et al., 2011; Marrec et al., 2017). We selected the fields in 1 km
144 landscapes representative of the average composition of the study area in other green
145 infrastructures, i.e., grasslands and woodlands (Table 1), excluding extremely simplified or
146 complex landscapes. Therefore, grassland or woodland covers were not correlated with the
147 gradient of hedgerow amount (Appendix A in supplementary material, Table. A.1). This
148 design allows us to disentangle the effects of local grassland plant species richness and hedge
149 length from other potentially confounding variables known to affect predator communities
150 (Chaplin-Kramer et al., 2011; Karp et al., 2018). In addition, we calculated hedge length
151 within 0.25 km radius and used it as an explanatory variable (see below) to explore its effect

152 at a local scale. We checked that it was not correlated with grassland plant species richness (r
153 = 0.19) (Appendix A in supplementary material, Fig. A.1). Selected field pairs were separated
154 from one another by at least around 1 km to avoid spatial autocorrelation and fields within
155 each pair were adjacent or in close proximity (Table 1).

156

157 2.2. *Estimating grassland plant species richness and predator communities in grasslands* 158 *and sunflower fields*

159 We conducted a botanical survey in July 2015 on the 23 selected grasslands. To
160 estimate plant species diversity, we randomly located 10 quadrats of 50 cm x 50 cm per
161 grassland. The total number of species recorded over the 10 quadrats was calculated as our
162 measurement of plant species richness.

163 In each grassland and sunflower field, we established ten sampling points, evenly
164 spaced every 5 m along a 45 m transect. The transects were established from the field
165 boundary to 45 m inside the field, the starting points being where the two fields of each pair
166 were at the smallest distance from each other. Weed seed and aphid predation rates in
167 sunflower fields were assessed at the 10 points using sentinel prey cards. While cards were
168 accessible to both vertebrates and invertebrates, we only tested the potential effects of
169 invertebrate community features. We sampled carabid beetles and spiders in grassland and
170 sunflower fields at 4 of the 10 points (i.e., inside the field at 1 m from field boundary, 16 m,
171 31 m and 46 m) while. Carabid beetles and spiders were sampled using one pitfall trap
172 (Thiele, 1977) at each of the 4 sampling points. The traps were plastic cups of 8.5 cm
173 diameter filled with a mixture of salted water and a drop of soap. Traps were established
174 between 17th and 27th July. The content of traps was collected four days after. We identified
175 carabid beetles and adult spiders at the species level, while juvenile spiders were identified at
176 the genus or at the family level. We considered carabid beetles to test their effect on seed and

177 aphid predation. For seed predation, we tested the effects of individual seed-eating
178 (granivorous and omnivorous) abundant species, or a functional subset of seed-eating species,
179 or all species pooled. For aphid predation, we tested the effects of a functional subset of
180 potentially aphid-eating species (carnivorous and omnivorous) or all species pooled. Carabid
181 beetle diets were obtained from Laroche (1990) and the online database ‘carabids.org’
182 (Homburg et al., 2014). In addition, spiders were also considered as potential predators of
183 aphids. We calculated the species richness (number of recorded species per field based on
184 adult carabid beetles and adult spiders) and Shannon index of carabid beetles and spiders, and
185 their activity-densities as the numbers of trapped individuals (juveniles and adults) per field
186 (cumulated over the 4 pitfall traps whatever their location in the field).

187

188 2.3. Estimating weed seed and aphid predation rates

189 Weed seed and aphid predation rates were quantified using sentinel preys (Chisolm et
190 al., 2014; Birkhofer et al., 2017). Sentinel preys consist in exposing seeds and aphids glued on
191 cards to predation to measure prey removal. We used methods adapted from Westerman et al.
192 (2003) and from Winqvist et al. (2011). We specify here that such approach makes it possible
193 to quantify biological pest control potential and not actual biological pest control services but
194 is extensively used in the literature. Weed seed predation was assessed using the very
195 common weed in the study area, *Viola arvensis* Murray. Ten seeds were glued on one side of
196 pieces (5 cm x 5 cm) of red sand paper (grain 120) using repositionable spray glue. These
197 cards were put top surface up on the ground and bound with a pin. Aphid predation was
198 assessed using three live pea aphid (*Acyrtosiphon pisum* Harris) adults or nymphs at the third
199 or fourth instar, which were glued with repositionable spray glue on one side of pieces (5 cm
200 x 6 cm) of black sand paper (grain 400) which were folded in half. These cards were bound
201 on the ground with a pin, top surface down. We placed one seed card and one aphid card at

202 each of the 10 points per sunflower field so that there was a total of 10 seed cards and 100
203 seeds, and 10 aphid cards and 30 aphids in each sunflower field. All cards were set on 30th
204 July and left in place during 4 effective-days for seed cards and 1 effective-day for aphid
205 cards. At that time, the number of consumed seeds or aphids per card was noted and allowed
206 us to calculate seed and aphid predation rates per field as i/ the number of seeds (ranging from
207 0 to 100) or aphids (ranging from 0 to 30) consumed and as ii/ the number of cards (ranging
208 from 0 to 10) with a predation event, i.e., with at least 1 consumed seed or aphid.

209

210 *2.4. Data analysis*

211 The number of cards with at least one event of seed or aphid predation was highly
212 correlated with respectively the number of consumed seeds ($r = 0.93$) or aphids ($r = 0.89$). We
213 thus analysed the proportion of preyed cards, i.e. with at least one event of seed or aphid
214 predation, as it provided smaller dispersion parameters than the proportion of preyed seeds or
215 aphids. Seed predation rates were analysed using the proportion of preyed cards with
216 generalized linear models (GLM) with a binomial error distribution. Aphid predation rates
217 were analysed using binary response variable (status of each individual aphid card: 0 if no
218 aphid has been preyed or 1 if at least one aphid has been preyed) with generalized linear
219 mixed effects models (GLMM) and a binomial error distribution to take into account
220 overdispersion. Sunflower field identity was set as random effect. We run two sets of
221 competing models to respectively analyze seed and aphid predation. In each set of models we
222 examined whether the response variable was related to: plant species richness in the adjacent
223 grassland (all models), predator species richness (Models 1, 4 and 7, 10), Shannon Index
224 (Models 2, 5 and 8, 11) and activity-density (Models 3, 6 and 9, 12) in the sunflower field,
225 hedge length in the landscape within 0.25 km radius (Models 1, 2, 3 and 7, 8, 9) and within 1
226 km radius (Models 4, 5, 6 and 10, 11, 12) (Table 2). An interaction term between grassland

227 plant species richness and hedge length was included to test for potential modulation of local
228 quality effects by landscape context at the two scales. The effects of distance from field
229 margin and of its interactions with grassland quality and hedge length were tested. As they
230 were not significant (Appendix B in supplementary material, Table B.1) they were not
231 discussed further. Model simplification (within each of the competing models) was done
232 using a backward stepwise procedure based on chi-squared statistics (Fox and Weisberg
233 2011). Then, we used an information-theoretic approach (AIC-based approach corrected for
234 small sample size; AICc; Burnham and Anderson, 2002) to select the best model among the
235 competing simplified models for seed and aphid predation (i.e., the model with the smallest
236 AICc and $\Delta AICc < 2$ among competing simplified models).

237 If predators (species richness, Shannon Index or activity-density) in the sunflower
238 fields impacted significantly pest predation then additional analyses were carried out to
239 determine whether predator communities were driven by: plant species richness in the
240 adjacent grassland, hedge length in the landscape within 0.25 km radius and 1 km radius and
241 predators (species richness, Shannon Index or activity-density) in the adjacent grassland. An
242 interaction term between grassland plant species richness and hedge length in the landscape
243 was included in the models. We also tested for the effect of grassland plant species richness
244 and hedge length in the landscape within 0.25 km radius and 1 km radius on predators in the
245 grassland fields. Predator response variables were only those which were retained in the
246 selected predation models and they were analysed with generalized linear models (GLM)
247 using adequate distributions. We checked for spatial autocorrelation in the residuals of the
248 final models using bubble plots and no spatial autocorrelation was detected (Appendix C in
249 supplementary material).

250 We performed statistical analyses in R 3.5.0 (R Development Core Team, 2018), using
251 the ‘lme4’ (Bates et al., 2015), ‘car’ (Fox and Weisberg, 2011), ‘ggplot2’ (Wickham, 2016)
252 and ‘MuMIn’ (Barton, 2018) packages.

253

254 3. Results

255 We recorded 81 plant species in the focal grasslands including *Medicago sativa* L.,
256 *Lolium perenne* sp., *Dactylis glomerata* L., *Festuca arundinacea* Scherb. and *Trifolium*
257 *pratense* L., *Picris hieracioides* L., *Plantago lanceolata* L., *Daucus carota* L.,
258 *Arrhenatherum elatius* L. and *Convolvulus arvensis* L. (Appendix D in supplementary
259 material, Table D.1). Grassland plant species richness ranged from 3 to 28 species (mean \pm
260 SE = 11.8 ± 1.6) per field and was significantly positively correlated with grassland age ($r =$
261 0.59 ; $p = 0.002$) (Appendix D in supplementary material, Fig. D.1).

262 In total, 22 carabid beetle species were trapped. Mean species richness per field was 2.2
263 ± 0.2 (mean \pm SE) in sunflower fields and 1.5 ± 0.4 in grassland fields. Mean cumulated
264 carabid beetle activity-density over the 4 pitfall traps per field was 13.4 ± 4.3 in sunflower
265 fields and 11.3 ± 7.8 in grasslands. Carabid beetle communities in sunflower fields were
266 dominated by three species, i.e., *Pseudoophonus rufipes* De Geer, *Poecilus cupreus* L. and
267 *Amara consularis* Duftschmid which were trapped respectively in 87%, 39% and 22% of the
268 fields. Numerically, these species represented more than 92% of the trapped carabid beetles
269 (*P. rufipes*: 73.5%, *P. cupreus*: 12.0%, *A. consularis*: 6.8%). In grassland fields, *P. rufipes*
270 and *P. cupreus* were also the most frequent species, being trapped in respectively 43% and
271 26% of the fields while *A. consularis* was not observed. Numerically, these species
272 encountered for 90% of the counts (*P. rufipes*: 16.9%, *P. cupreus*: 73.2% mainly due to one
273 grassland field).

274 For spiders, we recorded 40 species and 29 genera. Mean species richness was 2.9 ± 0.3
275 (mean \pm SE) in sunflower fields and 3.7 ± 0.5 in grasslands. Mean cumulated spider activity-
276 density over the 4 pitfall traps per field was 12.5 ± 2.1 (juveniles and adults) in sunflower
277 fields and 25.1 ± 7.2 in grasslands. Lycosidae family was trapped in 95% of the sunflower
278 fields and 78% of the grasslands. Numerically, this family encountered for 68% of the counts
279 in the sunflower fields and 85% in the grasslands. Linyphiidae family was also well
280 represented in sunflower fields with 20 % of the counts while in grasslands they only
281 represented 4% of the counts. *Pardosa agrestis* Westring and *Oedothorax apicatus* Blackwall
282 were the main species in sunflower fields, being trapped in respectively 74% and 43% of the
283 fields, while *O. apicatus* was rarely trapped in grasslands where the main species were
284 *Pardosa proxima*, *P. agrestis*, *Pardosa vittata* and *Xysticus ninnii* trapped respectively in
285 48%, 43%, 39% and 35% of the grasslands.

286 The complete list of species and their activity-density are provided in Appendix E in
287 supplementary material (Table E.1).

288

289 3.1. Weed seed predation

290 Seed predation rates of *V. arvensis* estimated at the end of July in sunflower fields
291 ranged from 0 to 60 % of preyed seed cards, i.e. with at least one predation event, and
292 averaged 23 ± 3 % (mean \pm SE) per field. The proportion of seeds which were consumed per
293 field was quite low ranging from 0 to 28 % of preyed seeds and averaged 7 ± 2 % per field.

294 The proportion of preyed cards increased with the amount of hedges in the landscape
295 within 0.25 km (Models 1, 2, 3: AICc = 82.7) and within 1 km (Models 4, 5, 6: AICc = 74.9)
296 (Appendix F in supplementary material, Table F.1). The plant species richness in grasslands
297 and the various metrics describing carabid beetle communities in the sunflower fields (species
298 richness, Shannon Index or the activity-density of individual species, granivorous and

299 omnivorous functional group, or all species pooled) had no effect on the proportion of preyed
300 cards (Appendix F in supplementary material, Table F.1). The model with the lowest AICc
301 (i.e. amount of hedges within 1 km) was then selected as the best model (Table 3 and Fig. 2).
302 We obtained the exact same results when using the proportion of preyed seeds instead of the
303 proportion of preyed cards as response variable (Appendix F in supplementary material, Table
304 F.3).

305

306 3.2. *Aphid predation*

307 The proportion of preyed aphid cards, i.e. with a predation event, ranged from 0 to 90 %
308 and averaged 43 ± 5 % (mean \pm SE) per field. Regarding the proportion of consumed aphids
309 per field, predation was high ranging from 0 to 86 % and averaged 32 ± 5 %.

310 Predator communities in sunflower fields, plant species richness in grasslands and
311 hedge length in the landscape had positive effects on aphid predation rates. Model 9 (Table 2)
312 was selected among competing models (Δ AICc >2 with the other competing models:
313 AICc = 289.8, 290.0, 282.5, 294.6, 295.0, and 290.2 respectively for Models 7, 8, 9, 10, 11
314 and 12) (Appendix F in supplementary material, Table F.2). The length of hedges within 0.25
315 km radius and grassland plant species richness had an interactive effect on the proportion of
316 preyed cards. Increasing either plant species richness in the adjacent grassland or hedge length
317 within 0.25 km resulted in an increase in aphid predation rates in sunflower fields. However,
318 the positive effect of grassland plant species richness on aphid predation rates vanished when
319 hedge length within 0.25 km was high, and the positive effect of hedge length on aphid
320 predation rates vanished when grassland plant species richness was high (Fig. 3). Aphid
321 predation was also explained by predator communities in sunflower fields, namely by spider
322 activity-density which had a positive effect on predation (Table 3). Carabid beetles metrics
323 (species richness, Shannon Index or the activity-density of carnivorous and omnivorous

324 functional group or all species pooled) had no effect on aphid predation (Appendix F in
325 supplementary material, Table F.2). We obtained the same results when using the proportion
326 of preyed aphids instead of the proportion of preyed cards (Appendix F in supplementary
327 material, Table F.4).

328

329 3.3. *Spider activity-density*

330 We only analysed spider activity-density since it was the only variable characterizing
331 ground-dwelling predator communities which had an effect on biological control in our study.

332 Spider activity-density in sunflower fields ranged from 0 to 35 spiders (mean \pm SE: 12.5
333 \pm 2.1) while it ranged from 0 to 116 spiders (mean \pm SE: 25.1 \pm 7.1) in grassland fields.

334 Grassland plant species richness and hedge length in the landscape within 0.25 km or 1
335 km radius landscapes had no effect on spider activity-density in sunflower fields. Spider
336 activity-density in sunflower field increased only with spider activity-density in the adjacent
337 grassland (Table 4).

338 Hedge length in the landscape within 1 km had a positive effect on spider activity-
339 density in grasslands (Table 4) while grassland plant species richness had a null or adverse
340 effect on spider activity-density in the grasslands depending on the amount of hedges in the
341 landscapes within 1 km (Fig. 4).

342

343 **4. Discussion**

344 In this study, we sampled arthropod predator communities (carabids and spiders) and
345 measured pest predation rates in crop fields along two independent environmental gradients: a
346 gradient of local green infrastructure quality and a gradient of green infrastructure amount in
347 the landscape. We show that increasing the amount or the quality of green infrastructures can

348 enhance pest predation rates in adjacent crops. Both weed seed and aphid predation rates in
349 the sunflower fields increased with the length of hedges but at different spatial scales. As
350 hypothesized, pest predation in the sunflower fields increased with plant species richness in
351 the adjacent grassland field, but this effect was observed only for aphid predation, and was
352 positive only when hedge length in the immediate landscape was low. In addition, we
353 highlight the key role of spider abundance in aphid pest control in our system.

354

355 *4.1. Effects of local grassland plant species richness and hedge amount in the landscape on*
356 *pest predation rates in sunflower fields*

357 We show that aphid predation rates depended on an interaction between the quality and
358 the quantity of green infrastructures in the immediate field surroundings. Therefore, our
359 results on aphid predation partly validate our hypothesis about a modulation of the local effect
360 of green infrastructure quality on biological control by the landscape context (Tschardt et
361 al., 2012) which acted however at a very local scale in our study. Aphid predation rates were
362 the weakest when sunflower field was adjacent to plant species poor grassland and when there
363 were few hedgerows in the 0.25 km radius landscape. From that point, increasing either plant
364 species richness in grassland or hedge length increased aphid predation rates. On one side,
365 increasing plant species richness in grasslands may increase the local pool of natural enemies
366 that could spillover in adjacent crops by local diffusion (Rand et al., 2006). On the other side,
367 increasing hedge length may increase the abundance and diversity of natural enemies thereby
368 increasing the flow of individuals towards crop habitats due to mass effect (i.e., immigration
369 of individuals from different patches in the immediate landscape). When grassland species
370 richness and hedge length were simultaneously high, aphid predation rates reached a plateau.
371 Such saturating effect may be explained because greater abundance and diversity of natural
372 enemies in crop habitats may result in higher competition and intra guild predation. This

373 could limit their efficiency in preying aphids thereby resulting in a slowdown or a decrease in
374 predation rates at some levels of natural enemy abundance and diversity (Caballero-Lopez et
375 al., 2012).

376 In contrast to aphid predation, weed seed predation only depended on the length of
377 hedges in the landscape at 1 km scale. This result is in line with previous studies (Trichard et
378 al., 2013) and suggests that weed seed predation in sunflower fields is mainly affected by
379 mass effects resulting in immigration of beneficial organisms mainly coming from hedgerows
380 at this scale and that characteristic of adjacent grassland is not a major factor explaining the
381 level of weed seed predation. This result does not validate our hypothesis about the positive
382 effects of local grassland plant species richness on weed seed predation.

383

384 *4.2. Which predators are in play?*

385 Our results clearly show that spiders were an important functional group involved in
386 aphid biological control as the activity-density of spiders in sunflower fields positively
387 affected aphid predation rates. This was also observed in wheat fields surrounded by
388 hedgerows (Garrat et al., 2017). Spider communities in our sunflower fields were largely
389 dominated by Lycosidae (68% of the total spider abundance) and by Linyphiidae (20 % of the
390 total spider abundance). Our results are therefore in line with what is known about the diet of
391 these two spider families. Several studies involving field or laboratory observations as well as
392 molecular analyses of predator gut contents have shown that aphids can represent a significant
393 part of Lycosidae's diet (Nyffeler and Benz, 1988; Roubinet et al., 2018).

394 However, our results also suggest that other groups of natural enemies may be
395 important for both aphid and weed seed predation. First of all, our results on aphid predation
396 indicate that spiders alone did not explain all the variability in aphid predation rates but that
397 carabid beetles did not affect aphid predation rates whatever the groups we considered (all

398 species pooled or carnivorous and omnivorous functional group). Our data support the
399 hypothesis that aphid predation rates partly depended on the spillover of spiders from
400 grassland to sunflower fields (i.e., there is a positive relationship between the activity-density
401 of spider in sunflower fields and the activity-density of spiders in grasslands). However, our
402 analyses about the environmental drivers of both the activity-density of spiders in grasslands
403 and the predation rates in sunflower fields indicate a positive effect of plant species richness
404 on aphid predation rates in 0.25 km radius landscapes with low amount of hedgerows despite
405 very low spider densities in the adjacent grassland (Fig 4). These results suggest that other
406 taxa may be involved in the spillover between habitats and that plant species richness in the
407 adjacent grassland can benefit aphid predation rates via other natural enemies. We particularly
408 suggest that ants, staphylinid beetles, true bugs or lacewings can be important groups to
409 consider that could contribute to the observed spillover effects on aphid predation rates
410 (Symondson et al., 2002; Thies et al., 2011; Garrat et al., 2017).

411 Secondly, our analyses indicate that no variables describing natural enemy communities
412 in the sunflower fields were important predictors of weed seed predation. We initially
413 hypothesized that carabids were the main group of natural enemies explaining weed seed
414 predation variability (Bohan et al., 2011; Trichard et al., 2013). In our study, carabid
415 communities were mainly dominated by *P. rufipes*, *P. cupreus* and *A. consularis*. Knowledge
416 about the diet of these species is variable but indicates that it ranges from omnivorous to
417 granivorous (Larochele, 1990; Honek et al., 2003; Homburg et al., 2014). In particular, *P.*
418 *rufipes* which has strong preferences for seeds of *V. arvensis* in laboratory diet assessment is
419 a good candidate for *V. arvensis* predation (Petit et al., 2014). However, activity-density of
420 both pooled, granivorous and omnivorous functional group and individual carabid species did
421 not significantly explain the level of weed seed predation in our experiment at that time. This
422 may be explained by the quite low activity-densities that we observed compared to other

423 studies establishing a positive effect of carabids on *V. arvensis* seed predation in field
424 conditions using a similar methodology (Petit et al., 2014). Recent studies have revealed that
425 vertebrates (including rodents or birds), much more than invertebrates, are responsible for
426 seed predation in agroecosystems (Tschumi et al., 2018). The fact that the only important
427 predictor for seed predation was the length of hedges at the 1 km scale is in line with the scale
428 at which rodents and birds operate in agricultural landscape and with other studies about seed
429 predation in agricultural landscapes (Baker et al., 2012; Trichard et al., 2013). Our results on
430 weed seed predation therefore highlight that dispersal abilities of species in play strongly
431 determine the scale of response of biological control services to green infrastructures.

432

433 *4.3 What is the optimal spatial scale to enhance biological control potential in sunflower* 434 *fields?*

435 Our study indicates that management options to enhance biological control potential in
436 agricultural landscapes depend on the type of pest considered. We found that management
437 options to enhance biological control of aphids in sunflower fields are more local than
438 management options to increase biological control of weed seeds. Several studies have shown
439 that aphid predation rates respond to the proportion of green infrastructures at large scales
440 such as in a 1 or 1.5 km radius (Roschewitz et al., 2005; Rusch et al., 2013; Rusch et al.,
441 2016). However, these studies did not explicitly examine the effects of both green
442 infrastructure quality and quantity at multiple scales on aphid predation rates. Here, we
443 demonstrate that taking into account both quality and quantity of green infrastructures at
444 different scales, i.e., adjacent habitats and immediate landscape, can help in explaining the
445 context-dependency of green infrastructure effects on aphid biological control. Our results
446 about the most important spatial scale to explain biological control of weed seed (i.e. 1 km)
447 are in line with other studies (Baker et al., 2012; Trichard et al, 2013). We demonstrate that

448 building functional landscape to optimize the delivery of ecosystem services in agricultural
449 landscapes needs a multi-spatial scale and a multi-taxa approach that takes into account
450 species traits, landscape structure as well as potential trade-offs in the delivery of multiple
451 ecosystem services (Nelson et al., 2009; Ekroos et al., 2016).

452

453 **5. Conclusions and applications**

454 Our study clearly highlights that both quality and quantity of green infrastructures in the
455 landscape are major drivers of spillover of beneficial organisms and biological control
456 services in agricultural landscapes. Our study highlights the benefit of having grassland fields
457 and hedgerow networks in the landscape mosaic which act as biodiversity reservoirs for
458 neighboring crop fields. We also show that increasing grassland quality through management
459 options may counteract in some extent the negative effect of landscape simplification on
460 aphid biological control. Our study therefore provides practical guidelines to help the
461 development of agri-environmental schemes aiming at maximising the flow of ecosystem
462 services in farmland. Indeed, our results suggest that efforts of local plant diversification to
463 enhance pest control services should be prioritized in landscapes with low amount of
464 hedgerows. Also, our results extend previous findings suggesting that the conservation or the
465 restoration of hedgerow networks in agricultural landscapes is a promising way to promote
466 pest control services without taking much land out of production.

467

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475

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687 **Captions for figures**

688

689 **Figure 1.** Map of the study area showing its location in France, the 1 km radius landscapes
690 around each of the 23 sampled sunflower-grassland fields and the paired design: a sunflower
691 field (in yellow) adjacent to a grassland field (in green).

692

693 **Figure 2.** Effect of the length of hedges within 1 km radius landscapes on seed predation
694 (proportion of preyed cards) in sunflower fields (See model parameters in Table 3). Black
695 dots represent the observed proportion of preyed cards in each sampled sunflower field.

696

697 **Figure 3.** Predicted effects of the length of hedges within 0.25 km radius landscapes and of
698 grassland quality (plant species richness) on aphid predation rate (proportion of preyed cards)
699 in sunflower fields (See model parameters in Table 3). Black dots represent the predicted
700 proportion of preyed cards in each sampled sunflower field.

701

702 **Figure 4.** Predicted effects of the length of hedges within 1 km radius landscapes and of
703 grassland quality (plant species diversity) on spider activity-density in the local grassland (See
704 model parameters in Table 4). Black dots represent the predicted spider activity-density in
705 each sampled grassland field.

706

707

708 **Table 1.** Characteristics of the 23 selected pairs of fields (a grassland field adjacent a
709 sunflower field) at the local scale and in 1 km radius buffers around each pair of fields.
710

Scale	Descriptor	Mean \pm SE	Range
Local	Grassland field area (ha)	3.4 \pm 0.4	0.7 – 8.5
	Sunflower field area (ha)	5.2 \pm 0.7	1.1 – 11.8
	Grassland age (yr)	7.2 \pm 1.6	1 - 38
	Between field distance within each pair (m)	8.8 \pm 2.8	0 - 40
	Grassland plant species richness	11.8 \pm 1.6	3 - 28
Landscape (1 km radius)	% grassland cover	10.0 \pm 0.6	5.2 – 16.7
	% woodland cover	2.9 \pm 0.7	0 – 13.0
	Hedge length (km)	10.1 \pm 0.8	4.4 – 17.5
	Minimal distance between pairs (km)	1.8 \pm 0.2	0.9 – 4.0

711 **Table 2.** Fitted GLMs with binomial error distribution for seed (*Viola arvensis*) predation (proportion of preyed cards) and GLMMs with
 712 binomial error distribution for aphid (*Acyrtosiphon pisum*) predation (proportion of preyed cards). Filled cells = explanatory variables included
 713 in the models.

714

	Model	Grassland	Predators in sunflower fields:			Predators in sunflower fields:			Landscape :	
		quality	Carabid beetles			Spiders			hedge length	
		Plant_SPR	Carab_SPR	Carab_Sh	Carab_AD	Spider_SPR	Spider_Sh	Spider_AD	H_0.25km	H_1km
Seed predation	1	■	■						■	
	2	■		■					■	
	3	■			■				■	
	4	■	■							■
	5	■		■						■
	6	■			■					■
Aphid predation	7	■	■			■			■	
	8	■		■		■	■		■	
	9	■			■			■	■	
	10	■	■			■				■
	11	■		■			■			■
	12	■			■			■		■

715

716 Plant_SPR is grassland plant species richness, Carab_SPR, Carab_Sh and Carab_AD are respectively carabid beetle species richness, Shannon

717 Index and activity-density (log-transformed) in sunflower field, Spider_SPR, Spider_Sh and Spider_AD are respectively spider adult species

718 richness, spider adult Shannon Index and activity-density (adults + juveniles) (log-transformed) in sunflower field, H_0.25km and H_1km are the

719 lengths of hedges in respectively 0.25 km and 1 km radius landscapes centred on each field pair. In all models, an interaction term between
720 grassland plant species richness and hedge length in the landscapes was included.

721 **Table 3.** Results of GLM with binomial error distribution fitted for seed predation (proportion
 722 of preyed cards) and GLMM with binomial error distribution fitted for aphid predation
 723 (proportion of preyed cards).

724

	Term	Est. \pm SE	P
Seed predation	Intercept	-2.78 \pm 0.50	< 0.001
	H_1km	0.15 \pm 0.04	0.0004
Aphid predation	Intercept	-4.19 \pm 0.85	< 0.001
	Spider_AD_Sun	0.74 \pm 0.22	0.001
	Plant_SPR	0.11 \pm 0.04	0.008
	H_0.25km	4.24 \pm 1.10	0.0001
	I(Plant_SPR: H_0.25km)	-0.21 \pm 0.06	0.001

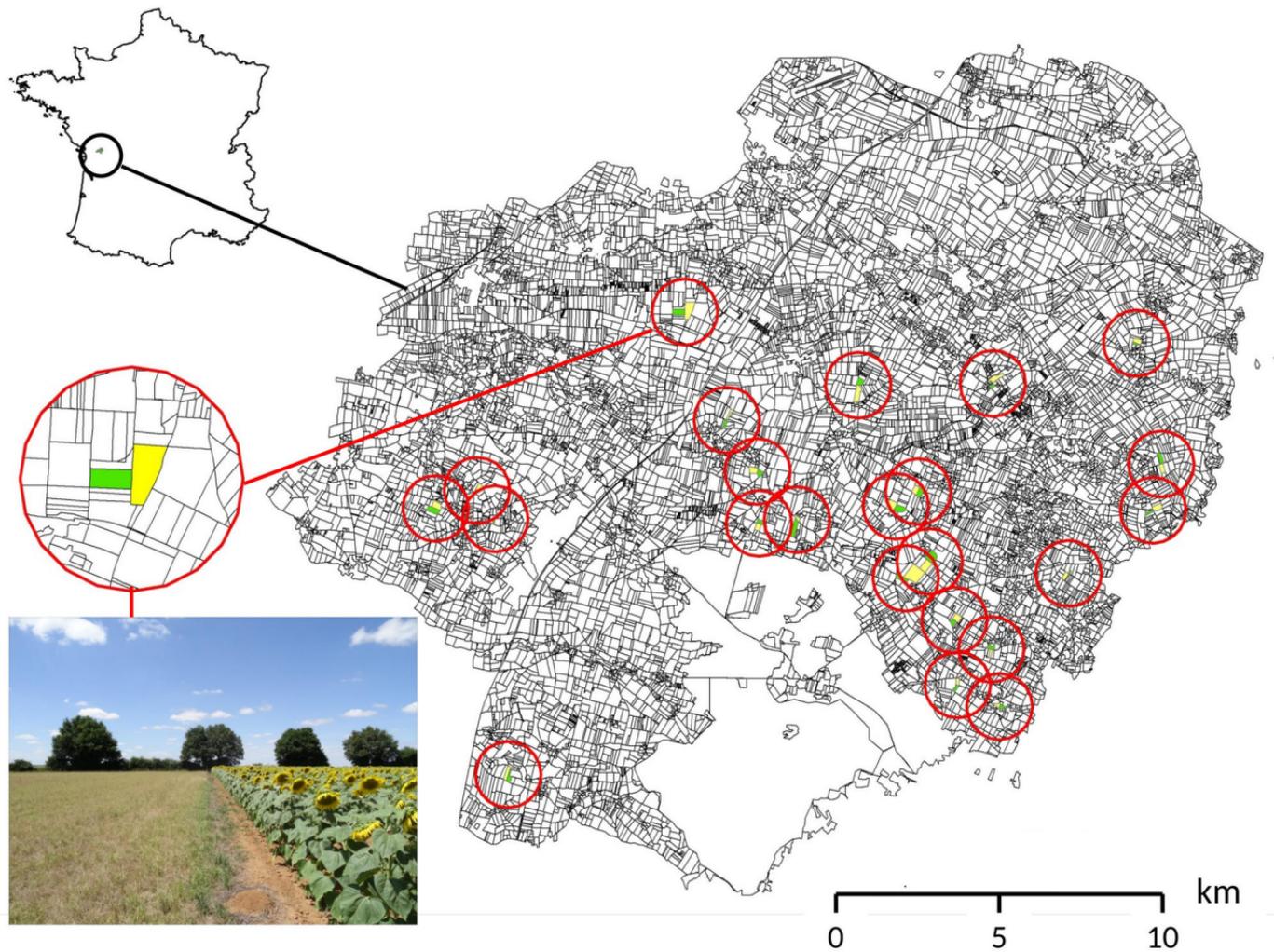
725 Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in GLM and
 726 GLMM with the proportion of cards with a predation event as response variable. Plant_SPR is
 727 grassland plant species richness, Spider_AD_Sun is spider activity-density in sunflower field,
 728 H_0.25km and H_1km are the lengths of hedges (km) in respectively 0.25 km and 1 km
 729 radius landscapes centred on each field pair. Spider_AD_Sun is log-transformed in the
 730 models.

731

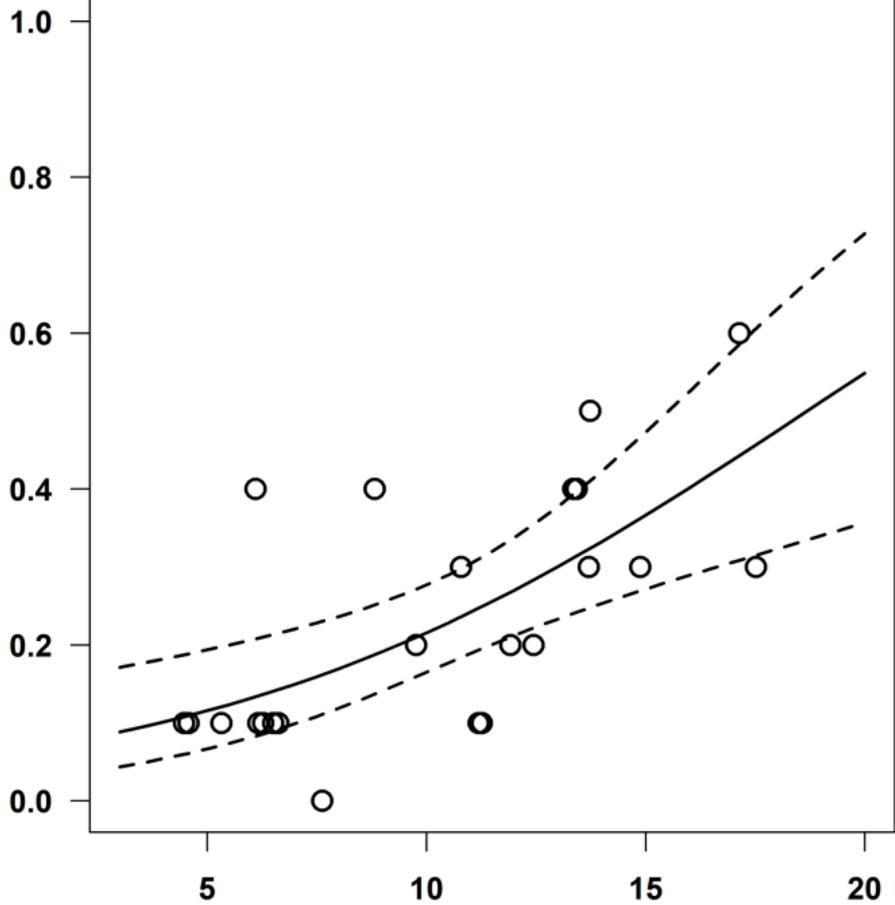
732 **Table 4.** Results of GLMs with binomial negative distribution fitted for spider activity-
 733 density in sunflower fields and in grassland fields

	Term	Est. \pm SE	P
Spider_AD_Sun	Intercept	1.74 \pm 0.39	<0.001
	Spider_AD_Grass	0.29 \pm 0.13	0.03
Spider_AD_Grass	Intercept	0.32 \pm 1.10	0.77
	Plant_SPR	0.11 \pm 0.08	0.22
	H_1km	0.37 \pm 0.11	0.001
	I(Plant_SPR:H_1km)	-0.02 \pm 0.01	0.02

734 Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in generalized
 735 linear models with spider activity-density in sunflower fields (Spider_AD_Sun) and in
 736 grassland fields (Spider_AD_Grass) as response variables. Plant_SPR is grassland plant
 737 species richness, H_1km is the length of hedges (km) within 1 km radius landscapes centred
 738 on each field pair. Spider_AD_Grass as an explanatory variable is log-transformed in the
 739 models.



Predation rate



Hedge length (km)

