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1 **Promoting generalist predators of crop pests in alley cropping agroforestry fields:**
2 **farming system matters**

3

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24 **Abstract**

25

26 Developing agroecological practices that enhance biological control of crop pests is a
27 major issue for the transition of agriculture towards sustainable and biodiversity-
28 friendly systems. Agroecological infrastructures (AEI) are devoted to the support of
29 ecosystem service providers, although they have mixed effects on natural enemies of
30 crop pests. In temperate regions, alley cropping agroforestry involves within-field AEI,
31 in the form of tree rows and associated understory vegetation strips. The objective of
32 this study was to assess the potential of generalist predators (carabid beetles and
33 cursorial spiders) to control weed seeds and invertebrate pests in alley cropping *vs* pure
34 crop systems, under two contrasting farming systems (conventional *vs* organic).
35 Predator surveys were carried out in May and June 2017 in South-Western France over
36 12 winter cereal fields. Our study revealed that the effect of alley cropping was
37 modulated by the farming system. Under conventional farming, alley cropping had a
38 negative effect on the activity-density and species richness of generalist predators,
39 especially regarding carnivorous carabids whose activity-density was reduced by nearly
40 50%. Under organic farming, alley cropping enhanced both the activity-density and
41 complementarity of generalist predators, with a two-fold increase in the activity-density
42 of seed-feeding carabids (predominantly granivorous and omnivorous), potentially
43 promoting weed seed and invertebrate pest control. Our results suggest that the
44 effectiveness of AEI in promoting natural enemies depends on the farming system at the
45 field scale, which affects resource availability and determines spillover intensity
46 between habitats. AEI are often perceived as sources of natural enemies. However, sink
47 and retention effects (*i.e.* reduced or delayed spillover into crop fields due to higher

48 attractiveness of AEI) are overlooked and very likely to explain the mixed impacts of
49 AEI on natural enemy communities.

50

51 **Keywords:** understory vegetation strip, natural enemy, agroecological infrastructure,
52 organic farming, spillover, source-sink dynamics

53 **1. Introduction**

54

55 The conservation of natural enemies of crop pests is of fundamental importance to the
56 sustainability of crop production (Begg et al., 2017). Generalist predators such as carabid
57 beetles and spiders play a key role in the functioning of agroecosystems. Studies have
58 demonstrated that carabids efficiently control various crop pests such as aphids (Collins et al.,
59 2002), flies (Finch, 1996) and slugs (Oberholzer and Frank, 2003). Furthermore, some species
60 are weed seed consumers and can contribute to reduce weed pressure in crop fields (Bohan et
61 al., 2011). Spiders are also recognized as efficient regulators of phytophagous pests such as
62 aphids, leafhoppers, beetles, and lepidopteran larvae (Michalko et al., 2019). However, as
63 many other arthropods, these predators are suffering from agricultural intensification, *i.e.* high
64 pesticide and fertilizer inputs, mechanization and simplification of agricultural landscapes
65 (Prieto-Benítez and Méndez, 2011; Brooks et al., 2012).

66 Agroecological infrastructures (AEI) such as hedgerows, beetle banks or wildflower
67 strips are devoted to shelter and support ecosystem service providers. AEI can be established
68 around or even within crop fields to promote the spillover of predators with limited dispersal
69 abilities (such as many carabid and spider species), whose abundance and diversity generally
70 decrease when farther from AEI (Rand et al., 2006). Yet, AEI can also have negative impacts
71 on predators. It has been shown that field boundaries, especially hedgerows, could act as a
72 barrier to the dispersal of carabids, preventing them from colonizing crop fields (Mauremooto
73 et al., 1995; Fernandez Garcia et al., 2000; Holland et al., 2004; Jowett et al., 2019), although
74 we found no evidence of barrier effects for cursorial spiders. Conversely, even agrobiont
75 spiders (*i.e.* reaching high densities in crops) do overwinter abundantly in AEI (Mestre et al.,
76 2018). Further, if AEI are highly attractive, they might lead to reduced or delayed
77 colonization of crop fields by carabids (Wamser et al., 2011; Jowett et al., 2019).

78 Although the presence of AEI nearby or within crop fields is of major importance to
79 promote predators, farming system is also decisive. Positive effects of organic farming on
80 predators can be explained by the absence of pesticides and synthetic fertilizers, which are
81 harmful for many carabid and spider species (Haughton et al., 1999; Navntoft et al., 2006;
82 Geiger et al., 2010; Li et al., 2018). Organic farming also favors the presence of a rich and
83 abundant weed flora, which provides additional habitats and trophic resources such as seeds
84 and pollen, but also phytophagous prey (Batáry et al., 2012). Alternative food is important
85 both to sustain predators when pest populations are low and to mitigate intraguild predation,
86 although it can also distract predators from main crop pests (Heij and Willenborg, 2020). It
87 has been shown that organic farming increases the abundance and species richness of carabid
88 communities (Djouidi et al., 2019), especially by favoring predominantly granivorous carabid
89 species and those with a large body length (Diekötter et al., 2016; Gallé et al., 2019).
90 Similarly, organic farming increases the activity-density¹ and species richness of spiders
91 (Feber et al., 1998; Batáry et al., 2012), but do not affect their functional structure
92 (considering their body size and hunting and dispersal strategies) (Gallé et al., 2019).
93 Furthermore, although rarely investigated, the combination of AEI and organic farming seems
94 very promising for promoting predators of crop pests. For example, some studies found a
95 negative effect of AEI on weed seed or aphid suppression in fields under conventional
96 farming, but a positive effect in fields under organic farming (Fischer et al., 2011; Winqvist et
97 al., 2011).

98 In agroforestry systems, the association of woody vegetation (trees or shrubs) with
99 crops and/or animals has been shown to provide various ecosystem services such as
100 sustainable biomass production, soil and water protection, biodiversity conservation and

¹ Pitfall trap catches depend on both population density and an organism's activity, to provide a quantity usually referred to as activity-density (Thomas et al. (1998).

101 carbon sequestration (Torralba et al., 2016; Kay et al., 2019). In temperate regions, alley
102 cropping agroforestry represents a great opportunity for restoring ecosystem services. Indeed,
103 in such systems, the absence of tillage operations on tree rows results in the formation of
104 understory vegetation strips (UVS), covering about 3 to 13% of the available agricultural area
105 and delimiting alleys (generally about 24 m wide) where arable crops are grown (Figure 1a).
106 Agroforestry systems are therefore very conducive to ecological engineering and innovations
107 (*e.g.* spatial and temporal diversification of crop vs non-crop habitats and their management
108 strategies). This increased interspersed of AEI and cropped areas within fields themselves
109 can affect ecosystem service flows (Mitchell et al., 2015). Although very few studies have
110 focused on the ecological functions of UVS, it has been shown that they are important refugia
111 for many plants and invertebrates (Boinot et al., 2019a; Boinot et al., 2019b; Pardon et al.,
112 2019; D’Hervilly et al., 2020). UVS provide overwintering habitats for most spiders and for
113 carabid species sensitive to agricultural intensification (characterized by a predominantly
114 granivorous diet and a large body length), whereas small and carnivorous carabids overwinter
115 mostly in crop alleys (Boinot et al., 2019b). These results suggest that alley cropping might
116 efficiently promote spiders and predominantly granivorous carabids compared to pure crop
117 systems, because UVS provide suitable overwintering habitats and enhanced plant and
118 invertebrate resources within fields themselves. On the other hand, alley cropping could have
119 detrimental effects on small and carnivorous carabids that forage and overwinter in arable
120 habitats (Baulechner et al., 2019; Boinot et al., 2019b), either because UVS hamper their
121 movements and/or host both competitors and predators. Nevertheless, to our knowledge no
122 study has compared generalist predator communities between alley cropping and pure crop
123 systems under contrasting farming systems.

124

125 **Figure 1.** (a) Alley cropping agroforestry system and pure crop control in the Gers
126 department, France. (b) Predator sampling design (pitfall traps are represented by the circles).
127

128 The objective of this study was to assess the potential of generalist predator
129 communities to control weed seeds and invertebrate pests in alley cropping *vs* pure crop
130 systems, under conventional *vs* organic farming. We hypothesized that **1)** predominantly
131 granivorous carabids and cursorial spiders are favored by alley cropping, whereas carnivorous
132 carabids, especially small ones that are adapted to highly disturbed habitats, are negatively
133 impacted by alley cropping. Further, we expected that **2)** the effect of alley cropping is
134 modulated by the farming system. Under conventional farming, alley cropping has an overall
135 negative impact on the predator community that is composed predominantly of species
136 adapted to highly disturbed habitats (*i.e.* small and carnivorous carabids), whereas alley
137 cropping under organic farming strongly favors more sensitive species (*i.e.* larger species and
138 granivorous carabids), by providing both undisturbed habitats under the trees and abundant
139 trophic resources in crop alleys. Consequently, we expected **3)** higher activity-density, larger
140 mean body size and enhanced complementarity (*i.e.* diversity of diet and body size) of
141 predator communities in more complex systems (*i.e.* alley cropping under organic farming),
142 which is likely to result in better biological control of weed seeds and invertebrate pests.

143

144 **2. Material and Methods**

145

146 *2.1. Study site*

147

148 The study was conducted in the Gers department (South-Western France), a hilly region (200-
149 400 m altitude) where agricultural areas are dominated by clay-limestone and clay to silt soils.

150 Climate is sub-Atlantic (hot summers and cool winters) and annual precipitation usually
151 varies from 700 to 900 mm. From a previous study assessing the effect of alley cropping on
152 plant communities (Boinot et al., 2019a), vegetation surveys were carried out in May 2017 in
153 fields growing either winter wheat (*Triticum aestivum* L.) or winter barley (*Hordeum vulgare*
154 L.), half under conventional farming and half under organic farming (*i.e.* generally more
155 diverse crop rotations, without pesticides and inorganic fertilizers). Three fields under organic
156 farming also contained leguminous crops, either garden pea (*Lathyrus oleraceus* Lam.) and/or
157 common vetch (*Vicia sativa* L.) but the proportion of legumes was always very low compared
158 to cereals (less than 15%). The same fields were used for predator sampling in May and June
159 2017, except that two pairs of fields were excluded from the analyses because the alley
160 cropping plot and its pure crop control were more than three km apart, thus not located in the
161 same landscape context. Indeed, carabids and cursorial spiders respond to landscape variables
162 at a lower scale, generally within a 500 m or 1 km radius around fields (*e.g.* Schmidt et al.,
163 2008; Wamser et al., 2011). This resulted in six pairs of fields (alley cropping *vs* pure crop
164 control), half under conventional farming and half under organic farming, located within the
165 same perimeter, similar in terms of pedo-climatic conditions and surrounding land use.
166 Although there is a great diversity of farming systems along a gradient from conventional to
167 organic farming (Puech et al., 2014), all farmers in our study performed shallow tillage
168 without mouldboard ploughing. Under conventional farming, all farmers used herbicides with
169 a wide spectrum of action and similar treatment frequency indices (*i.e.* the sum of the ratio of
170 the applied dose to the recommended dose of all the treatments applied in a year). No
171 insecticide was employed. Each pair of fields was cultivated by the same farmer, with similar
172 crop management over the three years preceding the study (see Table S1 in Supplementary
173 material). Features of alley cropping systems (*i.e.* tree species and basic metrics) are given in
174 Table 1.

175

176 **Table 1.** Description of alley cropping agroforestry fields.

177

178 *2.2. Predator sampling*

179

180 Carabid beetles and cursorial spiders were sampled with pitfall traps (depth: 16 cm, diameter:
181 6.2 cm, exposure time: 48h), on three different sampling periods in May and June 2017. In
182 each alley cropping field, pitfall traps were positioned along three transects 20 m apart and
183 running perpendicularly to tree rows (Figure 1b). These transects were located in field cores,
184 at around 50 m and 100 m from the two nearest field boundaries. Each transect comprised
185 pairs of pitfall traps (10 m apart) located in UVS and in adjacent crop alleys, at two distances
186 from UVS (2 m and 8 m). During field work, the content of each pair of pitfall traps was
187 collected in the same plastic bag and considered as one sampling unit. The same protocol was
188 used for pure crop controls with the transects placed at equivalent locations in the field in the
189 absence of UVS. This resulted in a dataset of 162 pairs of pitfall traps sampled over three
190 periods (pure crops: $n = 72$, crop alleys: $n = 72$, UVS: $n = 18$).

191

192 *2.3. Biological control potential of predator communities*

193

194 To estimate the potential of common generalist predators to control weed seeds and
195 invertebrate pests, we measured the activity-density and species richness of carabids
196 (granivorous, omnivorous, carnivorous) and cursorial spiders in pure crop controls and alley
197 cropping systems (crop alleys vs UVS) under conventional vs organic farming. Further, we
198 measured the activity-density, species richness, community-weighted mean (CWM) and
199 functional divergence (FDvar) of body length and diet of the total predator community. CWM

200 corresponds to the average of trait values weighted by the relative abundance of each species.
201 FDvar is a relevant metric for assessing complementarity between species (Woodcock et al.,
202 2019), which has been shown to enhance pest suppression (Dainese et al., 2017; Greenop et
203 al., 2018). It varies from 0 to 1; FDvar is low if species and/or abundances are clustered
204 around the mean body length value (*i.e.* low complementarity), whereas it is high if they are
205 clustered towards one or both margins of the trait distribution (*i.e.* high complementarity).
206 Formulas are given in Table A1 in Appendix A. Information on the diet and body length of
207 carabid beetles were collected in databases (Hedde et al., 2012; Homburg et al., 2014) and
208 through a search in scientific literature (references are given in Supplementary Material).
209 Information on the body length of spiders was collected from the BETSI database (Hedde et
210 al., 2012).

211

212 2.4. Data analysis

213

214 Data from the three sampling periods were summed per pitfall trap to analyze the global effect
215 of cropping and farming systems. To assess hypotheses 1 and 2, we used generalized linear
216 mixed effects models (GLMMs) and compared the activity-density and species richness of
217 each functional group (*i.e.* granivorous, omnivorous, carnivorous carabids and cursorial
218 spiders) between pure crop controls and alley cropping systems (crop alleys *vs* UVS) under
219 conventional *vs* organic farming. To assess hypothesis 3, we used GLMMs to compare the
220 activity-density, species richness, CWM and FDvar of body length and diet of predator
221 communities in pure crop controls, crop alleys and UVS under conventional *vs* organic
222 farming. Field pairs were included as a random effect on the intercept to take into account the
223 spatial auto-correlation between pitfall traps located within the same perimeter. When
224 GLMMs revealed significant interactions between farming system (conventional *vs* organic

225 farming) and habitats (pure crop, crop alleys, UVS), least-square means were used to compare
226 habitats under conventional *vs* organic farming separately. Activity-density and species
227 richness were assumed to follow a Poisson distribution, CWM Body length was assumed to
228 follow a Gaussian distribution and variables varying from 0 to 1 (CWM Diet, FDvar Diet,
229 FDvar Body length) were assumed to follow a Beta distribution. When the latter included 0
230 and/or 1 value(s), the transformation $(FDvar \times (N - 1) + 0.5) / N$ was employed following
231 Zuur et al. (2013), where N is the sample size. We used the package lme4 for fitting Gaussian
232 LMMs (Bates et al., 2015) and the package glmmTMB (Brooks et al., 2017) for fitting
233 Poisson and Beta GLMMs, with the link functions log and logit respectively. When Poisson
234 GLMMs revealed under- or over-dispersion, Conway-Maxwell-Poisson GLMMs were fitted
235 instead as suggested by (Lynch et al., 2014). The package lsmeans was used for least-square
236 means post-hoc comparisons (Lenth, 2016). All analyses were performed using the statistical
237 software R 5.1 (R Core Team, 2018).

238

239 **3. Results**

240

241 A considerably high number of carabids and cursorial spiders were sampled during the survey
242 (Table 2).

243

244 **Table 2.** Total number of individuals and species sampled per functional group during the
245 whole survey.

246

247 *3.1. Activity-density and species richness of generalist predators*

248

249 Independently from the farming system (conventional *vs* organic farming), alley cropping had
250 a clear negative effect on the activity-density and species richness of carnivorous carabids,

251 which were much lower both in crop alleys and UVS as opposed to pure crop controls (Table
252 3, Figure 2). This result was largely driven by the reduced activity-density of small and
253 dominant carabids such as *Anchomenus dorsalis* and Trechini species, especially under
254 conventional farming, but also by the reduced activity-density of the large *Carabus auratus*
255 under organic farming (Figure A1 in Appendix A). Other functional groups responded
256 differently to alley cropping depending on the farming system. Granivorous carabids tended
257 to have lower activity-density in crop alleys than in pure crop controls under conventional
258 farming, but higher activity-density and species richness in crop alleys and UVS under
259 organic farming (Table 3, Figures 2a, 2b). Under conventional farming, granivorous carabids
260 were mostly represented by *Harpalus dimidiatus*, whereas some species benefited from the
261 combination of alley cropping and organic farming, such as *Harpalus affinis*, *Harpalus*
262 *pygmaeus* and *Amara* spp. (Figure A1 in Appendix A). Omnivorous carabids had lower
263 activity-density only in UVS under conventional farming, whereas their activity-density
264 strongly increased in crop alleys under organic farming compared to pure crop controls (Table
265 3, Figure 2a), especially for *Poecilus cupreus* and *Brachinus crepitans* (Figure A1 in
266 Appendix A). Cursorial spiders had lower activity-density in crop alleys than in pure crop
267 controls under conventional farming, but similar activity-density between all habitats under
268 organic farming (Table 3, Figure 2a). Consequently, activity-density of the total predator
269 community was much lower in crop alleys and UVS as opposed to pure crop controls under
270 conventional farming (Table 3, Figure 2a). Species richness of the predator community was
271 even reduced in crop alleys under conventional farming (Table 3, Figure 2b). On the other
272 hand, activity-density of the predator community was higher in crop alleys than in pure crop
273 controls under organic farming (Table 3, Figure 2a).

274

275 **Table 3.** Results of GLMMs comparing activity-density, species richness and functional
276 structure of predator communities between pure crop (reference level), crop alleys and
277 understory vegetation strips (UVS), under conventional farming (reference level) vs organic
278 farming. When GLMMs revealed significant interactions between habitats and farming
279 system, least-square means were used to compare habitats under conventional vs organic
280 farming separately (see Table S2 in Supplementary material for detailed outputs). CMP =
281 Conway-Maxwell Poisson. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

282

283 **Figure 2.** Mean and standard deviation of **(a)** activity-density and **(b)** species richness of each
284 functional group and total predator community. Stars at the top of barplots are based on the p-
285 values of least-square means post-hoc comparisons, when there was a significant interaction
286 between habitats and farming systems. Stars indicate significant difference between pure crop
287 controls (reference level) vs crop alleys and understory vegetation strips (UVS). See Table S2
288 in Supplementary material for detailed outputs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

289

290 *3.2. Functional structure of generalist predator communities*

291

292 CWM Diet of predator community was close to 1 (*i.e.* towards carnivorous diet) and similar
293 between all habitats under conventional farming, whereas it was lower in crop alleys and UVS
294 as opposed to pure crop controls under organic farming (Table 3, Figure 3a). Although FDvar
295 Diet tended to be higher in alley cropping, especially under organic farming (Figure 3c), no
296 significant effect was detected (Table 3). CWM Body length was significantly higher in crop
297 alleys than in pure crop controls (Table 3, Figure 3b), but the difference was small (+0.6 mm
298 on average per trap). FDvar Body length was higher in crop alleys than in pure crop controls

299 under conventional farming, but lower in crop alleys under organic farming (Table 3, Figure
300 3d).

301

302 **Figure 3.** Functional structure of total predator community. **(a)** Community-weighted mean
303 (CWM) of diet (granivorous: 0, omnivorous: 0.5 and carnivorous: 1), **(b)** CWM of body
304 length, **(c)** Functional divergence (FDvar) of body length and **(d)** FDvar of body length (low
305 complementarity: 0, high complementarity: 1). Stars at the top of boxplots are based on p-
306 values of least-square means post-hoc comparisons, when there was a significant interaction
307 between habitats and farming systems. Stars indicate significant difference between pure crop
308 controls (reference level) vs crop alleys and understory vegetation strips (UVS). See Table S2
309 in Supplementary material for detailed outputs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

310

311 **4. Discussion**

312

313 Our study on the distribution of generalist predators in alley cropping agroforestry vs pure
314 crop systems revealed that the effect of alley cropping was modulated by the farming system.
315 Under conventional farming, alley cropping had a negative effect on the activity-density and
316 species richness of generalist predators, especially regarding carnivorous carabids whose
317 activity-density was reduced by nearly 50%. Under organic farming, alley cropping enhanced
318 both the activity-density and complementarity of generalist predators, with a two-fold
319 increase in the activity-density of seed-feeding carabids (predominantly granivorous and
320 omnivorous).

321

322 *4.1. Negative effects of alley cropping agroforestry on generalist predators under*
323 *conventional farming*

324

325 We confirmed that the activity-density and species richness of carnivorous carabids were
326 clearly reduced by alley cropping, independently from the farming system (hypothesis 1).
327 This was especially true for small species such as *Anchomenus dorsalis* and Trechini species,
328 and corroborates previous studies showing that carnivorous species, particularly small ones,
329 thrive in disturbed and open habitats (Navntoft et al., 2006; Hanson et al., 2016; Baulechner et
330 al., 2019). In alley cropping systems, UVS seem to act as a sink (*i.e.* unfavorable habitat) or a
331 barrier hampering their movements, as their activity-density was even lower in UVS than in
332 crop alleys, which is in line with the results of Richard et al. (2019). Moreover, Boinot et al.
333 (2019b) showed that small and carnivorous carabids spent the winter in crop alleys, whereas
334 larger carabids were found mostly in UVS. Therefore, small and carnivorous species might
335 have suffered from both competition with other predators and intraguild predation in alley
336 cropping systems. The reduction of such predatory species may result in lower biological
337 control in alley cropping systems, especially regarding small crop pests such as aphids, on
338 which they mostly feed (Rusch et al., 2015).

339 However, alley cropping alone was not enough to promote predominantly seed-
340 feeding carabids (granivorous and omnivorous) and cursorial spiders in crop alleys. The
341 presence of overwintering habitats and trophic resources in UVS might not have compensated
342 for the very poor weed flora observed in fields under conventional farming (Boinot et al.,
343 2019a). Indeed, previous studies have shown that organic farming favors seed-feeding
344 carabids and spiders (Feber et al., 1998; Batáry et al., 2012; Diekötter et al., 2016),
345 presumably because of the presence of a rich and abundant weed flora that provides additional
346 habitats (*e.g.* hunting and hiding structures) and trophic resources such as seeds, but also
347 phytophagous and detritivore prey. Probably, these predators also directly suffered from

348 herbicide and synthetic fertilizer applications in the conventional farming fields surveyed
349 (Haughton et al., 1999; Navntoft et al., 2006; Geiger et al., 2010; Li et al., 2018).

350 Conversely to our expectations, granivorous carabids (mostly represented by *Harpalus*
351 *dimidiatus*) and cursorial spiders were even less active in crop alleys than in pure crop
352 controls under conventional farming. In alley cropping systems, they probably foraged in
353 UVS where plant and invertebrate resources are more abundant and diversified than in crop
354 alleys (Boinot et al., 2019a; Boinot et al., 2019b), resulting in a retention effect. This result is
355 consistent with those from Wamser et al. (2011), who showed that high availability of
356 overwintering habitats in the landscape reduces or delays the spillover of carabid beetles in
357 fields under conventional farming. Similarly, Boetzi et al. (2019) found that the percentage of
358 granivorous carabids in oilseed rape under conventional farming decreased by nearly 50%
359 when adjacent to AEI. This could be explained by the spillover of some carnivorous species
360 from AEI towards crop fields, but also by the retention of granivorous carabids outside crop
361 fields due to higher food supply in adjacent AEI. Finally, Schoeny et al. (2019) also found
362 low spider spillover from flower strips towards melon crops, presumably because of low
363 attractiveness of the crop and/or high attractiveness of the field margins, which would provide
364 suitable microclimate, shelters and prey.

365

366 *4.2. Positive effects of alley cropping agroforestry on generalist predators under organic* 367 *farming*

368

369 The effect of alley cropping was modulated by the farming system, thereby confirming
370 hypothesis 2. Indeed, although alley cropping had a negative impact on predator communities
371 under conventional farming, it was the opposite under organic farming. First, the total
372 activity-density of seed-feeding carabids (granivorous and omnivorous) was doubled in crop

373 alleys of alley cropping systems as opposed to pure crop controls. This could be explained by
374 (i) the presence of UVS that are favorable overwintering habitats for seed-feeding carabids in
375 alley cropping systems (Boinot et al., 2019b), and (ii) a rich and abundant weed flora
376 enhancing habitat and resource availability under organic farming, including associated
377 phytophagous and detritivore prey (Batáry et al., 2012; Diehl et al., 2012; Boinot et al.,
378 2019a), thereby favoring the spillover of predators associated to UVS towards crop alleys (*i.e.*
379 source effect). Second, alley cropping no longer had a negative effect on the activity-density
380 of cursorial spiders, which was similar in all habitats (pure crops, crop alleys, UVS).
381 Although we expected cursorial spiders to benefit from UVS in alley cropping systems, they
382 might have been limited by the high activity of omnivorous carabids that can feed on them
383 (Roubinet et al., 2017).

384 Considering the whole community, the total activity-density of predators was higher in
385 crop alleys than in pure crop controls. Besides, CWM Diet of predator communities was close
386 to 1 in pure crop controls (indicating a high dominance of carnivorous diet), whereas it was
387 getting closer to 0.5 in crop alleys (indicating a higher complementarity between predators
388 with various diet), thereby partly confirming hypothesis 3. However, we expected higher
389 difference in CWM and FDvar of body length between cropping systems than those observed
390 in our study. It is likely that we did not detect a clear effect of cropping and farming systems
391 on these variables because we focused on circulating predators during spring, which might
392 partly come from adjacent habitats and arable fields. Indeed, using emergence traps, Boinot et
393 al. (2019b) showed that carabids overwintering in UVS are larger than those associated with
394 crop alleys. This result was consistent with previous studies showing that large carabids are
395 more sensitive to agricultural disturbances (Winqvist et al., 2014; da Silva et al., 2017).
396 Distinguishing overwintering from circulating individuals would help disentangling the effect
397 of local and landscape factors on predator communities in arable fields (Djouidi et al., 2019).

398 Nevertheless, although spillover might have occurred between an alley cropping field and its
399 adjacent pure crop control, or between AEI and arable fields, there were still very large
400 variations of activity-density for all functional groups, in response to the different
401 combinations of cropping and farming systems. Alley cropping combined with organic
402 farming can enhance both the activity-density and complementarity of predator communities
403 within fields during spring, even in relatively small fields such as those observed in the Gers
404 department (generally less than 10 ha).

405 In conclusion, the combination of alley cropping and organic farming should be the
406 best option for enhancing both weed seed and invertebrate pest control, provided that niche
407 complementarity outweighs intraguild predation (Straub et al., 2008; Heij and Willenborg,
408 2020). Our results are in line with those of Caro et al. (2016) and Fusser et al. (2018), who
409 found that AEI had stronger effect on carabid diversity when combined with organic farming.
410 Other studies also revealed contrasting effects of AEI on weed seed or aphid suppression,
411 depending on the local farming system and pesticide use intensity (*i.e.* positive effects under
412 organic farming and low pesticide use intensity, negative ones under conventional farming
413 and high pesticide use intensity) (Fischer et al., 2011; Winqvist et al., 2011; Ricci et al.,
414 2019). All these results highlight the key role of organic farming to promote the spillover of
415 predators from AEI towards cropped areas, most likely by increasing resource availability – a
416 major factor driving the movement of organisms between habitats (Dunning et al., 1992;
417 Corbett and Plant, 1993; Blitzer et al., 2012; Tschardt et al., 2016). An alternative but not
418 exclusive hypothesis is that increased soil organic matter under organic farming promotes
419 predator spillover into crop fields, by improving structural habitat complexity and soil
420 microclimate (Aldebron et al., 2020). All in all, the establishment of AEI alone cannot
421 guarantee the restoration of biological pest control, and should therefore be coupled with
422 within-field plant diversification, which is a key factor in promoting beneficial trophic

423 interactions (Wan et al., 2020). More precisely, fine-grained interspersion of crop(s) and
424 alternate vegetation, such as weeds, is of major importance for generalist predators (especially
425 for species suffering from agricultural intensification), although this might not be the case for
426 specialist ones (Sheehan, 1986). Plant diversification should additionally reduce pest pressure
427 through the resource concentration hypothesis, which predicts that specialist pests are more
428 likely to locate and remain on host plants (*i.e.* crops) occurring in large, dense, pure stands
429 compared to species-rich environment, where host chemical cues are disrupted (Root, 1973).

430

431 *4.3. Future research on biological control in alley cropping agroforestry*

432

433 Since alley cropping agroforestry is a marginal farming practice in Europe, it is very
434 challenging to find old systems, especially when looking for adjacent pure crop controls.
435 Therefore, our results do not apply to alley cropping in general, but rather to systems in
436 transition (less than 12 years old), where farmers performed shallow tillage without
437 mouldboard ploughing and grew winter cereals during the study year. In this study, we
438 focused on the presence of UVS, which was indeed the major difference between alley
439 cropping and pure crop systems (tree canopy was never very imposing, although some trees
440 could already reach up to seven meters). However, trees and shrubs might greatly enhance
441 natural enemy communities by providing additional trophic resources and sites for
442 reproduction, overwintering and estivation (Stamps and Linit, 1998), especially in older
443 systems (> 15-20 years). Higher trophic taxa such as birds and small mammals have also been
444 shown to benefit from the presence of tree rows and UVS in alley cropping systems (Klaa et
445 al., 2005; Gibbs et al., 2016), and their effects on weed and invertebrate pest suppression are
446 mixed (Tschumi et al., 2018). Besides, agroforestry farmers are currently using contrasting
447 strategies for UVS management (*e.g.* minimalist management, maintaining bushes, mowing

448 the vegetation, sowing plant mixtures). UVS width also varies from one alley cropping system
449 to another and is expected to have an impact on the quality and quantity of habitats and
450 trophic resources (Aavik and Liira, 2010; Fried et al., 2018). Ecological engineering of UVS
451 is still in its infancy, and future research should assess how these management strategies
452 affect biological control level in crop alleys. Although our results and those of a recent meta-
453 analysis (Staton et al., 2019) show that natural enemies generally benefit from agroforestry, a
454 broader food web perspective is required to describe the processes that enhance or reduce
455 biological control of invertebrate pests and weeds in temperate agroforestry systems.
456 Encouragingly, diversified natural enemy communities generally improve biological control
457 through higher niche complementarity (Straub et al., 2008; Holland et al., 2012; Woodcock et
458 al., 2016; Dainese et al., 2017; Greenop et al., 2018).

459

460 **5. Conclusions**

461

462 Under conventional farming, the presence of understory vegetation strips within fields has a
463 negative effect on the activity-density and species richness of generalist predators in crops,
464 but is still useful for biodiversity conservation. On the other hand, the combination of alley
465 cropping agroforestry and organic farming greatly enhances both the activity-density and
466 complementarity of generalist predators, potentially making biodiversity conservation and
467 crop pest control compatible. Our results suggest that the establishment of other
468 agroecological infrastructures such as wildflower strips, beetle banks or hedgerows within
469 fields would enhance biological control by generalist predators under organic farming,
470 although it could well be the opposite under conventional farming. We emphasize that
471 agroecological infrastructures and agrochemicals are intrinsically antagonistic strategies to
472 control pests; the former are dedicated to the promotion of biodiversity whereas the latter lead

473 to the destruction of biodiversity (in sprayed areas and even beyond). This antagonism can
474 lead to strong sink or retention effects on predatory species, depending on their life strategies
475 and associated ecological preferences. We suggest that within-field plant diversification and
476 fine-grained interspersed crop(s) and alternate vegetation, such as weeds, are key to
477 promote the positive functions of agroecological infrastructures.

478

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480

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487

488 **Appendix A.**

489

490 **Table A1.** Single trait indices. S is total number of species, w_i is the relative abundance of
491 species i and x_i is the trait value for species i . FDvar modified is used for variables that contain
492 0 values.

493

494 **Table A2.** Functional trait values of carabid and cursorial spider species (diet; granivorous: 0,
495 omnivorous: 0.5 and carnivorous: 1). References are given in Supplementary Material.

496

497 **Figure A1.** Mean activity-density of common species (*i.e.* occurring in at least five pitfall
498 traps) in each functional group (G: granivorous carabids, O: omnivorous carabids, C:
499 carnivorous carabids, S: cursorial spiders) under **a)** conventional farming and **b)** organic
500 farming.

501

502 **Supplementary material**

503

504 **Table S1.** Crop management for each pair of agroforestry fields and pure crop controls.

505 **Table S2.** Results of least-square means post-hoc comparisons.

506

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Table 1. Description of alley cropping agroforestry fields.

Field	Farming system	Age of the system (years)	Field size (ha)	Crop alley width (m)	UVS width (m)	UVS management	Dominant plant species in UVS	Tree species
1	Conventional	10	9	25	2	Unmanaged	<i>Bromus</i> spp., <i>Galium aparine</i> , <i>Geranium columbinum</i>	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Pyrus pyraister</i> , <i>Prunus avium</i> , <i>Quercus petraea</i>
2	Conventional	6	12	28	1.5	Unmanaged	<i>Bromus</i> spp., <i>Schedonorus arundinaceus</i> , <i>Galium aparine</i>	<i>Juglans regia</i> , <i>Pyrus pyraister</i> , <i>Prunus avium</i> , <i>Quercus pubescens</i> , <i>Sorbus domestica</i>
3	Conventional	5	6	38	2	Unmanaged	<i>Festuca rubra</i> (sown), <i>Avena</i> spp., <i>Galium aparine</i>	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Sorbus domestica</i> , <i>Tilia cordata</i>
4	Organic	2	8	26	1	Unmanaged	<i>Avena</i> spp., <i>Myosotis arvensis</i> , <i>Rubus</i> spp.	<i>Juglans regia</i> , <i>Prunus avium</i> , <i>Quercus petraea</i> , <i>Sorbus torminalis</i> , <i>Fraxinus excelsior</i>
5	Organic	8	3	17	1	Unmanaged	<i>Dactylis glomerata</i> , <i>Potentilla reptans</i> , <i>Lactuca serriola</i>	<i>Pyrus pyraister</i> , <i>Quercus petraea</i> , <i>Sorbus domestica</i> , <i>Sorbus torminalis</i> , <i>Fraxinus excelsior</i> , <i>Cornus sanguinea</i> .
6	Organic	5	6	32	2	Mown twice a year (before crop sowing/after harvest)	<i>Lolium</i> spp., <i>Convolvulus arvensis</i> , <i>Bromus</i> spp.	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Sorbus domestica</i> , <i>Fraxinus excelsior</i> , <i>Ulmus campestris</i>

Table 2. Total number of individuals and species sampled per functional group during the whole survey.

	Total number of individuals	Total number of species
Carabids		
Granivorous	560	15
Omnivorous	1492	8
Carnivorous	803	25
Total	2855	48
Cursorial spiders	3006	63

Table 3. Estimates and standard errors of GLMMs comparing activity-density, species richness and functional structure of predator communities between pure crop (reference level), crop alleys and understory vegetation strips (UVS), under conventional farming (reference level) vs organic farming. When GLMMs revealed significant interactions between habitats and farming system, least-square means were used to compare habitats under conventional vs organic farming separately (see Table S2 in Supplementary material for detailed outputs). CMP = Conway-Maxwell Poisson. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

	Distribution	Main effects			Interactions	
		Crop alleys	UVS	Organic farming	Crop alleys x Organic farming	UVS x Organic farming
Granivorous carabids						
Activity-density	CMP	-0.48 ± 0.247	0.05 ± 0.337	0.19 ± 0.906	$1.23 \pm 0.337^{***}$	$1.04 \pm 0.456^*$
Species richness	CMP	-0.13 ± 0.256	0.02 ± 0.372	0.16 ± 0.482	$0.68 \pm 0.333^*$	$0.96 \pm 0.456^*$
Omnivorous carabids						
Activity-density	CMP	-0.43 ± 0.254	$-1.25 \pm 0.464^{**}$	0.82 ± 1.023	$1.20 \pm 0.305^{***}$	$1.69 \pm 0.536^{**}$
Species richness	CMP	$-0.45 \pm 0.180^*$	-0.60 ± 0.325	0.62 ± 0.508	$0.55 \pm 0.213^{**}$	$0.74 \pm 0.371^*$
Carnivorous carabids						
Activity-density	CMP	$-0.73 \pm 0.165^{***}$	$-1.31 \pm 0.336^{***}$	-0.25 ± 0.520	0.11 ± 0.244	0.53 ± 0.461
Species richness	CMP	$-0.38 \pm 0.130^{**}$	$-0.95 \pm 0.281^{***}$	-0.15 ± 0.314	-0.11 ± 0.199	0.62 ± 0.366
Cursorial spiders						
Activity-density	CMP	$-0.47 \pm 0.107^{***}$	-0.22 ± 0.161	0.14 ± 0.126	$0.49 \pm 0.139^{***}$	0.20 ± 0.216
Species richness	CMP	-0.08 ± 0.088	0.22 ± 0.126	0.05 ± 0.125	0.12 ± 0.121	-0.03 ± 0.174
TOTAL						
Activity-density	CMP	$-0.55 \pm 0.100^{***}$	$-0.47 \pm 0.161^{**}$	0.07 ± 0.271	$0.78 \pm 0.127^{***}$	$0.58 \pm 0.205^{**}$
Species richness	CMP	$-0.18 \pm 0.077^*$	-0.05 ± 0.115	-0.07 ± 0.137	$0.21 \pm 0.104^*$	0.24 ± 0.155
CWM Diet	Beta	-0.11 ± 0.187	-0.32 ± 0.266	-0.37 ± 0.546	$-0.54 \pm 0.249^*$	-0.44 ± 0.373
FDvar Diet	Beta	0.21 ± 0.163	0.33 ± 0.234	0.21 ± 0.534	0.26 ± 0.227	0.48 ± 0.323
CWM Body length	Gaussian	$0.84 \pm 0.221^{***}$	0.53 ± 0.350	0.42 ± 0.999	-0.38 ± 0.313	0.01 ± 0.495
FDvar Body length	Beta	$0.41 \pm 0.123^{***}$	0.02 ± 0.194	0.24 ± 0.454	$-0.76 \pm 0.173^{***}$	0.17 ± 0.273

Table A1. Single trait indices. S is total number of species, w_i is the relative abundance of species i and x_i is the trait value for species i . FDvar modified is used for variables that contain 0 values.

Name	Abbreviation	Formula
Community-weighted mean	CWM	$\sum_{i=1}^S w_i x_i$
Functional divergence	FDvar	$\frac{2}{\pi} \arctan \left[5 \left(\sum_{i=1}^S w_i (\ln x_i - \overline{\ln x})^2 \right) \right]$
		$\overline{\ln x} = \sum_{i=1}^S w_i \ln x_i$
	FDvar modified	$\sum_{i=1}^S w_i (x_i - \bar{x})^2$
		$\bar{x} = CWM$

Table A2. Functional trait values of carabid and cursorial spider species (diet; granivorous: 0, omnivorous: 0.5 and carnivorous: 1). References are given in Supplementary Material.

Code	Latin name	Diet	Body length (mm)
Carabids			
Acin.pici	<i>Acinopus picipes</i>	0	14.5
Acup.meri	<i>Acupalpus meridianus</i>	1	3.625
Agon.muel	<i>Agonum muelleri</i>	0.5	7.5
Amar.sp	<i>Amara</i> spp.	0	7.5
Anch.dors	<i>Anchomenus dorsalis</i>	1	6.5
Anis.bino	<i>Anisodactylus binotatus</i>	0	10.5
Asap.stie	<i>Asaphidion stierlini</i>	1	3.5
Badi.bull	<i>Badister bullatus</i>	1	5.25
Bemb.sp	<i>Bembidion</i> spp.	1	NA
Brac.crep	<i>Brachinus crepitans</i>	0.5	8.25
Brac.expl	<i>Brachinus explodens</i>	1	5.75
Cala.fusc	<i>Calathus fuscipes</i>	0.5	12.5
Call.luna	<i>Callistus lunatus</i>	1	6
Cara.aura	<i>Carabus auratus</i>	1	23.5
Cara.purp	<i>Carabus purpurascens</i>	0.5	28.5
Chla.chry	<i>Chlaenius chrysocephalus</i>	1	8.5
Cici.camp	<i>Cicindela campestris</i>	1	12.75
Cyli.germ	<i>Cylindera germanica</i>	1	9.5
Deme.atri	<i>Demetrius atricapillus</i>	1	5
Diac.germ	<i>Diachromus germanus</i>	0	8.75
Harp.affi	<i>Harpalus affinis</i>	0	10.25
Harp.cupr	<i>Harpalus cupreus</i>	0	12.75
Harp.dimi	<i>Harpalus dimidiatus</i>	0	12.5
Harp.dist	<i>Harpalus distinguendus</i>	0.5	9.5
Harp.obli	<i>Harpalus oblitus</i>	0	10
Harp.pygm	<i>Harpalus pygmaeus</i>	0	6.125
Harp.smar	<i>Harpalus smaragdinus</i>	0	9.5
Harp.tene	<i>Harpalus tenebrosus</i>	0	9
Leis.fulv	<i>Leistus fulvibarbis</i>	1	7.5
Lori.pili	<i>Loricera pilicornis</i>	1	7.25
Meta.lamp	<i>Metallina lampros</i>	1	3.125
Meta.prop	<i>Metallina properans</i>	1	3.5

Micr.sp	<i>Microlestes</i> spp.	1	2.5
Nebr.brev	<i>Nebria brevicollis</i>	1	11.5
Nebr.sali	<i>Nebria salina</i>	1	11
Noti.bigu	<i>Notiophilus biguttatus</i>	1	4.875
Noti.quad	<i>Notiophilus quadripunctatus</i>	1	4.625
Opho.ardo	<i>Ophonus ardosiacus</i>	0	12
Opho.azur	<i>Ophonus azureus</i>	0	7.75
Paro.mend	<i>Parophonus mendax</i>	0	7.75
Phil.bigu	<i>Philochthus biguttatus</i>	1	3.625
Phil.gutt	<i>Philochthus guttula</i>	1	2.875
Poec.cupr	<i>Poecilus cupreus</i>	0.5	11
Pseu.rufi	<i>Pseudoophonus rufipes</i>	0.5	13.5
Pter.madi	<i>Pterostichus madidus</i>	0.5	16.5
Sten.skri	<i>Stenolophus skrimshiranus</i>	0.5	5.875
Stom.pumi	<i>Stomis pumicatus</i>	1	7
Synt.obsc	<i>Syntomus obscuroguttatus</i>	1	2.875
Trec.sp	<i>Trechinii</i> spp.	1	3.55
Zabr.tene	<i>Zabrus tenebrioides</i>	0	15

Cursorial spiders

Agra.line	<i>Agraecina lineata</i>	1	6.1
Agro.lusa	<i>Agroeca lusatica</i>	1	5.3
Alop.albo	<i>Alopecosa albofasciata</i>	1	9.8
Alop.cune	<i>Alopecosa cuneata</i>	1	7.3
Alop.pulv	<i>Alopecosa pulverulenta</i>	1	8.5
Arct.peri	<i>Arctosa perita</i>	1	7
Aulo.albi	<i>Aulonia albimana</i>	1	4.1
Chal.nigr	<i>Chalcoscirtus nigrinus</i>	1	3.5
Civi.civi	<i>Civizelotes civicus</i>	1	4.4
Dipl.grae	<i>Diplocephalus graecus</i>	1	1.9
Dras.lapi	<i>Drassodes lapidosus</i>	1	10.8
Dras.pube	<i>Drassodes pubescens</i>	1	7.1
Dras.lute	<i>Drassyllus lutetianus</i>	1	5.7
Dras.pumi	<i>Drassyllus pumilus</i>	1	3.8
Dras.pusi	<i>Drassyllus pusillus</i>	1	4.4
Dras.prae	<i>Drassyllus praeficus</i>	1	6.2

Dysd.eryt	<i>Dysdera erythrina</i>	1	9.3
Erig.dent	<i>Erigone dentipalpis</i>	1	2.3
Hapl.dalm	<i>Haplodrassus dalmatensis</i>	1	5.4
Hapl.sign	<i>Haplodrassus signifer</i>	1	7.3
Hogn.radi	<i>Hogna radiata</i>	1	16
Lasi.hirs	<i>Lasiargus hirsutus</i>	1	2.6
Liop.flav	<i>Liophrurillus flavitarsis</i>	1	5
Merm.tril	<i>Mermessus trilobatus</i>	1	1.9
Mica.albo	<i>Micaria albovittata</i>	1	5.3
Mica.puli	<i>Micaria pulicaria</i>	1	3.6
Micr.aper	<i>Micrargus apertus</i>	1	1.9
Nomi.exor	<i>Nomisia exornata</i>	1	5.9
Oedo.apic	<i>Oedothorax apicatus</i>	1	2.6
Ozyp.simp	<i>Ozyptila simplex</i>	1	3.5
Pard.agre	<i>Pardosa agrestis</i>	1	4.8
Pard.hort	<i>Pardosa hortensis</i>	1	5.2
Pard.nigr	<i>Pardosa nigriceps</i>	1	5.4
Pard.palu	<i>Pardosa palustris</i>	1	6
Pard.prat	<i>Pardosa prativaga</i>	1	6.1
Pard.prox	<i>Pardosa proxima</i>	1	6.7
Pard.pull	<i>Pardosa pullata</i>	1	4.8
Pard.salt	<i>Pardosa saltans</i>	1	5.8
Pard.vitt	<i>Pardosa vittata</i>	1	6.2
Pele.para	<i>Pelecopsis parallela</i>	1	1.5
Phle.bres	<i>Phlegra bresnieri</i>	1	5
Phru.fest	<i>Phrurolithus festivus</i>	1	2.7
Phru.nigr	<i>Phrurolithus nigrinus</i>	1	2.8
Poca.junc	<i>Pocadicnemis juncea</i>	1	1.9
Seta.carm	<i>Setaphis carmeli</i>	1	4
Sibi.auro	<i>Sibianor aurocinctus</i>	1	3.4
Tala.aper	<i>Talavera aperta</i>	1	2.5
Than.atra	<i>Thanatus atratus</i>	1	4.6
Tibe.oblo	<i>Tibellus oblongus</i>	1	7.6
Trac.fusc	<i>Trachyzelotes fuscipes</i>	1	4.6
Trac.pede	<i>Trachyzelotes pedestris</i>	1	6.6
Troc.hisp	<i>Trochosa hispanica</i>	1	10.5

Troc.robust	<i>Trochosa robusta</i>	1	14
Walck.capito	<i>Walckenaeria capito</i>	1	2.7
Xyst.acerbus	<i>Xysticus acerbus</i>	1	6.5
Xyst.cristatus	<i>Xysticus cristatus</i>	1	5.6
Xyst.kochi	<i>Xysticus kochi</i>	1	6.6
Zelotes.atrocaeruleus	<i>Zelotes atrocaeruleus</i>	1	6.9
Zelotes.latreillei	<i>Zelotes latreillei</i>	1	6.7
Zelotes.petrensis	<i>Zelotes petrensis</i>	1	5.8
Zodarion.italicum	<i>Zodarion italicum</i>	1	2.7
Pardosa spp.	<i>Pardosa</i> spp.	1	5.7
Xysticus spp.	<i>Xysticus</i> spp.	1	6
Zelotes spp.	<i>Zelotes</i> spp.	1	6.5

Figure 1

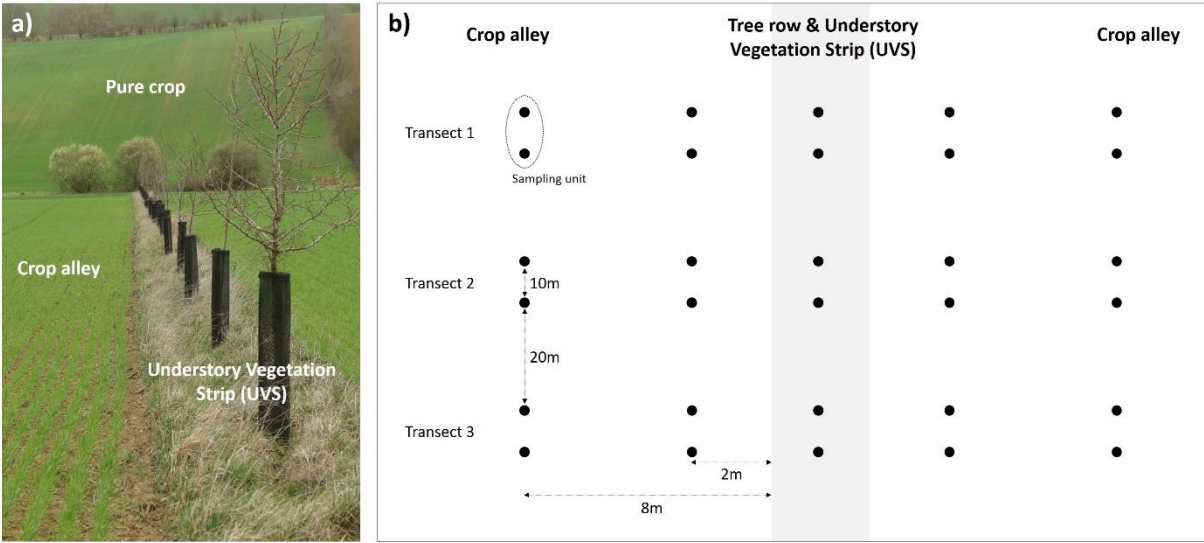


Figure 2

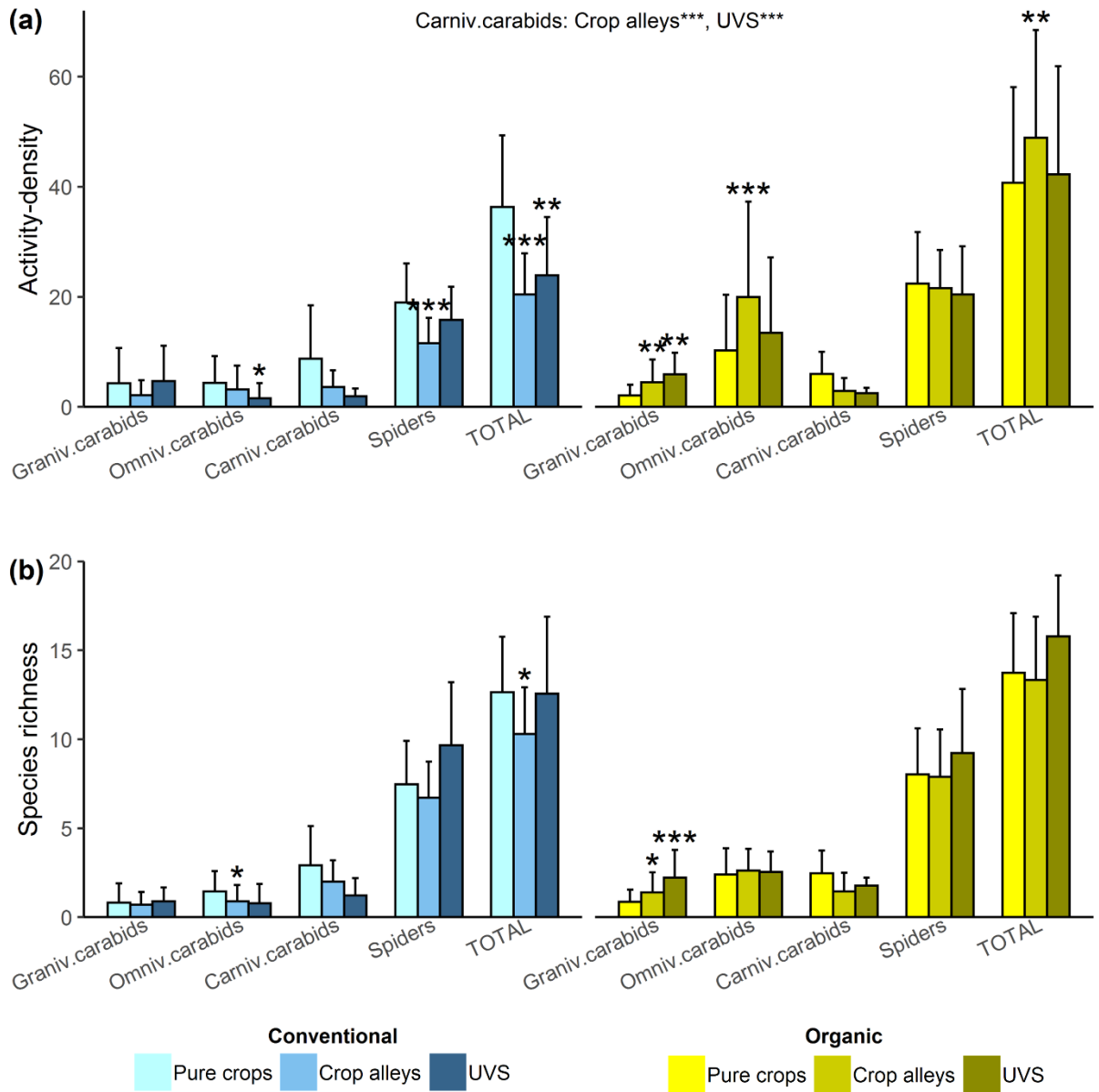


Figure 3

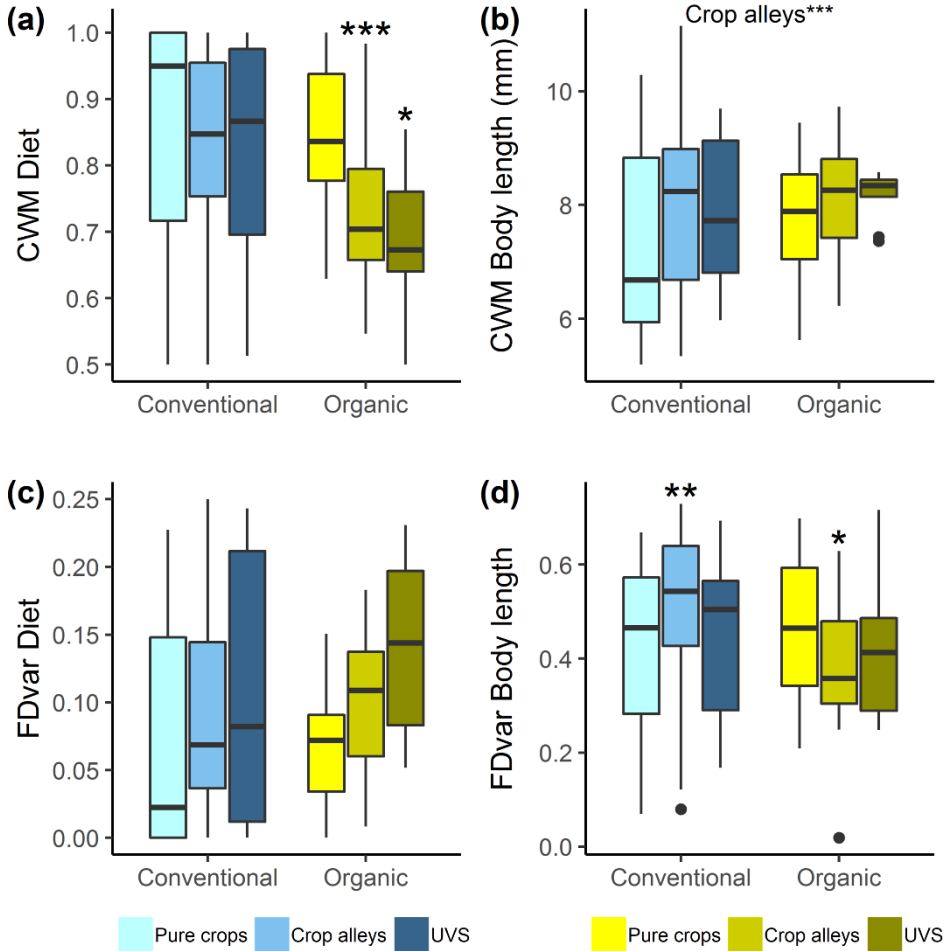
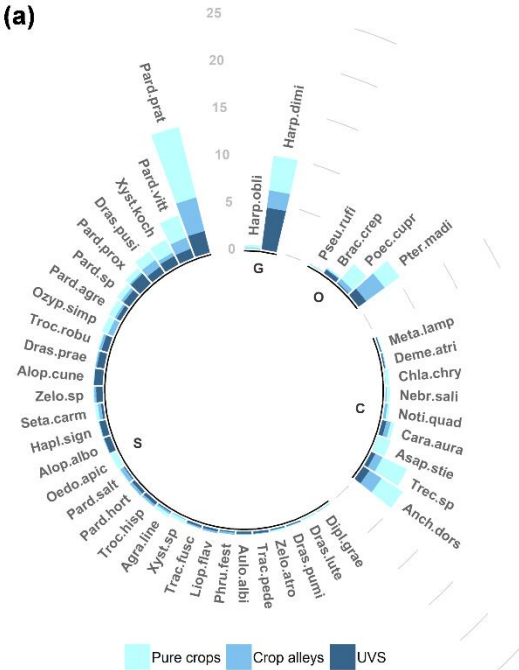


Figure A1

(a)



(b)

