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# Distribution of overwintering invertebrates in temperate agroforestry systems: Implications for biodiversity conservation and biological control of crop pests

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1 **Distribution of overwintering invertebrates in agroforestry systems: implications for**  
2 **biodiversity conservation and biological control of crop pests**

3

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22

23 **Declaration of interest:** none

24

25 The dramatic decline of invertebrates at a global scale is mainly driven by habitat loss,  
26 agricultural intensification and urbanization. Alley cropping agroforestry is a land use practice  
27 in which arable crops are grown between tree rows. In such systems, understory vegetation  
28 strips (UVS) develop in the tree rows, providing habitats undisturbed by soil tillage. We  
29 investigated whether UVS are major overwintering habitats for invertebrates. We focused on  
30 carabid communities, which are dominant beneficial invertebrates in crop fields, but suffer  
31 from agricultural intensification. We described carabid communities with functional traits  
32 related to sensitivity to agricultural disturbances and ecological functions (i.e. pest control).  
33 Sampling of invertebrates were carried out from February to June 2018 over seven  
34 agroforestry fields in Restinclières Estate (South France), one of the oldest experimental sites  
35 in Europe. The study revealed that 55% of invertebrate taxonomic groups were more  
36 abundant in UVS, whereas only 14% were more abundant in crop alleys. Crop pests were  
37 overwintering mainly in crop alleys while beneficial invertebrates were more dependent on  
38 UVS. Finally, UVS hosted carabids sensitive to agricultural disturbances, characterized by  
39 larger body length, predominantly granivorous diet and overwintering in adult stage. On the  
40 other hand, crop alleys were home to smaller carnivorous species overwintering in both larval  
41 and adult stages, which can tolerate high levels of disturbance. Environmental and agricultural  
42 policies should consider agroforestry systems, especially understory vegetation strips, as  
43 valuable habitats for biodiversity conservation and biological control in agricultural  
44 landscapes.

45

46

47 **Keywords:** alley cropping, understory vegetation strip, semi-natural habitat, natural enemy,  
48 carabid beetle, functional trait

49

## 50 **1. Introduction**

51

52 The dramatic decline of invertebrates at a global scale is mainly driven by habitat loss and  
53 conversion to intensive agriculture and urbanization (Sánchez-Bayo and Wyckhuys, 2019;  
54 Habel et al., 2019). Semi-natural habitats are of major importance for the survival of  
55 invertebrates, especially by offering them resources and overwintering habitats undisturbed by  
56 soil tillage (Pywell et al., 2005; Mallinger et al., 2016). Indeed, ploughing significantly  
57 reduces the emergence of many invertebrates (Holland and Reynolds, 2003; Ganser et al.,  
58 2019). Moreover, the success of hibernation is a key factor driving the population dynamics in  
59 crops during spring and summer (Leather et al., 1993). Thus, overwintering success of  
60 invertebrates in uncropped habitats has a direct influence on the conservation of higher  
61 trophic taxa such as birds and mammals, by conditioning resource availability. The presence  
62 of suitable overwintering habitats also has an impact on the agroecosystem functioning. It can  
63 reduce crop yields if it promotes the spillover of emerging crop pests within fields, or  
64 conversely increase crop yields if it favors the dispersal of beneficial invertebrates such as  
65 pollinators and predators of crop pests (Blitzer et al., 2012). Agri-environmental measures are  
66 more and more implemented for reconciling crop production with the conservation of  
67 biodiversity and the ecosystem services it provides. For example, sown grass strips,  
68 wildflower strips and conservation headlands can take place in field margins, providing  
69 resources and overwintering habitats for invertebrates (Smith et al., 2008; Feltham et al.,  
70 2015; Ganser et al., 2019). Although these measures reduce the surface available for crop  
71 production, it can even lead to higher yields and economic profitability by promoting the  
72 dispersal of beneficial invertebrates within crops (Pywell et al., 2015), making production and  
73 biodiversity conservation compatible. However, if cropland dominates in the landscape, agri-  
74 environmental measures at field edges might not be sufficient for biodiversity conservation

75 and promotion of ecosystem service flows in cropland (Mitchell et al., 2015). Then,  
76 implementation needs to take place within fields themselves, as in the case of within-field  
77 wildflowers strips that support natural enemies of crop pests (Hatt et al., 2017).

78

79 Agroforestry is land use practice integrating woody vegetation (trees or shrubs) with  
80 crop and/or animal production systems. Such systems have been shown to provide a wide  
81 range of ecosystem services from the same area of land, such as sustainable food, timber and  
82 biomass production, soil and water protection, biodiversity conservation and carbon  
83 sequestration (Jose, 2009; Quinkenstein et al., 2009; Torralba et al., 2016; Kay et al., 2019).  
84 In temperate regions, alley cropping agroforestry systems, in which arable crops are grown  
85 between tree rows, represent a great opportunity for the reintegration of semi-natural habitats  
86 directly within fields. Indeed, the presence of tree rows entails the growth of understory  
87 vegetation strips (UVS) that are not disturbed by soil tillage. However, only a few studies  
88 have assessed the potential of alley cropping systems for enhancing biodiversity, most of  
89 them revealing promising results (Peng et al., 1993; Burgess, 1999; Stamps et al., 2002;  
90 Akbulut et al., 2003; Naeem et al., 2010; Smits et al., 2012; Varah et al., 2013), and even less  
91 have focused on the ecological functions of UVS. Boinot et al. (2019) showed that UVS  
92 constitute refugia for plant diversity, harboring species that are poorly tolerant to agricultural  
93 disturbances. Recent studies revealed that abundance and diversity of woodlice and millipedes  
94 (Pardon et al., 2019) and earthworms (Cardinael et al., 2019) were higher in UVS than in  
95 adjacent crop alleys. Yet these results were obtained in spring and to our knowledge, no study  
96 has described the distribution of overwintering invertebrates in agroforestry systems and  
97 assessed the potential of UVS in promoting successful overwintering of a wide range of  
98 invertebrates.

99           The objective of this study was to investigate the importance of understory vegetation  
100 strips (UVS) associated to tree rows in promoting successful overwintering of invertebrates  
101 within agroforestry fields, as opposed to crop alleys that are disturbed by soil tillage (in non-  
102 conservation agricultural systems). We also identified families of crop pests and beneficial  
103 invertebrates that were dominant during the survey. We gave a focus on carabid communities  
104 because (i) they suffer from agricultural intensification and can be used as bioindicators  
105 (Rainio and Niemelä, 2003; Brooks et al., 2012), (ii) they are common prey for other  
106 invertebrates, birds, micro-mammals, reptiles and amphibians (Holland, 2002; Laroche and  
107 Larivière, 2003), (iii) they are important predators of crop pests and weed seed consumers  
108 (Kromp, 1999; Bohan et al., 2011) and (iv) knowledge on carabid communities in  
109 agroforestry systems is currently poor (but see Martin-Chave et al., 2019; Pardon et al., 2019;  
110 Richard et al., 2019). We hypothesized that **1)** for most taxonomic groups, UVS are better  
111 overwintering habitats than crop alleys that are disturbed by soil tillage, which reduces the  
112 emergence of many invertebrates. Moreover, we hypothesize that **2)** crop pests successfully  
113 overwinter in crop alleys whereas beneficial invertebrates tend to be more dependent on UVS,  
114 because so-called “r-strategist” characterized by smaller size, shorter life-cycle and higher  
115 fecundity are generally performing better than “K-strategist” in highly disturbed habitats  
116 (Thomas et al., 1992; Schirmel et al., 2016). Finally, we expect that **3)** UVS are overwintering  
117 refugia for carabid species that are sensitive to agricultural disturbances, which are  
118 characterized by a unique overwintering stage (adult), large size and mixed diet (Table 1). On  
119 the other hand, small and exclusively carnivorous carabids that overwinter at both larval and  
120 adult stages can successfully spend the winter in disturbed crop alleys.

121

## 122 **2. Materials and Methods**

123

## 124 2.1. Study site

125

126 The study was conducted over seven agroforestry fields, in Restinclières Estate (South  
127 France, Hérault department), which is characterized by a Mediterranean climate with mild  
128 winters and warm summers. Trees were planted in 1995 on rows spaced 13 m apart (a list of  
129 tree species associated to sampled UVS can be found in Table S1 in Supplementary material,  
130 along with the area covered by UVS). Each field was cultivated by the same farmer, growing  
131 winter barley and winter wheat during the study (crop rotation is composed of winter wheat,  
132 winter barley and winter pea). Between crop harvest in summer and following sowing in  
133 autumn, crop alleys are dominated by spontaneous vegetation. A ploughing tillage was  
134 performed in October 2017, followed by one herbicide treatment and fertilization in February-  
135 March 2018. No insecticides were used and UVS, on average two meters wide, were  
136 composed of spontaneous vegetation rarely managed (one crush every five to six years).

137

## 138 2.2. Invertebrate sampling

139

140 Overwintering invertebrates were sampled from February 16<sup>th</sup> to June 15<sup>th</sup> within 0.36 m<sup>2</sup>  
141 emergence traps buried up to 10 cm in the ground. Per field, five emergence traps at least 10  
142 m apart were set up in one understory vegetation strip and compared to five emergence traps  
143 in the adjacent crop alley (Figure 1). Due to damage caused by boars, the dataset was  
144 restricted to a total of 51 emergence traps, which were undamaged during the whole  
145 experiment ( $n = 26$  in UVS and  $n = 25$  in crop alleys). Each emergence trap contained an  
146 aerial trap for flying and climbing invertebrates and a pitfall trap at ground level for ground-  
147 dwellers. Traps were filled with propylene glycol and collected every two weeks. All  
148 individuals found within traps (whether they were adults or larvae) were identified to the

149 order level using the guide from Chinery (2012). Families of dominant crop pests and  
150 beneficial invertebrates were also recorded. Adult carabid beetles were identified to the  
151 species level using Jeannel (1941), Jeannel (1942), Coulon et al. (2011a) and Coulon et al.  
152 (2011b).

153

154 **Figure 1.** Emergence traps used for sampling overwintering invertebrates in agroforestry  
155 fields (Restinclières Estate, South France, Hérault department).

156

### 157 *2.3. Functional structure of overwintering carabid communities*

158

159 We used a functional approach to describe the dominant life strategies in crop alleys vs UVS,  
160 but also to assess the nature and intensity of ecosystem services provided by carabid  
161 communities in each habitat. We described overwintering carabid communities with  
162 functional traits related to sensitivity to agricultural disturbances and ecological functions (i.e.  
163 crop pest control) (Table 1). Functional trait values were collected in databases (Hedde et al.,  
164 2012; Homburg et al., 2014) and through an extensive research in literature (Thiele, 1977;  
165 Ribera et al., 1999; Ribera et al., 2001; Woodcock et al., 2010; Jaskuła and Soszyńska-Maj,  
166 2011; Petit et al., 2011; Pilon et al., 2013; Birkhofer et al., 2014; Marrec et al., 2015; Talarico  
167 et al., 2016; Hanson et al., 2017).

168

169 Community-weighted mean (CWM) and functional divergence (FDvar) of each trait  
170 were then computed for carabid communities sampled in each emergence trap, following  
171 Garnier and Navas (2012) and Schleuter et al. (2010). Formulas are given in Table A1 in  
172 Appendix A. CWM corresponds to the average of trait values weighted by the relative  
173 abundance of each species. FDvar is an expression of the variance of trait values within a



174 community, weighted by the relative abundance of each species. FDvar varies from 0 to 1; it  
175 is low if species and/or abundances are clustered around the mean trait value, whereas it is  
176 high if they are clustered towards one or both margins of the trait distribution. This metric is  
177 relevant for assessing to what extent functional attributes are constrained by natural or  
178 anthropogenic selection, but also for assessing complementarity between species (Woodcock  
179 et al., 2019). Regarding biological control, it is expected that predator communities  
180 characterized by different ecological strategies (i.e. non-overlapping trait distributions)  
181 control more efficiently a wide range of crop pests.

182

183 **Table 1.** Carabid functional traits related to sensitivity to agricultural disturbances and  
184 ecological functions.

185

#### 186 *2.4. Data analysis*

187

188 To assess hypotheses 1 and 2, we used generalized linear mixed effects models (GLMMs) and  
189 compared the total density of each taxonomic group per emergence trap between UVS and  
190 crop alleys. Fields were included as a random effect on the intercept to take into account the  
191 spatial auto-correlation between emergence traps located in a same field. To assess hypothesis  
192 3, we described the functional structure of carabid communities with traits related to  
193 sensitivity to agricultural disturbances. GLMMs were used to compare CWM and FDvar of  
194 each trait between UVS and crop alleys. Density (individuals / m<sup>2</sup>) and species richness were  
195 assumed to follow a Poisson distribution, CWM of body length was assumed to follow a  
196 Gaussian distribution and all other variables (proportional CWM and FDvar varying from 0 to  
197 1) were assumed to follow a Beta distribution. When proportional variables included 0 and/or  
198 1 value(s), the transformation  $(Y \times (N - 1) + 0.5) / N$  was employed following Zuur et al.

199 (2013), where Y is the response variable and N is the sample size. We used the package lme4  
200 for fitting Gaussian LMMs (Bates et al., 2015) and the package glmmTMB (Brooks et al.,  
201 2017) for fitting Poisson and Beta GLMMs (with the link functions log and logit  
202 respectively). When Poisson GLMMs revealed over-dispersion, Conway-Maxwell-Poisson  
203 GLMMs were fitted instead as suggested by Lynch et al. (2014). All figures were built using  
204 raw data. All analyses were performed using the statistical software R 5.1 (R Core Team,  
205 2018).

206

### 207 **3. Results**

208

209 Many taxonomic groups of invertebrates were found during the survey, with huge differences  
210 in abundance and relative proportion: Homoptera ( $n = 46441$ , 47%), Coleoptera ( $n = 13324$ ,  
211 13%), Diptera ( $n = 12466$ , 13%), Hymenoptera ( $n = 8187$ , 8%), Collembola ( $n = 7907$ , 8%),  
212 Myriapoda ( $n = 2257$ , 2%), Araneae ( $n = 1885$ , 2%), Isopoda ( $n = 1778$ , 2%),  
213 Stylommatophora ( $n = 1429$ , 1%). There were also other groups below 1%: Acarina ( $n =$   
214 785), Dermaptera ( $n = 762$ ), Heteroptera ( $n = 528$ ), Orthoptera ( $n = 354$ ), Psocoptera ( $n =$   
215 323), Blattoptera ( $n = 239$ ), Lepidoptera ( $n = 172$ ), Opiliones ( $n = 75$ ), Neuroptera ( $n = 21$ ),  
216 Pseudoscorpionida ( $n = 19$ ), Thysanoptera ( $n = 14$ ), Thysanura ( $n = 5$ ), Trichoptera ( $n = 4$ ),  
217 Megaloptera ( $n = 2$ ). Density differences between UVS and crop alleys could not be  
218 statistically tested for Thysanura, Trichoptera and Megaloptera because too few individuals  
219 were captured. This was also the case for Apoidae family ( $n = 3$ ). Regarding carabid beetles, a  
220 total of 1538 individuals belonging to 50 species were collected.

221

#### 222 *3.1. Overwintering invertebrates in crop alleys and understory vegetation strips*

223

224 Out of the 22 invertebrate taxonomic groups found during the survey, 12 were more abundant  
225 in UVS whereas only 3 were more abundant in crop alleys (Figure 2, Table 2).

226

227 **Table 2.** Results of Conway-Maxwell-Poisson GLMMs comparing invertebrate density  
228 (individuals / m<sup>2</sup>) between crop alleys (reference level) and understory vegetation strips.

229

230 **Figure 2.** Mean and standard deviation of group density (individuals / m<sup>2</sup>) in crop alleys and  
231 understory vegetation strips (UVS). Only groups showing significant differences in density  
232 between habitats were represented (see Figure S1 in Supplementary material for other  
233 groups). Stars indicate significant difference between crop alleys and UVS at 0.05 threshold  
234 based on p-values of GLMMs (\* P ≤ 0.05, \*\* P ≤ 0.01, \*\*\* P ≤ 0.001).

235

### 236 *3.2. Overwintering of crop pests vs beneficial invertebrates*

237

238 Crop pests (i.e. Aphidae, Elateridae and slugs) overwintered predominantly in crop alleys  
239 (Figure 3, Table 2). On the other hand, snails were more abundant in UVS. The response was  
240 less dichotomic for the families of beneficial invertebrates considered in this study.

241 Coccinellidae, Formicidae and Chrysopidae overwintered mostly in UVS, whereas Carabidae,  
242 Staphylinidae and Syrphidae were more abundant in crop alleys.

243

244 **Figure 3.** Mean and standard deviation of dominant crop pest and beneficial invertebrate  
245 density (individuals / m<sup>2</sup>) in crop alleys and understory vegetation strips (UVS). Stars indicate  
246 significant difference between crop alleys and UVS at 0.05 threshold based on p-values of  
247 GLMMs (\* P ≤ 0.05, \*\* P ≤ 0.01, \*\*\* P ≤ 0.001).

248

249 3.3. Functional structure of overwintering carabid communities

250

251 There was a clear shift in the functional structure of carabid communities between habitats in  
252 agroforestry systems. UVS hosted larger carabids than crop alleys (Figure 4, Table 3). Crop  
253 alleys hosted mainly carnivorous species, such as *Trechus quadristriatus*, *Metallina lampros*  
254 and *Apotomus rufus*, whereas predominantly granivorous species, such as *Ophonus azureus*,  
255 *Parophonus mendax* and *Harpalus dimitiatus*, were clearly associated to UVS (Figure 4,  
256 Table 3, see Figure S2 in Supplementary Material for the analysis of species composition).  
257 The response was more variable for omnivorous species; *Brachinus crepitans* and *Scybalicus*  
258 *oblongiusculus* were associated to UVS whereas *Phyla obtusa* was more abundant in crop  
259 alleys and *Pseudoophonus rufipes* was found equally in both habitats. Finally, CWM and  
260 FDvar of overwintering stages were respectively close to 1 and 0 in UVS, indicating that  
261 species overwintering in adult stage were strongly dependent on the presence of UVS (Figure  
262 4, Table 3). On the other hand, species overwintering in both larval and adult stages were  
263 found in high abundances in crop alleys.

264

265 **Table 3.** Results of GLMMs comparing species richness and functional structure of carabid  
266 communities between crop alleys (reference level) and understory vegetation strips.

267

268 **Figure 4.** Functional structure of carabid communities overwintering in crop alleys vs  
269 understory vegetation strips (UVS). (a) Community-weighted mean (CWM) of body length;  
270 (b) CWM of diet (granivorous: 0, omnivorous: 0.5 and carnivorous: 1); (c) CWM of  
271 overwintering stage (overwintering in both larval and adult stages: 0, overwintering in adult  
272 stage: 1); (d) Functional divergence (FDvar) of body length; (e) FDvar of diet; (f) FDvar of

273 overwintering stage. Stars indicate significant difference at 0.05 threshold based on p-values  
274 of GLMMs (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ).

275

## 276 **4. Discussion**

277

278 Our study on the distribution of overwintering invertebrates in agroforestry systems revealed  
279 that understory vegetation strips (UVS) are home to a wide range of overwintering  
280 invertebrates, as opposed to crop alleys. Crop pests overwintered predominantly in crop alleys  
281 while beneficial invertebrates were often associated to UVS. Moreover, carabid species that  
282 are sensitive to agricultural disturbances were overwintering mostly in UVS.

283

### 284 *4.1. Understory vegetation strips provide overwintering habitats for many invertebrates*

285

286 Even if UVS are surrounded by crop alleys, with potential disturbances induced by pesticides  
287 and fertilizers drifts, our results show that UVS are semi-natural habitats of major importance  
288 for invertebrate conservation. Indeed, 55% of the taxonomic groups of invertebrates found  
289 during the survey were more abundant in UVS whereas only 14% were more abundant in crop  
290 alleys. This is in line with previous studies showing that semi-natural habitats provide suitable  
291 habitats for overwintering invertebrates (Sotherton, 1984; Pfiffner and Luka, 2000; Pywell et  
292 al., 2005; Geiger et al., 2009; Schaffers et al., 2012; Sutter et al., 2017). Butterflies,  
293 characterized by a high degree of host-plant specialization and sensitivity to habitat  
294 degradation, are drastically declining in many European countries (van Strien et al., 2019).  
295 Lepidoptera (butterflies and moths confounded) were more abundant in UVS, indicating that  
296 this habitat has higher environmental quality than crop alleys. Detritivores (Collembola,  
297 Isopoda, some Acarina and Blattoptera) were also more abundant in UVS, which is not

298 surprising given the permanent litter quantity available at the ground level, although  
299 Myriapoda (Diplopoda and Chilopoda confounded) were more abundant in crop alleys. All  
300 Arachnida groups found during the survey (Acarina, Araneae, Opiliones and  
301 Pseudoscorpionida) were overwintering in great majority in UVS. Araneae are not able to dig  
302 into the soil to find refuges and rely on the presence of vegetation and crevices for  
303 overwintering (Lemke and Poehling, 2002). This seems to be the case for Opiliones too,  
304 which are favored by the presence of grassy field margins in spring and autumn (Holland et  
305 al., 2016). However, Apoidae did not seem to overwinter in UVS, neither in crop alleys. They  
306 probably preferred overwintering habitats located outside the fields, such as grasslands and  
307 scrublands, which are very diversified in Restinclières Estate (Smits et al., 2012). UVS cover  
308 about 3 to 13% of the available agricultural area and thus greatly enhance the conservation of  
309 plants (Boinot et al., 2019) and invertebrates directly within crop fields. Moreover, trees and  
310 shrubs associated to UVS were not sampled in this study, but are very likely to offer  
311 permanent overwintering habitats for invertebrates (Dix et al., 1995); Stamps and Linit,  
312 1998). Further studies should assess to what extent improved plant and invertebrate resources  
313 in agroforestry systems favor higher trophic taxa such as threatened farmland species (Donald  
314 et al., 2001; Fischer et al., 2011).

315

316 *4.2. Crop pests and beneficial invertebrates are not equally dependent on undisturbed*  
317 *habitats for overwintering*

318

319 Overall, beneficial invertebrates were more dependent on UVS for overwintering, considering  
320 groups composed in majority of detritivore species (Collembola, Isopoda, Acarina,  
321 Blattoptera and Myriapoda), predators (Araneae, Opiliones, Carabidae, Staphylinidae,  
322 Syrphidae, Chrysopidae, Coccinellidae) and weed controllers (predominantly granivorous

323 carabids and harvester ants). However, Syrphidae, Carabidae and Staphylinidae were more  
324 abundant in crop alleys. We found only two species of Syrphidae: *Episyrphus balteatus* and  
325 *Sphaerophoria scripta*. Raymond et al. (2014) showed that these aphidophagous syrphid  
326 species mainly overwinter in crop fields whereas non aphidophagous species preferred field  
327 margins. Many species of Carabidae and Staphylinidae are also major predator of aphids  
328 (Sunderland and Vickerman, 1980), which could explain their higher presence in crop alleys,  
329 where aphids were overwintering. On the other hand, lacewings (aphid predators) were found  
330 in UVS. Coccinellidae, both carnivorous species such as *Scymnus* spp. and mycophagous ones  
331 such as *Psyllobora vigintiduopunctata*, also preferred UVS and often overwintered in  
332 aggregated groups. Formicidae, which can control crop pests, weeds and plant diseases  
333 depending on the species (Offenberg, 2015), were also more abundant in UVS.

334

335 On the other hand, crop pests overwintered predominantly in crops, which could  
336 explain higher probability of pest outbreaks when suitable overwintering habitats for  
337 predators are missing (Bianchi et al., 2006; Rusch et al., 2016). Homoptera were much more  
338 abundant in crop alleys, a result driven by aphids which probably reproduced under the  
339 emergence traps and benefited from their protection. Elateridae and slugs were also  
340 overwintering predominantly in crop alleys. Griffiths et al. (1998) showed that slugs were  
341 more abundant in agroforestry fields than in pure crop controls, however our results suggest  
342 that this would not be due to the presence of less disturbed overwintering habitats in  
343 agroforestry fields. Slugs might have been favored by a more suitable microclimate in  
344 agroforestry fields. Finally, snails were the only dominant crop pest more abundant in UVS.

345

346 It is likely that species overwintering in UVS are strongly dependent on semi-natural  
347 habitats for overwintering and thus poorly represented in the field core of pure crops. Indeed,

348 many studies have shown that habitats such as hedges, wildflower strips or grassy field  
349 margins provide more suitable overwintering habitats than arable land (e.g. Pfiffner and Luka,  
350 2000; Ganser et al., 2019). This explains why so-called “edge-effects” or “edge-biased  
351 distribution” are frequently observed among invertebrates, resulting in decreased abundance  
352 and diversity in the field core (Rand et al., 2006; Nguyen and Nansen, 2018). The great extent  
353 and spatial configuration of UVS could promote the spillover of many invertebrates between  
354 cropped and uncropped habitats, especially regarding poorly dispersive species that hardly  
355 move between field edges and field cores, such as some Carabidae species (e.g. *Amara*  
356 species, *Metallina lampros*) and spiders of the Lycosidae family (Holland et al., 1999). Then,  
357 a wide range of overwintering predators, from specialist to generalist and from ground-  
358 dwelling to aerial ones, would improve biological control in agroforestry systems through a  
359 process of complementarity and additive effects (Woodcock et al., 2016). On the other hand,  
360 if intra-guild predation or competition is enhanced, this could reduce the efficiency of  
361 predator community to control crop pests, although field studies generally contradict this  
362 hypothesis (Woodcock et al., 2016). Finally, semi-natural habitats have also been shown to  
363 have negative impacts on the dispersal of invertebrates, especially agrobiont ones, by either  
364 acting as a sink habitat or a physical barrier (Holland et al., 2009). Further studies are thus  
365 needed to assess the positive and negative impacts of the presence of UVS on the dispersal of  
366 a wide range of invertebrates, from emergence to the return in semi-natural habitats at the end  
367 of the season or cycle.

368

#### 369 4.3. Understory vegetation strips are refugia for sensitive carabid species

370

371 Although Carabidae were overall more abundant in crop alleys, this varied from one species  
372 to another according to their sensitivity to agricultural disturbances. Higher density of carabid



373 beetles in crop alleys is explained by the dominance of small carabids with higher  
374 reproductive output such as *Trechus quadristriatus*, *Metallina lampros* or *Apotomus rufus*. On  
375 the other hand, UVS hosted carabid species with higher sensitivity to agricultural disturbances  
376 (such as *Harpalus dimidiatus*, *Parophonus mendax* and *Ophonus* spp.), which are  
377 characterized by a unique overwintering stage (adult), a large body length and a  
378 predominantly granivorous diet (Holland et al., 2009; Vanbergen et al., 2010; Winqvist et al.,  
379 2014; da Silva et al., 2017; Baulechner et al., 2019). This is in line with the results of Hanson  
380 et al. (2016), who demonstrated that increasing management intensity reduces the average  
381 body size of overwintering carabid beetles and the proportion of mixed feeders. Such  
382 sensitive species probably moved to undisturbed UVS after crop harvest and/or suffered from  
383 ploughing in crop alleys, which is known to greatly reduce the emergence of many  
384 invertebrates (Holland and Reynolds, 2003; Ganser et al., 2019). Our results also confirm that  
385 overwintering stage is an important trait explaining the response of carabid beetles to  
386 agricultural disturbances. Species overwintering in both larval and adult stages are able to  
387 adapt to environmental changes by shifting their reproductive period and are also more likely  
388 to tolerate fluctuating biotic and abiotic conditions, given that they are composed of different  
389 age classes (Nolte et al., 2017).

390

391 A negative relationship was observed between the community-average value of body  
392 size of ground-dwelling predators and predation rates of aphids (Rusch et al., 2015).  
393 Presumably, smaller carnivorous species at larval stage were overwintering in crop alleys both  
394 to consume aphids and to avoid intra-guild predation by larger carabids or spiders found in  
395 UVS, which hardly tolerate tillage disturbances. Indeed, many species found abundantly in  
396 crop alleys, such as *Anchomenus dorsalis*, *Metallina lampros* and *Trechus quadristriatus*, are  
397 known to feed on aphids (Sunderland and Vickerman, 1980; Sunderland et al., 1987; Hedde et

398 al., 2012). Given their differences in terms of phenology, body length and habitat preferences,  
399 carabids that overwinter predominantly in crop alleys and those associated to UVS can be  
400 complementary. Such complementarity could lead to enhanced biological control in  
401 agroforestry fields, whereas large carabids and mixed feeders are particularly affected by crop  
402 management in fields with high land-use intensity (Hanson et al., 2016). A successful  
403 overwintering of large carabid species within agroforestry fields could enhance the control of  
404 a wider range of prey (Rouabah et al., 2014), provided that these species do disperse towards  
405 crop alleys after emergence. Moreover, the spread of granivorous and omnivorous species that  
406 overwinter in UVS should be favored in agroforestry field core, whereas these species need to  
407 cover larger distances to recolonize pure crops after emergence from adjacent habitats.  
408 Species that consume weed seeds can help reduce weed pressure (Menalled et al., 2007;  
409 Bohan et al., 2011). Overall, these results suggest that carabid communities in agroforestry  
410 systems are likely to offer various and enhanced ecosystem services compared to those  
411 associated to crop fields or restricted to adjacent habitats, which are too far from the field  
412 core. This effect of agroforestry systems on the functional structure of carabid communities  
413 should be of particular interest in intensively cultivated agricultural landscapes, where semi-  
414 natural habitats are missing.

415

## 416 **5. Conclusions**

417

418 The massive decline of invertebrates is driven by habitat loss, intensive agricultural practices  
419 and urbanization. This study revealed that understory vegetation strips are home to a wide  
420 range of overwintering invertebrates in agroforestry systems, as opposed to crop alleys. Crop  
421 pests overwintered predominantly in crop alleys while beneficial invertebrates were often  
422 associated to understory vegetation strips. Carabid species that are sensitive to agricultural

423 disturbances were overwintering mostly in understory vegetation strips. The presence of rich  
424 invertebrate communities within understory vegetation strips could favor higher trophic taxa  
425 such as birds, mammals, reptiles and amphibians. We also expect enhanced spillover of  
426 beneficial invertebrates in agroforestry fields, due to the presence of undisturbed habitats  
427 within fields themselves, which could have strong impacts on the biological control of crop  
428 pests. To our knowledge, this is the first study to describe the distribution of overwintering  
429 invertebrate communities in alley cropping agroforestry systems, and accounting for the  
430 effects of the non-crop herbaceous strips under the tree rows. Given the context of climate  
431 change and biodiversity extinction crisis we are facing, such semi-natural habitats should be  
432 used for biodiversity conservation purposes and the enhancement of ecosystem service flows  
433 in the agroecosystem.

434

## 435 **Appendix A.**

436

437 **Table A1.** Single trait indices.  $S$  is total number of species,  $w_i$  is the relative abundance of  
438 species  $i$  and  $x_i$  is the trait value for species  $i$ . FDvar modified is used for variables that contain  
439 0 values.

440

441 **Table A2.** Functional trait values of carabid species (**diet**; granivorous: 0, omnivorous: 0.5  
442 and carnivorous: 1 / **overwintering stage**; overwintering in both larval and adult stages: 0,  
443 overwintering in adult stage: 1).

444

445

446

447

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449

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456

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458

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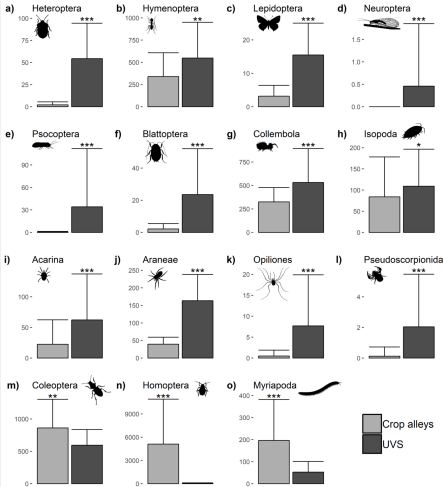
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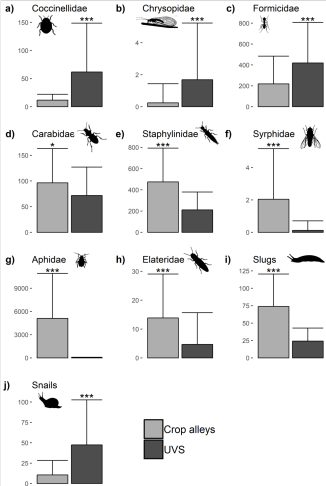
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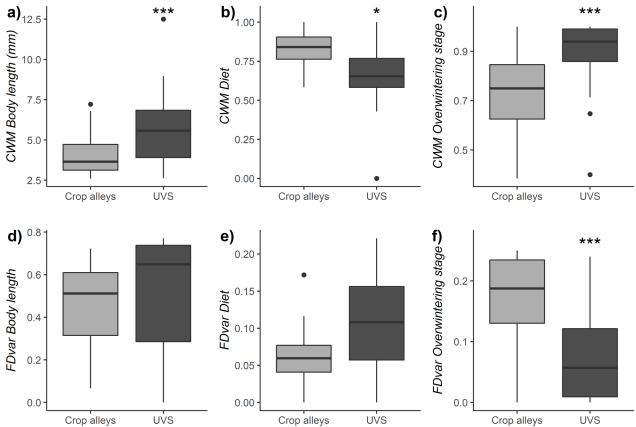
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**Table 1.** Carabid functional traits related to sensitivity to agricultural disturbances and ecological functions.

	<b>Sensitivity to agricultural disturbances</b>	<b>Ecological functions</b>
<b>Body length</b>	Large species, characterized by lower reproductive output and longer growth time, are less tolerant to agricultural intensification such as soil tillage. Smaller carabids are unaffected, or even positively influenced by agricultural intensification (Winqvist et al., 2014; da Silva et al., 2017).	The ratio between predator and prey body sizes is often considered as a good predictor of predator-prey dynamics (Rusch et al., 2015). The amount and range of prey consumed increase with increasing carabid body length (Rouabah et al., 2014).
<b>Diet</b>	Predominantly granivorous species are more impacted by local agricultural intensification than carnivorous species because of reduced weed cover and thus reduced resources. Carnivorous species usually hunt prey over larger scales and are more impacted by landscape composition and configuration (Vanbergen et al., 2010; Winqvist et al., 2014; Baulechner et al., 2019).	Carnivorous species are important predators of crop pests and granivorous species are weed seed consumers (Kromp, 1999; Bohan et al., 2011).
<b>Overwintering stage</b>	Species that hibernate in both larval and adult stages are predominantly found in arable soils whereas species that hibernate in adult stage are often found in field boundaries and need to recolonize field core after emergence (Holland et al., 2009).	Overwintering larvae in arable fields could favor early (thus more effective) regulation of crop pests (Holland et al., 2009).

**Table 2.** Results of Conway-Maxwell-Poisson GLMMs comparing invertebrate density (individuals / m<sup>2</sup>) between crop alleys (reference level) and understory vegetation strips.

	<b>Estimate</b>	<b>SE</b>	<b>d.f.</b>	<b>z-value</b>	<b>p-value</b>
<b>Coleoptera (tot.)</b>	<b>-0.33</b>	0.106	47	-3.160	0.002
<i>Carabidae</i>	<b>-0.33</b>	0.148	47	-2.213	0.027
<i>Staphylinidae</i>	<b>-0.76</b>	0.182	47	-4.180	< 0.001
<i>Coccinellidae</i>	<b>1.65</b>	0.292	47	5.653	< 0.001
<i>Elateridae</i>	<b>-1.39</b>	0.362	47	-3.835	< 0.001
<b>Diptera (tot.)</b>	-0.27	0.158	47	-1.700	0.089
<i>Syrphidae</i>	<b>-3.29</b>	0.847	47	-3.885	< 0.001
<b>Hymenoptera (tot.)</b>	<b>0.47</b>	0.142	47	3.289	0.001
<i>Formicidae</i>	<b>0.71</b>	0.221	47	3.188	0.001
<b>Homoptera (tot.)</b>	<b>-4.74</b>	0.313	47	35.350	< 0.001
<i>Aphidae</i>	<b>-5.17</b>	0.313	47	-16.500	< 0.001
<b>Neuroptera (tot.)</b>	<b>2.47</b>	0.629	47	3.918	< 0.001
<i>Chrysopidae</i>	<b>2.28</b>	0.634	47	3.599	< 0.001
<b>Heteroptera</b>	<b>3.25</b>	0.274	47	11.857	< 0.001
<b>Collembola</b>	<b>0.56</b>	0.114	47	4.863	< 0.001
<b>Dermaptera</b>	-0.31	0.262	47	-1.201	0.230
<b>Psocoptera</b>	<b>4.57</b>	0.515	47	8.882	< 0.001
<b>Orthoptera</b>	-0.06	0.331	47	-0.182	0.856
<b>Lepidoptera</b>	<b>1.59</b>	0.236	47	6.731	< 0.001
<b>Blattoptera</b>	<b>2.43</b>	0.344	47	7.080	< 0.001
<b>Thysanoptera</b>	-0.18	0.467	47	-0.387	0.698
<b>Myriapoda</b>	<b>-1.11</b>	0.211	47	-5.237	< 0.001
<b>Isopoda</b>	<b>0.36</b>	0.183	47	1.984	0.047
<b>Araneae</b>	<b>1.43</b>	0.145	47	9.822	< 0.001
<b>Opiliones</b>	<b>2.82</b>	0.470	47	5.997	< 0.001
<b>Acarina</b>	<b>1.49</b>	0.279	47	5.325	< 0.001
<b>Pseudoscorpionida</b>	<b>3.12</b>	0.740	47	4.215	< 0.001
<b>Stylommatophora (tot.)</b>	-0.20	0.187	47	-1.094	0.274
<i>Snails</i>	<b>1.62</b>	0.318	47	5.106	< 0.001
<i>Slugs</i>	<b>-1.14</b>	0.196	47	-5.833	< 0.001

SE: standard error of the estimates, d.f.: degrees of freedom

**Table 3.** Results of GLMMs comparing species richness and functional structure of carabid communities between crop alleys (reference level) and understory vegetation strips.

	Distribution	Estimate	SE	d.f.	z/t-value	p-value
<b>Species richness</b>	Poisson	-0.11	0.098	48	-1.155	0.248
<b>Body length</b>						
CWM	Gaussian	<b>1.54</b>	0.429	44	3.595	< 0.001
FDvar	Beta	0.08	0.249	47	0.316	0.752
<b>Diet</b>						
CWM	Beta	<b>-0.52</b>	0.241	47	-2.145	0.032
FDvar	Beta	0.29	0.176	47	1.658	0.097
<b>Overwintering stage</b>						
CWM	Beta	<b>1.02</b>	0.239	47	4.245	< 0.001
FDvar	Beta	<b>-0.92</b>	0.191	47	-4.841	< 0.001

SE: standard error of the estimates, d.f.: degrees of freedom

**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 species (**diet**; granivorous: 0, omnivorous: 0.5 and carnivorous: 1 / **overwintering stage**; overwintering in both larval and adult stages: 0, overwintering in adult stage: 1).

<b>Latin name</b>	<b>Diet</b>	<b>Body length</b>	<b>Overwintering stage</b>
<i>Acinopus picipes</i>	0	14.5	0
<i>Acupalpus meridianus</i>	1	3.6	1
<i>Anchomenus dorsalis</i>	1	6.5	1
<i>Apotomus rufus</i>	1	4	NA
<i>Badister bullatus</i>	1	5.3	0
<i>Brachinus crepitans</i>	0.5	8.3	1
<i>Brachynidius sclopeta</i>	1	5.6	1
<i>Calathus cinctus</i>	1	7.5	0
<i>Calathus fuscipes</i>	0.5	12.5	0
<i>Carterus fulvipes</i>	0.5	10.5	NA
<i>Demetrias atricapillus</i>	1	5	1
<i>Dinodes decipiens</i>	NA	11.5	1
<i>Dixus capito</i>	0	12.5	1
<i>Harpalus dimidiatus</i>	0	12.5	1
<i>Harpalus oblitus</i>	0	10	1
<i>Harpalus serripes</i>	0	11	NA
<i>Metallina lampros</i>	1	3.1	1
<i>Metoponus laticollis</i>	0	9.5	1
<i>Metoponus</i> spp.	NA	NA	NA
<i>Microlestes abeillei</i>	1	2.6	1

<i>Microlestes fissuralis</i>	1	2.5	1
<i>Microlestes fulvibasis</i>	1	2.5	1
<i>Microlestes minutulus</i>	1	2.7	1
<i>Microlestes negrita</i>	1	2	1
<i>Nebria brevicollis</i>	1	11.5	0
<i>Ocys harpaloides</i>	NA	NA	NA
<i>Ocys quinquestriatus</i>	1	4	NA
<i>Olisthopus fuscatus</i>	NA	5.5	NA
<i>Ophonus azureus</i>	0	7.8	1
<i>Ophonus sabulicola</i>	0	15	1
<i>Ophonus subquadratus</i>	0	7.3	1
<i>Paradromius linearis</i>	1	4.5	1
<i>Parophonus maculicornis</i>	0	6.3	1
<i>Parophonus mendax</i>	0	7.8	1
<i>Philorhizus crucifer confusus</i>	NA	2.5	1
<i>Philorhizus quadrisignatus</i>	NA	3.5	1
<i>Phyla obtusa</i>	0.5	2.5	1
<i>Poecilus cupreus</i>	0.5	11	1
<i>Poecilus sericeus</i>	1	12.8	1
<i>Pseudoophonus rufipes</i>	0.5	13.5	0
<i>Scybalicus oblongiusculus</i>	0.5	11.5	0
<i>Syntomus obscuroguttatus</i>	1	2.9	1
<i>Tachyura</i> spp.	NA	NA	NA
<i>Trechus aubei</i>	NA	NA	NA
<i>Trechus austriacus</i>	1	3.5	0

<i>Trechus fulvus</i>	1	4.5	0
<i>Trechus obtusus</i>	1	3.6	0
<i>Trechus quadristriatus</i>	1	3.6	0
<i>Trechus</i> spp.	1	3.6	0
<i>Zuphium olens</i>	NA	9	NA

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