

1 **Title:** Functional traits of carabid beetles reveal seasonal variation in community assembly in  
2 annual crops

3

4 **Authors:** Ronan Marrec<sup>1,2\*†</sup>, Nicolas Gross<sup>2,3,4,5\*</sup>, Isabelle Badenhaut<sup>2,3,5,6</sup>, Aurélie  
5 Dupeyron<sup>2</sup>, Gaël Caro<sup>2,7</sup>, Vincent Bretagnolle<sup>2,3</sup>, Marilyn Roncoroni<sup>2,3,4,5</sup> and Bertrand  
6 Gauffre<sup>2,3,5,8\*</sup>

7

8 **Affiliations:**

9 <sup>1</sup> UMR CNRS 7058 EDYSAN, Université de Picardie Jules Verne, F-80039 Amiens, France

10 <sup>2</sup> CEBC UMR CNRS 7372, Université de La Rochelle, F-79360 Villiers-en-Bois, France

11 <sup>3</sup> LTSER « Zone Atelier Plaine & Val de Sèvre », F-79360 Villiers-en-Bois, France

12 <sup>4</sup> UMR INRAE 0874 Ecosystème Prairial, Université Clermont-Auvergne, VetAgro Sup, F-  
13 63000 Clermont-Ferrand, France

14 <sup>5</sup> INRAE, USC 1339 CEBC, Villiers-en-Bois, F-79360 Niort, France

15 <sup>6</sup> URP3F, INRAE, F-86600 Lusignan, France

16 <sup>7</sup> UMR INRAE 1121 LAE, Université de Lorraine, F-54518 Vandœuvre, France

17 <sup>8</sup> UR 1115 Plantes et Systèmes de Cultures Horticoles, INRAE, F- 84914 Avignon, France

18 \*These authors contributed equally

19 **†Correspondence author:**

20 Ronan Marrec

21 EDYSAN (*Ecologie et Dynamique des Systèmes Anthropisés*), UMR CNRS 7058, Université  
22 de Picardie Jules Verne, 33 rue Saint Leu, F-80039 Amiens, France

23 E-mail: [ronan.marrec@u-picardie.fr](mailto:ronan.marrec@u-picardie.fr)

24 **Abstract**

25 **1.** Trait-based community assembly studies have mostly been addressed along spatial  
26 gradients, and do not consider explicitly a fundamental dimension governing community  
27 assembly, the time. Nevertheless, such consideration seems particularly necessary in systems  
28 in which organisms have to face regular disturbances and rapid changes in vegetation  
29 phenology, such as in intensively managed farmlands.

30 **2.** In this study, we aimed at understanding how the functional diversity of carabid beetle  
31 communities varied across the growing season in response to crop type. We tested three  
32 alternative hypotheses on mechanisms underlying the community assembly.

33 **3.** We used data from a long-term monitoring conducted over nine years in an intensively-  
34 managed farmland in central western France, in a total of 625 fields. First, we measured  
35 morphological traits related to body size, dispersal mode, and resource acquisition on the 13  
36 dominant carabid species (> 85 % of all trapped individuals) and identified three independent  
37 dimensions of functional specialization within our species pool along axes of a PCA and  
38 highlighted key traits for community assembly. Second, we evaluated the community  
39 assembly temporal dynamics and the impact of habitat filtering and niche differentiation in  
40 the different crop types with time, using linear mixed-effects models.

41 **4.** We showed that functional species assembly of carabid beetle communities occurring in  
42 crop fields varies importantly intra-annually, with strong variations in these dynamics  
43 depending on crop type and crop phenology. Each crop acted as a filter on carabid  
44 communities for body size and resource-acquisition traits, and functional differentiation  
45 between crops increased with time. We did not find any evidence of habitat filtering on traits  
46 related to dispersal mode.

47 **5.** Our results emphasize the major role of crop phenology but also disturbances involved by  
48 agricultural practices such as crop harvesting on changes in community assembly, likely due

49 to seasonal and inter-annual redistributions of species in agricultural landscapes in response to  
50 such changes. The temporal dimension cannot be ignored to understand the assembly of local  
51 carabid communities in farmlands.

52

53 **Keywords:** agriculture, arthropods, body size, carabid beetles, crop phenology, functional  
54 traits, seasonal dynamics, spatiotemporal dynamics

55        **1. INTRODUCTION**

56        Trait-based approaches are considered as one of the most prominent tool for the study of  
57        community assembly for both plants (e.g., Kraft et al., 2008; Le Bagousse & Pinguet et al.,  
58        2017) and animals (e.g., Gaüzère et al., 2015; Le Provost et al., 2017). Deterministic  
59        processes that shape plant and animal communities can be broadly separated into two distinct  
60        families with opposite effects on species assemblage. First, habitat filtering corresponds to  
61        any process that selects species with similar trait values (Keddy, 1992; Maire et al., 2012). At  
62        the community level, habitat filtering leads to trait convergence toward an optimal trait value  
63        that matches the local abiotic/biotic environment (Grime, 2006). Second, niche differentiation  
64        (e.g., limiting similarity, MacArthur & Levins, 1967) favours individual species with  
65        contrasted traits values (Maire et al., 2012). At the community level, niche differentiation can  
66        lead to high trait diversity by promoting species exploiting locally contrasted resources  
67        (HilleRisLambers et al., 2012). Trait-based community assembly studies have mostly been  
68        addressed along spatial gradients (e.g., Le Bagousse & Pinguet et al., 2017; Vanneste et al.,  
69        2019). While these studies are useful to detect how environmental conditions shape the  
70        functional structure of communities, they do not consider explicitly the temporal dynamics of  
71        communities and their environments.

72        Ecological communities face recurrent disturbances which may create transient  
73        community dynamics (Mouquet, et al., 2003) and instable equilibrium states (Scheffer et al.,  
74        2001). This source of variation may blur our ability to detect how trait differences between  
75        species determine community assembly. For instance, the trait diversity within communities  
76        has been shown to increase with time after disturbance (Fukami et al., 2005). In addition,  
77        most organisms are characterized by seasonal dynamics which may have profound  
78        implications for the study of community assembly (Fitzgerald et al., 2017; Habel et al., 2018).  
79        How disturbance interacts with seasonal dynamics of organisms in real situation is however

80 largely unknown although assembly time and disturbance regime are theoretically predicted to  
81 interact and determine the relative importance of stochastic vs. deterministic processes on  
82 community assembly (Mouquet et al., 2003).

83 In agricultural landscapes, wild organisms have to face regular disturbances, such as  
84 direct destruction of their habitat, regular ploughing, and chemical treatment application,  
85 which strongly alter their abundance and taxonomical and functional diversities (Newbold et  
86 al., 2015). This is typically the case of carabid beetle communities which represent a  
87 functionally diverse guild of predators (Kromp, 1999). Carabid beetles exhibit a large  
88 interspecific variation in body size and in habitat and feeding preferences (Kotze et al., 2011;  
89 Lövei & Sunderland, 1996; Ribera et al., 2001). However, land-use intensification tends to  
90 reduce functional diversity of carabid communities (Woodcock et al., 2014), and for instance,  
91 select for smaller carabid species with higher dispersal abilities (Ribera et al., 2001) and lower  
92 feeding niche breadth (Winqvist et al., 2014). By selecting species with similar traits, we could  
93 predict that the dynamic of species assembly within carabid communities is random due to  
94 high functional equivalence between species (Chesson, 2000; Gross et al., 2015; Hubbell,  
95 2005). However, carabid beetle community structure has been shown to vary among different  
96 crop types (Eyre et al., 2013; Marrec et al., 2015). For instance, grassland habitat may offer  
97 stable habitat over time within agricultural landscape, and has been shown to promote  
98 functional diversity for plants and arthropods (Le Provost, Badenhausser, Le Bagousse-  
99 Pinguet, et al., 2020; Le Provost, Badenhausser, Violle, et al., 2020; Le Provost et al., 2017).

100 In addition, carabid beetles may be sufficiently mobile (Ribera et al., 2001) to develop  
101 temporal strategy of habitat use, especially in response to seasonal environmental changes  
102 such as crop rotations (Holland et al., 2009; Marrec et al., 2015; Thomas et al., 2001).

103 However, how such strategies and environmental influences affect carabid functional  
104 assembly remains unknown. Understanding how carabid communities change over time

105 within and between crop types may help to design landscape-level management practices  
106 aiming at supporting key ecosystem services such as pest control, essential for global food  
107 production (Woodcock et al., 2014).

108 Here, we tested how the functional diversity of carabid beetle communities varied across  
109 the growing season in response to crop type. We used data from a long-term monitoring  
110 design conducted over nine years in an intensively-managed farmland (covering ca. 430 km<sup>2</sup>  
111 in central western France). Carabid communities have been surveyed in a total of 625 fields  
112 from 2005 to 2013 over the spring-summer growing season. We first evaluated how  
113 morphological traits co-vary between species in order to identify independent dimensions of  
114 functional specialization within our species pool and highlight key traits for community  
115 assembly (Maire et al., 2012). We then tested three alternative, but non-exclusive, hypotheses  
116 on mechanisms underlying the community assembly of carabid communities:

117 *Hypothesis 1*, community assembly is driven by random processes due to high functional  
118 equivalence between carabid species (Hubbell, 2005). In that case changes in community  
119 diversity are mostly due to the seasonal phenology of carabid communities and apparent  
120 random redistribution of individuals across communities. That would result in no differences  
121 in community structure between different crop types at a given time.

122 *Hypothesis 2*, farmland carabid beetles are adapted to high disturbance rate (Marrec et al.,  
123 2015) and characterized by fast assembly time (Mouquet et al., 2003). In that case, they are  
124 able to follow high temporal fluctuations of crop distribution, phenology, and resources. That  
125 would result in the fact that each crop may act as a filter on carabid communities and that  
126 functional differentiation between crops increases with time during the crop growing season  
127 (Fukami et al., 2005).

128 *Hypothesis 3*, functional diversity of carabid communities is higher in grasslands than in  
129 annual crops because grasslands show higher stability over time and present a more complex

130 and diverse vegetation (Pakeman & Stockan, 2014). That would result in high functional  
131 diversity for all trait dimensions in grasslands during the entire season.

132

## 133 **2. MATERIALS AND METHODS**

### 134 **2.1. Study area**

135 The study was conducted in the Long Term Ecological Research “Zone Atelier Plaine & Val  
136 de Sèvre” area (LTER ZA-PVS) located in central western France (46°23’N, 0°41’ W). It is a  
137 farmland area of ca. 430 km<sup>2</sup> mostly dedicated to cereal crop production. Since 1994, land use  
138 has been recorded annually for each field (~ 13 000 fields) and mapped with a Geographical  
139 Information System (ArcGis 9.2 - ESRI Redlands, CA, USA). From 2005 to 2013, land cover  
140 was dominated by annual crops, mostly winter cereals (36.9 % ± 0.4 of the total area), oilseed  
141 rape (10.1 % ± 0.7), and sunflower (10.8 % ± 0.5). Other crop types accounted for 18.2 % ±  
142 3.4 of the land use. Temporary (sown with pure grasses or with mixed grasses with or without  
143 legume species and < 6 yr-old) and permanent grasslands (> 5 yr-old) represented 8.5 % ± 0.4  
144 of the total area, and artificial grasslands (sown with pure legume species and < 6 yr-old;  
145 exclusively alfalfa in the study site) represented 3.4 % ± 0.3. Other main land uses were urban  
146 areas (9.3 % ± 0.3) and woodland (2.9 % ± 0.1) (Bretagnolle et al., 2018a).

147

### 148 **2.2. Carabid beetle sampling**

149 From 2005 to 2013, carabid beetles were sampled in the five dominant crop types in the study  
150 region (i.e., alfalfa, grassland, oilseed rape, sunflower, and winter cereals). The surveyed  
151 fields were randomly selected within the study area (see Appendix S1 for a full description of  
152 the data set). The comparative crop calendar of these crops in the study area can be found in  
153 Fig. 1. We used pitfall traps, the standard method to estimate carabid beetle abundance-

154 activity (AA) during their activity period (Thiele, 1977). One to seven trapping sessions were  
155 conducted per field in a given year.

156 # Figure 1 here #

157 Three pitfall traps were placed between 10 and 30 m from the field margin and at 10 m  
158 from each other. Traps were filled with a 50 % preservative solution of ethylene glycol (2005  
159 to 2010), monopropylene glycol (2009 and 2010), or ethanol (2011 to 2013) (Bretagnolle et  
160 al., 2018b). The different preservative solutions used may affect catch probability (Skvarla et  
161 al., 2014) but the differences in AA among crops are robust for this bias (Marrec et al., 2015).  
162 Pitfall traps were left in place for five (2005-2010) or four (2011-2013) trapping-effective  
163 days and, for a given year, were set up at the same location for all sessions (see Appendix S1  
164 for a complete description of the dataset). Carabid beetles were stored in the lab in a 96°  
165 ethanol solution and identified at the species level following Jeannel (1941, 1942). Species  
166 names follow *Fauna Europaea* (de Jong et al., 2014). Data from all the pitfall traps were  
167 aggregated per field and date, and used as the statistical unit in the following analyses. Overall  
168 1,209 carabid communities were obtained from 625 fields and five crop types.

169

### 170 **2.3. Species selection and trait measurements**

171 In this study, we considered the 13 dominant carabid beetle species which accounted for 87.8  
172 % of the catches in pitfall traps along the nine trapping years (57,409 individuals in total). The  
173 same 13 species were among the most abundant species in each year of the study: *Poecilus*  
174 *cupreus* (32.8 %), *Brachinus sclopeta* (19.0 %), *Anchomenus dorsalis* (13.6 %), *Calathus*  
175 *fuscipes* (4.3 %), *Nebria salina* (4.2 %), *Brachinus crepitans* (4.1 %), *Pterostichus melanarius*  
176 (2.4 %), *Harpalus dimidiatus* (2.2 %), *Harpalus distenguentus* (1.5 %), *Amara consularis* (1.4  
177 %), *Pseudoophonus rufipes* (1.3 %), *Microlestes minutulus* (0.6 %), and *Microlestes maurus*  
178 (0.4 %). Morphological traits were measured on these 13 selected dominant species according



179 to standardized protocols (Le Provost, Badenhausser, Le Bagousse-Pinguet, et al., 2020).  
180 Twelve individuals per species and per sex from our local species collection were measured.  
181 Measured individuals were selected randomly from 2011 and 2012 samples irrespectively of  
182 the crop type from which they have been trapped.

183 On each individual, we measured three sets of traits related to body size, movement  
184 ability, and resource acquisition that describe leading dimension of forms and functions in  
185 arthropods (Le Provost, Badenhausser, Le Bagousse-Pinguet, et al., 2020; Moretti et al.,  
186 2017). Body size is an important trait related to metabolic rate (Brown et al., 2004) and  
187 thermoregulation (Uvarov, 1977). For carabid beetles, body size is also a critical trait related  
188 to predation and pest control (Rusch et al., 2015). Movement ability traits may much vary  
189 between carabid beetles especially regarding their flight and running ability (Evans &  
190 Forsythe, 1984; Lövei & Sunderland, 1996). Finally, resource acquisition traits may also vary  
191 since carabid beetles have large range of feeding preferences ranging from granivory and  
192 herbivory to specialized carnivory (e.g., ectoparasitoids like many *Brachinus* species) (Lövei  
193 & Sunderland, 1996). The measured morphological traits were:

194 (i) *Body size and shape-related traits*: body surface ( $Bs$ ;  $\text{mm}^2$ ), measured as the sum of  
195 head, pronotum, and elytra areas; body length (sum of head, pronotum, and elytra lengths) vs.  
196 body width (abdominal maximum width) ratio ( $Bl:Bw$ ;  $\text{mm}.\text{mm}^{-1}$ ); head length vs. head width  
197 ratio ( $Hl:Hw$ ;  $\text{mm}.\text{mm}^{-1}$ );

198 (ii) *Mobility-related traits*: membranous wing surface ( $Wg$ ;  $\text{mm}^2$ ); posterior leg length  
199 ( $Lg$ ;  $\text{mm}$ ); femur volume of the posterior leg ( $Fm$ ;  $\text{mm}^3$ ); femur volume of the posterior leg vs.  
200 body surface ratio ( $Fm:Bs$ ;  $\text{mm}^3.\text{mm}^{-2}$ ); femur volume vs. tibia length of the posterior leg ratio  
201 ( $Fm:Tb$ ;  $\text{mm}^3.\text{mm}^{-1}$ ); membranous wing surface vs. body surface ratio ( $Wg:Bs$ ;  $\text{mm}^2.\text{mm}^{-2}$ );

202 (iii) *Resource acquisition-related traits*: mandible length vs. head surface ratio ( $Md:Hd$ ;  
203  $\text{mm}.\text{mm}^{-2}$ ); mandible length vs. labrum length ratio ( $Md:Lb$ ;  $\text{mm}.\text{mm}^{-1}$ ).

204 All measurements were performed using a stereo-microscope (Leica Microsystems M50)  
205 equipped with an integrated high definition microscope camera (Leica IC80 HD).

206

## 207 **2.4. Statistical analyses**

### 208 *Functional trait variations across carabid beetle species*

209 We performed a principal component analysis (PCA) on the average traits of the 13 dominant  
210 species \* 2 sexes to evaluate trait co-variations among species (Mouillot et al., 2013). We  
211 used a VARIMAX procedure to maximize correlations between PCA axes and traits. We then  
212 selected PCA axes with eigenvalue > 1 and recorded the PCA coordinates of each species.  
213 Then, for each species we calculated the mean values of each of the selected PCA axes that  
214 we used as species traits in the following analyses. This procedure has the advantage to select  
215 independent traits for analyses and help to define important leading dimensions of  
216 morphological variations between species (Maire et al., 2012).

217 *An a priori* hypothesis when using a mean trait value for each species is that intraspecific  
218 variability is sufficiently low so that the mean trait value of a species can be realistically used  
219 as a proxy for the species (Violle et al., 2012). To validate our approach, we thus estimated  
220 for each selected PCA axis the relative importance of intra and interspecific variability. In a  
221 linear model, we tested for the effect of species identity and sex on observed trait variability.  
222 Sex was nested within species. We then conducted a variance decomposition analysis based  
223 on the sum of square to estimate the importance of species and sex in explaining observed  
224 trait values. In a second analysis, we performed a linear discriminant analysis which finds the  
225 best linear combination of continuous explanatory variables (morphological traits of carabid  
226 beetles) separating different classes (here species) of a categorical variable. This analysis  
227 corresponds to another way to measure the importance of intraspecific trait variability (Albert  
228 et al., 2010).

229

230 *Functional characterization of communities*

231 We calculated the community-weighted mean (CWM) and variance (CWV) for each PCA  
232 axis separately:

$$CWM_{PCA} = \sum_{i=1}^n p_i \cdot T_i \quad Eq. 1$$

$$CWV_{PCA} = \sum_{i=1}^n p_i \cdot (T_i - CWM)^2 \quad Eq. 2$$

233 where  $n$  is the number of species in the community,  $p_i$  is the relative abundance of species  $i$  in  
234 a given community,  $T_i$  is its PCA-based trait value.  $CWM_{PCA}$  reflects the mean PCA-based  
235 trait value of the community weighted by the abundance of each species (Violle et al., 2007).  
236 It reflects the functional identity of dominant species in a given community.  $CWV_{PCA}$  is a  
237 measurement of the functional diversity and quantifies the dispersion of PCA-based trait  
238 values within a given community (Le Bagousse & Pinguet et al., 2017). Calculated for each  
239 PCA-based trait separately, it is similar to commonly used distance-based indices of  
240 functional diversity such as functional dispersion or Rao index (Laliberté & Legendre, 2010).  
241

242 *Evaluation of the community assembly temporal dynamics*

243 To investigate seasonal trends in community assembly and their variation between crops,  
244 linear mixed-effects models were run on  $CWM_{PCAS}$  and  $CWV_{PCAS}$  calculated on each selected  
245 PCA-based trait with the R package LME4 (Bates et al., 2015).  $CWM_{PCA}$  and  $CWV_{PCA}$  of each  
246 PCA-based trait were modelled separately as the response variable. To test whether carabid  
247 community assembly exhibited contrasted temporal trajectory in different crop types, we  
248 tested for an interaction between crop types (*Crop*) and time. Time was modelled as the  
249 scaled annual Julian date (*JD*; scaled with mean = 0). As carabid communities may be

250 impacted by crop phenology or agricultural practices such as harvesting over the season  
251 (Marrec et al., 2015), we integrated in the model a polynomial order 3 for time to test for non-  
252 linear relationships. Sampling year (*Year*;  $n = 9$ ) and preservative solution (*Solution*;  $n = 3$ )  
253 were included to account for sampling design. Field identity (*FieldID*;  $n = 625$  levels) was  
254 included as a random intercept in all models, to account for within-year multi-sampling.  
255 Complete model formula was:

$$CWM_{PCA} \text{ or } CWV_{PCA} \sim (1|Field ID) + Year + Solution + (JD + JD^2 + JD^3)$$

\* Crop      Eq. 3

256 The best sub-model was selected by comparing AIC values ( $\Delta AIC < 4$ ) between all  
257 possible biologically relevant sub-models ( $n = 23$ ) (Barton, 2013). Final model was estimated  
258 using restricted maximum likelihood (REML). To remove potential outliers, we excluded in  
259 prior analyses data points outside the upper quantile 99.9 % and then communities with less  
260 than three individuals (162 out of 1209 communities).

261

### 262 *Evaluation of the impact of habitat filtering and niche differentiation*

263 A null model approach was used to quantify the strength of PCA-based trait convergence and  
264 divergence in carabid beetle communities ( $CWV_{PCA}$ ) to isolate the impact of habitat filtering  
265 and niche differentiation (Götzenberger et al., 2016). The null hypothesis was that local  
266 communities should simply reflect a random distribution of individuals drawn from a regional  
267 species pool. As such, the regional species pool used to generate the null predictions must be  
268 carefully considered when inferring ecological processes from observed patterns (de Bello et  
269 al., 2012). As the regional species pool may vary over the season due to contrasted phenology  
270 between carabid beetles (Matalin, 2007) we constructed two alternative null models:

- 271 (i) a global null model which considered the species pool observed throughout the  
272 growing season;

273 (ii) a seasonal null model which took into account variations of carabid species pools  
274 over the growing season due to variation in phenology and agricultural practices  
275 between crop types.

276 A matrix describing the individual AA of each of the 13 species observed at the field  
277 scale was randomly shuffled 1,000 times across communities using the *permatful* function in  
278 the R package VEGAN (Oksanen et al., 2018). For the seasonal null model, the AA matrix was  
279 split according to three successive time periods (early spring: April 1 to May 15; late spring:  
280 May 15 to July 10; summer: July 10 to August 30; Fig. 1). Randomization was performed  
281 independently for each time period. Overall, the procedure kept species AA constant at the  
282 regional scale, but allowed species richness and AA to randomly vary between communities.  
283 Our individual-based randomization had the advantage to directly reflect our sampling design  
284 by taking into account the pattern of local AA of all sampled individuals at the community  
285 level. The size of the null envelope is only determined by species AA at the regional scale,  
286 consistently with our null hypothesis.

287 For each of the 1,000 randomizations and for the two null models, we used the matrix of  
288 trait values of each individual species to calculate the  $CWV_{PCA}$  at the community level. We  
289 then calculated the 95 % confidence interval to compare the observed  $CWV_{PCA}$  values to the  
290 predictions of the null model. If observed data fell outside of the null envelope, it indicated  
291 that deterministic processes led to less or more divergent community trait distribution than  
292 expected by chance. Specifically, observed  $CWV_{PCA}$  values below the null envelope indicated  
293 that traits within communities were forced to converge more than expected by chance,  
294 suggesting habitat filtering. In contrast, the impact of niche differentiation was detected when  
295 communities exhibited observed  $CWV_{PCA}$  values above the null envelope, i.e., coexisting  
296 species showed stronger functional differences than expected under the null hypothesis. As  
297 multiple assembly processes can simultaneously affect community structure and influence

298 different traits independently (Gross et al., 2013; Spasojevic & Suding, 2012), we ran this  
299 analysis separately for each selected trait. For the seasonal null model, we also tested whether  
300 different crop types exhibited contrasted levels of trait dispersion ( $CWV_{PCA}$ ). To do so, we ran  
301 a linear mixed model such as described above for each period of time separately (early spring,  
302 late spring, and summer). The model had the following form:

$$CWV_{PCA} \sim (1|Field\ ID) + Year + Solution + Crop \quad Eq. 4$$

303 All statistical analyses were performed using the R environment (R. Core Team, 2018)  
304 and JMP11 (The SAS Institute, Cary, NC, USA).

305

### 306 **3. RESULTS**

#### 307 **3.1. Functional variations across carabid species**

308 Body size, mobility, and resources acquisition traits defined three independent leading  
309 dimensions along which carabid species differentiated (total variance explained: 74 %; Fig. 2;  
310 see Table S3 in Appendix S2 for correlation tables). The first PCA axis (42 %) was associated  
311 to carabid body size and body shape (correlation with PCA axis for *Bs*: 0.93; *Bl:Bw*: 0.65),  
312 posterior leg size (*Lg*: 0.95; *Fm:Tb*: 0.51), femur size of the posterior leg (*Fm*: 0.95), and the  
313 relative proportion of their head surface and mandible length (*Md:Hd*: -0.87) (Fig. 2). The  
314 axis particularly opposed small species such as *Microlestes* spp. against large species such as  
315 *C. fuscipes* and *P. melanarius*.

316 The second PCA axis (22 %) segregated species according to mobility traits and opposed  
317 species with large wings (*Wg*: 0.85; *Wg:Bs*: 0.74) to species with massive posterior legs  
318 (*Fm:Bs*: -0.67) and head larger than long (*Hl:Hw*: -0.56) (Fig. 2). The axis particularly  
319 opposed *A. consularis* and *H. distinguendus* against *M. maurus*, *C. fuscipes* and *P.*  
320 *melanarius*.

321 The third PCA axis (10 %) was mainly characterized by morphological traits linked to  
322 resource acquisition, and opposed species based on the relative length of their mandibles and  
323 labrum ( $Md:Lb$ : 0.59) and on the shape of their head ( $Hl:Hw$ : 0.56) (Fig. 2). The axis mainly  
324 opposed *Brachinus* spp. and *A. dorsalis* against *H. distinguendus* and *A. consularis*.  
325 # Figure 2 here #

326 For the three PCA-based traits, intraspecific variability was very low compared to  
327 interspecific variability ( $\%r^2 = 0$  to 3 %; Table 1). In addition, the linear discriminant analysis  
328 indicated only 11 % of misclassification due to intraspecific variability, confirming that  
329 interspecific variability was much stronger.  
330 # Table 1 here #

331

### 332 3.2. Seasonal trends in the functional structure of carabid communities

333 For each response variable (hereafter named  $CWM_{PCA1}$ ,  $CWV_{PCA1}$ ,  $CWM_{PCA2}$ ,  $CWV_{PCA2}$ ,  
334  $CWM_{PCA3}$ ,  $CWV_{PCA3}$  respectively for mean and dispersion of PCA axes 1, 2, and 3), 23  
335 biologically relevant models were tested. The full model was the best or second best model  
336 for all response variables but  $CWM_{PCA2}$  (Appendix S3).  $CWM_{PCA}$  and  $CWV_{PCA}$  of all PCA-  
337 based traits varied significantly between crop types (except  $CWV_{PCA3}$ , which was marginally  
338 significant) and community assembly significantly varied through the season, showing  
339 different trends among crops, for all PCA-based traits (Table 2).  
340 # Table 2 here #

341 For all PCA-based traits,  $CWM_{PCAS}$  were not significantly different between crops at the  
342 very beginning and end of the growing season, but showed strong differences in their seasonal  
343 dynamic (Fig. 3).  $CWM_{PCA1}$  mainly linked to variation in body size, increased in sunflower to  
344 peak around June 9 and then decreased to the starting value (Fig. 3b). By contrast,  $CWM_{PCA1}$   
345 decreased significantly in oilseed rape until ca. June 30 and then increased to the starting

346 value (Fig. 3b). For the three other crops (alfalfa, grassland, and winter cereals), a gradual  
347 increase of  $CWM_{PCA1}$  was observed, to peak at the end of the season (Fig. 3a-b). For  
348  $CWM_{PCA2}$ , almost no temporal variation and differences between crops were observed, except  
349 for sunflower, in which it was lower than anywhere else in mid-spring, around ca. May 10-  
350 June 10, indicating communities mainly dominated by species with smaller wings and larger  
351 legs (Fig. 3d). For  $CWM_{PCA3}$ , variations were mainly observed in annual crops, with higher  
352 values in oilseed rape than in other crops from ca. May 10 and which peaked around ca. June  
353 30 and then decreased (Fig. 3f). This pattern tends to indicate that during this period,  
354 communities were dominated by species with relatively longer mandibles and heads. The  
355 exact opposite pattern was observed in sunflower during the same period (Fig. 3f). In winter  
356 cereals,  $CWM_{PCA3}$  was the highest around ca. April 30 and then decreased until the end of the  
357 season (Fig. 3f).

358 *# Figure 3 here #*

359

### 360 **3.3. Evaluation of the impact of habitat filtering and niche differentiation**

361 When considering the global null model, trait dispersion ( $CWV_{PCA}$ ) did not depart from  
362 the null envelop for any PCA-based trait and crop in the mid-season, except in sunflower for  
363  $CWV_{PCA2}$  that was higher than expected by chance around ca. June 10-30 (Fig. 4d).  $CWV_{PCA1}$   
364 and  $CWV_{PCA2}$  were lower than expected in alfalfa at the beginning of the season, and in  
365 winter cereals for  $CWV_{PCA1}$  at the end of the season (Fig. 4a-c). Functional diversity was not  
366 significantly higher in perennial crops than annual crops at any time, but tended to be higher  
367 in grassland at the very beginning of the season for  $CWV_{PCA1}$  (Fig. 4a).

368 *# Figure 4 here #*

369



370 When considering the seasonal null model, carabid community assembly highly changed  
371 through time for  $CWV_{PCA1}$  and  $CWV_{PCA3}$  while it was not the case for  $CWV_{PCA2}$  (Fig. 5).  
372 Community assembly did not significantly depart from the null envelop for any of the PCA-  
373 based traits in early spring, except for  $CWV_{PCA1}$  values which converged more than expected  
374 by chance in winter cereals. In late spring,  $CWV_{PCA1}$  and  $CWV_{PCA3}$  values were lower than  
375 expected by chance in all crops, suggesting trait convergence. Similar pattern was observed in  
376 summer, except in oilseed rape where values did not depart from the null expectation.

377

## 378 **4. DISCUSSION**

379 In this multi-year study, we showed that the functional structure of carabid beetle  
380 communities varies importantly across the growing season in crops. This dynamic of  
381 community assembly for carabid beetles also strongly depends on the crop type. Although  
382 carabid beetles forms and functions widely vary across species, crops act as a habitat filter  
383 and strongly reduce the functional variation of co-occurring species within a field. However,  
384 we also showed that each crop type selects carabid species according to contrasting trait  
385 values and that dominant trait value could shift even within a single crop type over the season.  
386 Such high variability within and between crop types calls for the maintenance of diverse crop  
387 mosaics in agricultural landscapes (Sirami et al., 2019) to promote carabid species  
388 persistence, a key agent of biological pest control in agricultural landscapes.

389

### 390 **4.1. Leading dimensions in functional traits across carabid species**

391 Much functional ecology studies generally consider qualitative traits selected after a literature  
392 review and only partially available for all species. This generally impedes a precise  
393 characterization of all functional dimensions, because of unavailability of data for many  
394 species or trait variation across species distribution area. In our study, we measured

395 continuous morphological traits on our sampled individuals. We found that carabid species'  
396 traits in arable field communities differentiate along three main dimensions of functional  
397 specialization, similar as previously shown for other taxa (Le Provost, Badenhauer, Le  
398 Bagousse-Pinguet, et al., 2020).

399 The first main dimension of interspecific differentiation was related to body size. Body  
400 size is associated with many life history traits and ecological characteristics that can explain  
401 its importance as a main driver of species assemblages. For instance, bigger carabid species  
402 have already been shown to be more prone to decline than smaller species when facing a loss  
403 of natural habitats, because of their lower reproductive rate and lower dispersal abilities  
404 (Kotze & O'Hara, 2003). Indeed, bigger species are expected to respond less rapidly to  
405 environmental changes than smaller species, which explains why communities found in  
406 farmlands are dominated by small and relatively unspecialized species (Aviron et al., 2005;  
407 Schweiger et al., 2005).

408 The second leading dimension was based on mobility traits. Species appear to importantly  
409 oppose according to whether they have larger, well developed wings, or larger and stronger  
410 legs. Carabid beetles exhibit a variety of wing attributes, including wing dimorphism, which  
411 can have implications for their dispersal abilities (Kotze et al., 2011). However, the shape of  
412 posterior legs is also correlated, in carabid beetles and other Coleoptera, to movement ability  
413 and ecological behaviour, especially speed attained and pushing force (Evans & Forsythe,  
414 1984). Relatively short legs or/and short and slender femora are expected in horizontal pusher  
415 species, with reduced movement abilities, in opposition with species with relatively long legs  
416 and large femora which are faster runners but weak pushers (Evans & Forsythe, 1984;  
417 Forsythe, 1983).

418 The last dimension of interspecific differentiation was based on resource-acquisition traits.  
419 An opposition appears between species with relatively longer head or/and mandibles and

420 species with relatively broader head or/and shorter mandibles. Previous studies (e.g., Acorn &  
421 Ball, 1991; Deroulers & Bretagnolle, 2019; Kulkarni et al., 2015) correlated a phytophagous  
422 diet to more robust, broader mandibles in carabids, which is in accordance with feeding niche  
423 information obtained from the literature for our species (Appendix S4). However, information  
424 about carabid diet is relatively unknown for most species, and current knowledge is often  
425 based on individual observations or lab experiments (Deroulers & Bretagnolle, 2019). Better  
426 evaluation of carabid diet is required, using alternative approaches, such as gut content  
427 analysis (Kamenova et al., 2018) or isotopic and fatty acid composition analysis (González  
428 Macé et al., 2019).

429

#### 430 **4.2. Habitat filtering shapes carabid communities in crops**

431 We find support for one of our research hypotheses: each crop type acts as a habitat filter on  
432 carabid beetles, filtering out species according to their functional trait values, when taking the  
433 seasonal variation of the species pool into account (hypothesis 2). Functional diversity was on  
434 average lower than expected by chance under a random assembly of local communities.  
435 Nonetheless, the strength of this pattern varied depending on the null model considered. When  
436 considering a global null model based on the entire species pool observed throughout the  
437 growing season, communities seem randomly assembled or even subject to niche  
438 differentiation processes in late spring, which could have led to an erroneous validation of  
439 hypothesis 1. In fact, this period corresponds in temperate regions to a transition in carabid  
440 community composition. In early spring, communities are composed of “spring breeders”  
441 (Thiele, 1977). From mid-spring, there is an increase of the regional species pool due to the  
442 emergence of “summer-autumn breeders” (Matalin, 2008). As a consequence, there is a  
443 sudden increase of the functional diversity in local assemblages which can falsely be  
444 interpreted as niche differentiation processes operating at the field scale. On the contrary,

445 when considering a seasonal null model, which takes into account variations of carabid  
446 species pools over the growing season, a clear habitat filtering pattern was revealed. To sum  
447 up, we showed that whether or not integrating temporal change in species pool when  
448 investigating functional assembly dynamics can lead to very different interpretations and  
449 conclusions. Although carabid communities may show strong patterns of temporal niche  
450 differentiation (e.g., in forest ecosystems, Loreau, 1989), especially through competition  
451 processes (Kamenova et al., 2015), they are generally strongly filtered within fields in  
452 response to crop type and crop phenology.

453 Habitat filtering was observed in all crop types, indicating high specialization of carabid  
454 communities at the crop level, as previously suggested (Marrec et al., 2015; Weibull &  
455 Östman, 2003). Crop habitat filtering was the highest in late spring, while it was almost  
456 inexistent in early spring. This seemingly random assembly of species in early spring can be  
457 explained by the fact that abundance-activity of carabid species in fields does not entirely  
458 depend on the present crop type, but mainly on the previous crop type(s) in the succession,  
459 and on the landscape context as carabid may colonize crops from nearby habitats at the onset  
460 of the growing season (e.g., Marrec et al., 2015, 2017). Because of crop rotation, farmlands  
461 are highly dynamic landscapes, both in space and time. To face induced brutal changeovers,  
462 carabid individuals of most species might have to redistribute between fields of different crop  
463 types, and between crops and non-crop habitats before winter to shelter for overwintering, and  
464 in early spring to find a new suitable habitat patch (Geiger et al., 2009; Holland et al., 2005;  
465 Marrec et al., 2015; Thomas et al., 2001). Similar distribution shifts of individuals among  
466 crops or/and non-crop habitats have also been reported in summer, when spring-summer crops  
467 become more attractive as they grow, while winter crops are ripening, drying, and then  
468 harvested (O'Rourke et al., 2014; Schneider et al., 2016). Similarly as in early spring, these  
469 summer distribution shifts may explain the lower habitat filtering we found in summer.

470 Crop types did not select the same trait values, and we observed high functional  
471 specializations. Carabid species distribution depends mainly on microclimatic conditions and  
472 availability of resources (Lövei & Sunderland, 1996), which differ importantly between crops,  
473 due to differences in crop practices, crop phenology, vegetation structure, etc. Body size and  
474 resource-acquisition traits were the most affected by crop type in all crops. In late spring,  
475 oilseed rape species assemblages were characterized by small species with relatively long  
476 mandibles, traits associated to small predators (such as *M. maurus*, *M. minutulus*, and *B.*  
477 *sclopeta*). Oilseed rape fields are generally highly affected by many pest species, and their  
478 understory moisture conditions shelter many arthropod species, which can be as many  
479 potential preys for predators (e.g., Zaller et al., 2009). The reverse pattern was observed in  
480 sunflower, with larger carabid species with shorter mandibles, more characteristic of  
481 phytophagous diets (such as *H. dimidiatus* and *H. distinguendus*). Sunflower fields are sown  
482 in April in our study area (Fig. 1), which means soils are disturbed in early spring, and  
483 vegetative ground cover and pest species abundance are still low in late spring. As a  
484 consequence, phytophagous species generally dominate carabid assemblages in more  
485 disturbed habitats (Ribera et al., 2001). Consistently, soil ploughing allows buried seeds to  
486 resurface, and then provide food resources for granivorous species. In a recent study  
487 (Labruyère et al., 2016), AA of generalist phytophagous and polyphagous carabid species was  
488 congruently shown to be higher in spring crops (sugar beet, maize, and spring oilseed rape)  
489 than in winter oilseed rape. Finally, intermediate morphologies are found in all other crops  
490 (winter cereals, alfalfa, and grassland). Higher medium-sized beetle activity has already been  
491 shown in grassy habitats compared to annual crops (Eyre et al., 2009), with body size  
492 decreasing in more intensively managed habitats (Blake et al., 1994).

493 On the other hand, our results did not show strong selection for species in considered crop  
494 types depending on mobility attributes, at any time. The first reason would be that the ability

495 to disperse is likely to be selected at a scale much larger than the field: the landscape scale.  
496 Dispersal-related traits might be filtered by landscape spatiotemporal structure. It has been  
497 previously shown that long-term land-use change to more intensive agricultural landscapes  
498 has impoverished the functional diversity of mobility traits in carabid assemblages (Le  
499 Provost, Badenhausser, Le Bagousse-Pinguet, et al., 2020), and selected species with higher  
500 dispersal abilities and tolerance against agricultural disturbances (Turin & Den Boer, 1988).  
501 Secondly, in some species, macropterous individuals do not necessarily possess functioning  
502 flight muscles and are therefore incapable of flight (Desender & Turin, 1989; Nelemans,  
503 1987), at least at certain periods of their life cycle (Van Huizen, 1977). Such an evaluation is  
504 arduous, especially in smaller species, but would allow to better understanding intra and  
505 interspecific variations between flying and walking strategies to reach new habitat patches.

506 Recent studies have highlighted the importance of crop diversity in the landscape to  
507 maintain diverse arthropod communities in farmlands (e.g., Fahrig et al., 2011; Sirami et al.,  
508 2019). Two distinct hypotheses have been proposed to explain the effect of crop diversity:  
509 crop diversity should benefit biodiversity if many species are either specialist of distinct crop  
510 types (i.e., habitat specialization; Weibull et al., 2003) or require multiple resources provided  
511 by different crop types (i.e., landscape complementation; Dunning et al., 1992). In our study,  
512 we showed that different crops host contrasted carabid communities as crop type filters  
513 specific trait values. Such strong functional specialization of carabid communities may  
514 explain the effect of crop diversity that has been observed across many agricultural regions  
515 (including ours, see Sirami et al., 2019) and supports the habitat specialization hypothesis.  
516 However, by focusing our study on seasonal changes observed over the spring-summer  
517 period, we also show that contrasted carabid communities can inhabit a same crop type but at  
518 different periods of the year. Therefore, our results also support the landscape  
519 complementation hypothesis operating over time on carabid communities.

520

## 521 **5. CONCLUSIONS**

522 Most studies on carabid beetles functional traits have focused on size-related traits or  
523 literature-based information. Recent studies have proposed that morphological diversification  
524 of carabid beetles strongly respond to environmental heterogeneity and help to identify  
525 contrasted functional specialization (other than size) axes by determining their response to  
526 increasing environmental pressure (Le Provost, Badenhausser, Le Bagousse-Pinguet, et al.,  
527 2020). Combining various morphological traits related to different ecological functions, we  
528 found support to our second hypothesis: each crop type acts as a filter on carabid communities  
529 for body size and resource-acquisition traits, and functional differentiation between crops  
530 increases with time during crop growing season. Such variations seem to be mainly related to  
531 crop type and phenology. However, other drivers such as disturbances involved by  
532 agricultural practices associated with crop types may also explain the observed patterns. As  
533 highly mobile organisms, carabid beetles are able to follow high temporal fluctuations of crop  
534 distribution and resources. As such, mobility traits were not selected by crop types, but more  
535 likely at the landscape scale. Indeed, intensive agricultural landscapes are dominated by crops  
536 with short rotation times even in the case of grasslands which are mainly temporary  
537 grasslands included in crop rotations. Consequently, because of the strong functional  
538 specialisation to habitat type, maintaining high diversity of crops and non-crop habitats seems  
539 crucial to sustain carabid communities in agroecosystems.

540

## 541 **ACKNOWLEDGEMENTS**

542 We are especially grateful to the numerous field workers who helped collect the data. We also  
543 thank all involved farmers for letting us work on their land. R.M. was funded by a Région

544 Poitou-Charentes and Département des Deux-Sèvres Ph.D. grant. This work is part of the  
545 Landscaphid project and was supported by the ANR Systerra program (French National  
546 Research agency, ANR-09-STRA-05) and by the French national DIVA2 program.

547 Authors declare to not having any conflict of interest.

548

## 549 **AUTHORS' CONTRIBUTIONS**

550 IB, VB, GC, BG, NG, and RM designed the study.

551 BG, NG, and RM wrote the manuscript.

552 BG, AD, RM, and MR collected the data.

553 MR sorted arthropods from the traps and identified the species.

554 AD measured the morphological traits.

555 AD and NG ran the statistical analyses.

556 All authors contributed critically to the drafts and gave final approval for publication.

557

## 558 **REFERENCES**

559 Acorn, J. H., & Ball, G. E. (1991). The mandibles of some adult ground beetles: Structure, function,  
560 and the evolution of herbivory (Coleoptera: Carabidae). *Canadian Journal of Zoology*, 69(3),  
561 638–650.

562 Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait  
563 approach reveals the structure and the relative importance of intra-vs. Interspecific  
564 variability in plant traits. *Functional Ecology*, 24(6), 1192–1201.

565 Aviron, S., Burel, F., Baudry, J., & Schermann, N. (2005). Carabid assemblages in agricultural  
566 landscapes: Impacts of habitat features, landscape context at different spatial scales and  
567 farming intensity. *Agriculture, Ecosystems & Environment*, 108(3), 205–217.



- 568 Barton, K. (2013). MuMIn: Multi-model inference, R package version 1.9.0. <http://R-Forge.r-Project.Org/Projects/Mumin/>.
- 569
- 570 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using
- 571 lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/doi:10.18637/jss.v067.i01>
- 572 Blake, S., Foster, G. N., Eyre, M. D., & Luff, M. L. (1994). Effects of habitat type and grassland
- 573 management practices on the body size distribution of carabid beetles. *Pedobiologia*, 38(6),
- 574 502–512.
- 575 Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer, I.,
- 576 Monceau, K., Fabrice, A., & Monestiez, P. (2018). Biodiversity, ecosystem services and citizen
- 577 science: The value of long term monitoring in farmland landscapes for sustainable
- 578 agriculture. *Sci. Total Environ*, 627, 822–834.
- 579 Bretagnolle, Vincent, Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer, I.,
- 580 Monceau, K., Allier, F., Monestiez, P., & Gaba, S. (2018). Description of long-term monitoring
- 581 of farmland biodiversity in a LTSER. *Data in Brief*, 19, 1310–1313.
- 582 <https://doi.org/10.1016/j.dib.2018.05.028>
- 583 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic
- 584 theory of ecology. *Ecology*, 85(7), 1771–1789.
- 585 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and*
- 586 *Systematics*, 31(1), 343–366.
- 587 de Bello, F., Price, J. N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger,
- 588 L., Lavergne, S., & Lepš, J. (2012). Functional species pool framework to test for biotic effects
- 589 on community assembly. *Ecology*, 93(10), 2263–2273.
- 590 de Jong, Y., Verbeek, M., Michelsen, V., de Place Bjørn, P., Los, W., Steeman, F., Bailly, N., Basire, C.,
- 591 Chylarecki, P., & Stloukal, E. (2014). Fauna Europaea—all European animal species on the
- 592 web. *Biodiversity Data Journal*, 2, e4034. <https://doi.org/10.3897/BDJ.2.e4034>

- 593 Deroulers, P., & Bretagnolle, V. (2019). The consumption pattern of 28 species of carabid beetles  
594 (Carabidae) to a weed seed, *Viola arvensis*. *Bulletin of Entomological Research*, *109*(2), 229–  
595 235.
- 596 Desender, K., & Turin, H. (1989). Loss of habitats and changes in the composition of the ground and  
597 tiger beetle fauna in four West European countries since 1950 (Coleoptera: Carabidae,  
598 Cicindelidae). *Biological Conservation*, *48*(4), 277–294. [https://doi.org/10.1016/0006-](https://doi.org/10.1016/0006-3207(89)90103-1)  
599 3207(89)90103-1
- 600 Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in  
601 complex landscapes. *Oikos*, 169–175.
- 602 Evans, M. E. G., & Forsythe, T. G. (1984). A comparison of adaptations to running, pushing and  
603 burrowing in some adult Coleoptera: Especially Carabidae. *Journal of Zoology*, *202*(4), 513–  
604 534.
- 605 Eyre, M. D., Labanowska-Bury, D., Avayanos, J. G., White, R., & Leifert, C. (2009). Ground beetles  
606 (Coleoptera, Carabidae) in an intensively managed vegetable crop landscape in eastern  
607 England. *Agriculture, Ecosystems & Environment*, *131*(3–4), 340–346.
- 608 Eyre, M. D., Luff, M. L., & Leifert, C. (2013). Crop, field boundary, productivity and disturbance  
609 influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem. *Agriculture,*  
610 *Ecosystems & Environment*, *165*, 60–67.
- 611 Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., &  
612 Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in  
613 agricultural landscapes. *Ecology Letters*, *14*(2), 101–112.
- 614 Fitzgerald, D. B., Winemiller, K. O., Sabaj Pérez, M. H., & Sousa, L. M. (2017). Seasonal changes in the  
615 assembly mechanisms structuring tropical fish communities. *Ecology*, *98*(1), 21–31.
- 616 Forsythe, T. G. (1983). Locomotion in ground beetles (Coleoptera Carabidae): An interpretation of leg  
617 structure in functional terms. *Journal of Zoology*, *200*(4), 493–507.

- 618 Fukami, T., Bezemer, T. M., Mortimer, S. R., & van der Putten, W. H. (2005). Species divergence and  
619 trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–  
620 1290.
- 621 Gaüzère, P., Jiguet, F., & Devictor, V. (2015). Rapid adjustment of bird community compositions to  
622 local climatic variations and its functional consequences. *Global Change Biology*, *21*(9), 3367–  
623 3378.
- 624 Geiger, F., Wäckers, F. L., & Bianchi, F. J. (2009). Hibernation of predatory arthropods in semi-natural  
625 habitats. *BioControl*, *54*(4), 529–535.
- 626 González Macé, O., Ebeling, A., Eisenhauer, N., Cesarz, S., & Scheu, S. (2019). Variations in trophic  
627 niches of generalist predators with plant community composition as indicated by stable  
628 isotopes and fatty acids. *SOIL ORGANISMS*, *91*(2), 45–59–45–59.
- 629 Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M., & de Bello, F. (2016). Which  
630 randomizations detect convergence and divergence in trait-based community assembly? A  
631 test of commonly used null models. *Journal of Vegetation Science*, *27*(6), 1275–1287.
- 632 Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities:  
633 Mechanisms and consequences. *Journal of Vegetation Science*, *17*(2), 255–260.
- 634 Gross, N., Börger, L., Soriano-Morales, S. I., Le Bagousse-Pinguet, Y., Quero, J. L., García-Gómez, M.,  
635 Valencia-Gómez, E., & Maestre, F. T. (2013). Uncovering multiscale effects of aridity and  
636 biotic interactions on the functional structure of Mediterranean shrublands. *Journal of*  
637 *Ecology*, *101*(3), 637–649.
- 638 Gross, N., Liancourt, P., Butters, R., Duncan, R. P., & Hulme, P. E. (2015). Functional equivalence,  
639 competitive hierarchy and facilitation determine species coexistence in highly invaded  
640 grasslands. *New Phytologist*, *206*(1), 175–186.
- 641 Habel, J. C., Seibold, S., Ulrich, W., & Schmitt, T. (2018). Seasonality overrides differences in butterfly  
642 species composition between natural and anthropogenic forest habitats. *Animal*  
643 *Conservation*.

- 644 HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking  
645 community assembly through the lens of coexistence theory. *Annual Review of Ecology,  
646 Evolution, and Systematics*, 43, 227–248.
- 647 Holland, J. M., Birkett, T., & Southway, S. (2009). Contrasting the farm-scale spatio-temporal  
648 dynamics of boundary and field overwintering predatory beetles in arable crops. *Biocontrol*,  
649 54(1), 19–33.
- 650 Holland, J. M., Thomas, C. F. G., Birkett, T., Southway, S., & Oaten, H. (2005). Farm-scale  
651 spatiotemporal dynamics of predatory beetles in arable crops. *Journal of Applied Ecology*,  
652 42(6), 1140–1152.
- 653 Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional  
654 equivalence. *Functional Ecology*, 19(1), 166–172.
- 655 Jeannel, R. (1941). *Coléoptères Carabiques, Faune de France*. Lechevalier.
- 656 Jeannel, R. (1942). *Coléoptères Carabiques II, Faune de France*. Lechevalier.
- 657 Kamenova, S., Mayer, R., Rubbmark, O. R., Coissac, E., Plantegenest, M., & Traugott, M. (2018).  
658 Comparing three types of dietary samples for prey DNA decay in an insect generalist  
659 predator. *Molecular Ecology Resources*, 18(5), 966–973.
- 660 Kamenova, S., Tougeron, K., Cateine, M., Marie, A., & Plantegenest, M. (2015). Behaviour-driven  
661 micro-scale niche differentiation in carabid beetles. *Entomologia Experimentalis et Applicata*,  
662 155(1), 39–46.
- 663 Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology.  
664 *Journal of Vegetation Science*, 3(2), 157–164.
- 665 Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L.,  
666 Mossakowski, D., Noordijk, J., & Paarmann, W. (2011). Forty years of carabid beetle research  
667 in Europe—from taxonomy, biology, ecology and population studies to bioindication, habitat  
668 assessment and conservation. *ZooKeys*, 100, 55.

- 669 Kotze, D. J., & O'Hara, R. B. (2003). Species decline—But why? Explanations of carabid beetle  
670 (Coleoptera, Carabidae) declines in Europe. *Oecologia*, *135*(1), 138–148.
- 671 Kraft, N. J., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community  
672 assembly in an Amazonian forest. *Science*, *322*(5901), 580–582.
- 673 Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy,  
674 cultivation impacts and enhancement. In *Invertebrate biodiversity as bioindicators of*  
675 *sustainable landscapes* (pp. 187–228). Elsevier.
- 676 Kulkarni, S. S., Dossdall, L. M., & Willenborg, C. J. (2015). The role of ground beetles (Coleoptera:  
677 Carabidae) in weed seed consumption: A review. *Weed Science*, *63*(2), 355–376.
- 678 Labruyère, S., Bohan, D. A., Biju-Duval, L., Ricci, B., & Petit, S. (2016). Local, neighbor and landscape  
679 effects on the abundance of weed seed-eating carabids in arable fields: A nationwide  
680 analysis. *Basic and Applied Ecology*, *17*(3), 230–239.
- 681 Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity  
682 from multiple traits. *Ecology*, *91*(1), 299–305.
- 683 Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., De Bello, F., Fonseca, C. R., Kattge, J.,  
684 Valencia, E., Leps, J., & Liancourt, P. (2017). Testing the environmental filtering concept in  
685 global drylands. *Journal of Ecology*, *105*(4), 1058–1069.
- 686 Le Provost, G., Badenhauer, I., Le Bagousse-Pinguet, Y., Clough, Y., Henckel, L., Violle, C.,  
687 Bretagnolle, V., Roncoroni, M., Manning, P., & Gross, N. (2020). Land-use history impacts  
688 functional diversity across multiple trophic groups. *Proceedings of the National Academy of*  
689 *Sciences*.
- 690 Le Provost, G., Badenhauer, I., Violle, C., Requier, F., D'Ottavio, M., Roncoroni, M., Gross, L., &  
691 Gross, N. (2020). Grassland-to-crop conversion in agricultural landscapes has lasting impact  
692 on the trait diversity of bees. *Landscape Ecology*, 1–15.

- 693 Le Provost, G., Gross, N., Börger, L., Deraison, H., Roncoroni, M., & Badenhausser, I. (2017).  
694 Trait-matching and mass effect determine the functional response of herbivore communities  
695 to land-use intensification. *Functional Ecology*, *31*(8), 1600–1611.
- 696 Loreau, M. (1989). On testing temporal niche differentiation in carabid beetles. *Oecologia*, *81*(1), 89–  
697 96.
- 698 Lövei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera:  
699 Carabidae). *Annual Review of Entomology*, *41*(1), 231–256.
- 700 MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting  
701 species. *The American Naturalist*, *101*(921), 377–385.
- 702 Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F.  
703 (2012). Habitat filtering and niche differentiation jointly explain species relative abundance  
704 within grassland communities along fertility and disturbance gradients. *New Phytologist*,  
705 *196*(2), 497–509.
- 706 Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N., & Gauffre, B.  
707 (2015). Crop succession and habitat preferences drive the distribution and abundance of  
708 carabid beetles in an agricultural landscape. *Agriculture, Ecosystems & Environment*, *199*,  
709 282–289.
- 710 Marrec, R., Caro, G., Miguët, P., Badenhausser, I., Plantegenest, M., Vialatte, A., Bretagnolle, V., &  
711 Gauffre, B. (2017). Spatiotemporal dynamics of the agricultural landscape mosaic drives  
712 distribution and abundance of dominant carabid beetles. *Landscape Ecology*, *32*(12), 2383–  
713 2398.
- 714 Matalin, A. V. (2007). Typology of life cycles of ground beetles (Coleoptera, Carabidae) in Western  
715 Palaearctic. *Entomological Review*, *87*(8), 947–972.
- 716 Matalin, Andrey V. (2008). Evolution of biennial life cycles in ground beetles (Coleoptera, Carabidae)  
717 of the Western Palaearctic. *Back to the Roots and Back to the Future. Proceedings of XIII*  
718 *European Carabidologist Meeting, Blagoevgrad*, 259–284.

- 719 Moretti, M., Dias, A. T., De Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B.,  
720 Hedde, M., & Hortal, J. (2017). Handbook of protocols for standardized measurement of  
721 terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567.
- 722 Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W., & Bellwood, D. R. (2013). A functional  
723 approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3),  
724 167–177.
- 725 Mouquet, N., Munguia, P., Kneitel, J. M., & Miller, T. E. (2003). Community assembly time and the  
726 relationship between local and regional species richness. *Oikos*, *103*(3), 618–626.
- 727 Nelemans, M. N. E. (1987). Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.).  
728 *Oecologia*, *72*(4), 502–509. <https://doi.org/10.1007/BF00378974>
- 729 Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J.,  
730 Choimes, A., & Collen, B. (2015). Global effects of land use on local terrestrial biodiversity.  
731 *Nature*, *520*(7545), 45.
- 732 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara,  
733 R. B., Simpson, G. L., Solymos, P., Stevens, H. H., Szoecs, E., & Wagner, H. (2018). *Vegan*:  
734 *Community Ecology Package. R package version 2.5-2*. [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)  
735 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan).
- 736 O'Rourke, M. E., Liebman, M., & Rice, M. E. (2014). Ground beetle (Coleoptera: Carabidae)  
737 assemblages in conventional and diversified crop rotation systems. *Environmental*  
738 *Entomology*, *37*(1), 121–130.
- 739 Pakeman, R. J., & Stockan, J. A. (2014). Drivers of carabid functional diversity: Abiotic environment,  
740 plant functional traits, or plant functional diversity? *Ecology*, *95*(5), 1213–1224.
- 741 R. Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for  
742 *Statistical Computing, Vienna, Austria*. URL <https://www.R-project.org/>.
- 743 Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on  
744 species traits of ground beetle assemblages. *Ecology*, *82*(4), 1112–1129.

- 745 Rusch, A., Birkhofer, K., Bommarco, R., Smith, H. G., & Ekbom, B. (2015). Predator body sizes and  
746 habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology*,  
747 16(3), 250–259.
- 748 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in  
749 ecosystems. *Nature*, 413(6856), 591.
- 750 Schneider, G., Krauss, J., Boetzi, F. A., Fritze, M.-A., & Steffan-Dewenter, I. (2016). Spillover from  
751 adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-  
752 natural grasslands. *Oecologia*, 182(4), 1141–1150.
- 753 Schweiger, O., Maelfait, J.-P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M.,  
754 Augenstein, I., Aukema, B., Aviron, S., & Bailey, D. (2005). Quantifying the impact of  
755 environmental factors on arthropod communities in agricultural landscapes across  
756 organizational levels and spatial scales. *Journal of Applied Ecology*, 42(6), 1129–1139.
- 757 Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C.,  
758 & Alignier, A. (2019). Increasing crop heterogeneity enhances multitrophic diversity across  
759 agricultural regions. *Proceedings of the National Academy of Sciences*, 116(33), 16442–  
760 16447.
- 761 Skvarla, M. J., Larson, J. L., & Dowling, A. P. G. (2014). Pitfalls and preservatives: A review. *The Journal*  
762 *of the Entomological Society of Ontario*, 145, 15–43.
- 763 Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional  
764 diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*,  
765 100(3), 652–661.
- 766 Thiele, H.-U. (1977). *Carabid Beetles in Their Environments. A Study on Habitat Selection by*  
767 *Adaptations in Physiology and Behaviour*. Springer-Verlag.
- 768 Thomas, C. F. G., Parkinson, L., Griffiths, G. J. K., Garcia, A. F., & Marshall, E. J. P. (2001). Aggregation  
769 and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal*  
770 *of Applied Ecology*, 38(1), 100–116.



- 771 Turin, H., & Den Boer, P. J. (1988). Changes in the distribution of carabid beetles in The Netherlands  
772 since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid  
773 species with different powers of dispersal (Coleoptera, Carabidae). *Biological Conservation*,  
774 44(3), 179–200.
- 775 Uvarov, B. (1977). *Grasshoppers and Locusts. A Handbook of General Acridology Vol. 2. Behaviour,*  
776 *Ecology, Biogeography, Population Dynamics.* Centre for Overseas Pest Research.
- 777 Van Huizen, T. H. P. (1977). The significance of flight activity in the life cycle of *Amara plebeja*  
778 Gyll.(Coleoptera, Carabidae). *Oecologia*, 29(1), 27–41.
- 779 Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., Brunet,  
780 J., Cousins, S. A., Deconchat, M., & De Smedt, P. (2019). Functional trait variation of forest  
781 understorey plant communities across Europe. *Basic and Applied Ecology*, 34, 1–14.
- 782 Violle, C., Enquist, B. J., McGill, B. J., Jiang, L. I. N., Albert, C. H., Hulshof, C., Jung, V., & Messier, J.  
783 (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in*  
784 *Ecology & Evolution*, 27(4), 244–252.
- 785 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the  
786 concept of trait be functional! *Oikos*, 116(5), 882–892.
- 787 Weibull, A.-C., & Östman, Ö. (2003). Species composition in agroecosystems: The effect of landscape,  
788 habitat, and farm management. *Basic and Applied Ecology*, 4(4), 349–361.
- 789 Weibull, A.-C., Östman, Ö., & Granqvist, Å. (2003). Species richness in agroecosystems: The effect of  
790 landscape, habitat and farm management. *Biodiversity & Conservation*, 12(7), 1335–1355.
- 791 Winqvist, C., Bengtsson, J., Öckinger, E., Aavik, T., Berendse, F., Clement, L. W., Fischer, C., Flohre, A.,  
792 Geiger, F., & Liira, J. (2014). Species' traits influence ground beetle responses to farm and  
793 landscape level agricultural intensification in Europe. *Journal of Insect Conservation*, 18(5),  
794 837–846.
- 795 Woodcock, B. A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A. J., Heard, M. S., Roy, D. B., &  
796 Pywell, R. F. (2014). National patterns of functional diversity and redundancy in predatory

797 ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology*,  
798 51(1), 142–151.  
799 Zaller, J. G., Moser, D., Drapela, T., & Frank, T. (2009). Ground-dwelling predators can affect within-  
800 field pest insect emergence in winter oilseed rape fields. *BioControl*, 54(2), 247.  
801

802 **Table 1.** Effect of interspecific differences and sexual dimorphism on trait variability. We  
803 indicated model parameter and proportion (%) of explained variance (% $r^2$ ) by species and sex.  
804 We tested the effect of species and sex nested within species as explanatory variables and  
805 traits (PCA axes, see Fig. 2) as response variables.

Traits	Adj. $r^2$	Species			Sex		
		Df	Fratio	% $r^2$	Df	Fratio	% $r^2$
PCA axis 1	0.97	12	676.5 ***	99.8 %	13	1.4	0%
PCA axis 2	0.92	12	245.7 ***	97.5 %	13	6.3 ***	3%
PCA axis 3	0.95	12	406.7 ***	97.9 %	13	8.3 ***	2%

806

807

808 **Table 2.** Effect of crop type and time on the functional structure of carabid communities.  
 809 Values and significance of Type II Wald chi square tests realized on fixed effects selected in  
 810 each of the ‘best’ (lower  $\Delta$ AIC) final tested models after the selection procedure (see  
 811 Appendix S3).

Response variable	Fixed effects	Chisq	P (>Chisq)	Response variable	Fixed effects	Chisq	P (>Chisq)
<b>CWM1</b>	Year	15.6	< 0.001	<b>CWV1</b>	Year	30.8742	< 0.001
	Solution	18.6	< 0.001		Solution	14.9308	< 0.001
	JD	2.89	0.089		JD	6.1195	0.0134
	JD <sup>2</sup>	10.16	0.001		JD <sup>2</sup>	42.2013	< 0.001
	JD <sup>3</sup>	20.49	< 0.001		JD <sup>3</sup>	8.3696	0.0038
	Crop	84.57	< 0.001		Crop	14.6505	0.0055
	JD:Crop	43.23	< 0.001		JD:Crop	15.2958	0.0041
	JD <sup>2</sup> :Crop	31.15	< 0.001		JD <sup>2</sup> :Crop	-	-
	JD <sup>3</sup> :Crop	-	-		JD <sup>3</sup> :Crop	19.882	< 0.001
<b>CWM2</b>	Year	2.11	0.146	<b>CWV2</b>	Year	13.652	< 0.001
	Solution	1.96	0.375		Solution	34.156	< 0.001
	JD	5.63	0.018		JD	50.93	< 0.001
	JD <sup>2</sup>	64.6	< 0.001		JD <sup>2</sup>	29.081	< 0.001
	JD <sup>3</sup>	4.26	0.039		JD <sup>3</sup>	19.787	< 0.001
	Crop	29.27	< 0.001		Crop	61.103	< 0.001
	JD:Crop	-	-		JD:Crop	20.486	< 0.001
	JD <sup>2</sup> :Crop	27.58	< 0.001		JD <sup>2</sup> :Crop	18.572	< 0.001
	JD <sup>3</sup> :Crop	-	-		JD <sup>3</sup> :Crop	13.132	0.0107
<b>CWM3</b>	Year	0.05	0.826	<b>CWV3</b>	Year	0.86	0.355
	Solution	3.84	0.146		Solution	1.86	0.395
	JD	19.67	< 0.001		JD	6.03	0.014
	JD <sup>2</sup>	5.11	0.024		JD <sup>2</sup>	1.6	0.205
	JD <sup>3</sup>	2.51	0.113		JD <sup>3</sup>	7.99	0.005
	Crop	98.36	< 0.001		Crop	9.14	0.058
	JD:Crop	50.92	< 0.001		JD:Crop	13.03	0.011
	JD <sup>2</sup> :Crop	20.7	< 0.001		JD <sup>2</sup> :Crop	-	-
	JD <sup>3</sup> :Crop	21.26	< 0.001		JD <sup>3</sup> :Crop	18.95	< 0.001

812

813

814 **Figure captions**

815 **Fig. 1.** Crop calendar in the study area of the five dominant and sampled crop types. The  
816 dashed, orange boxes delineate the three time periods of sampling: early spring, April 1 to  
817 May 15; late spring, May 15 to July 10; summer, July 10 to August 30. T: soil tillage; S:  
818 sowing; H: harvesting.

819

820 **Fig. 2.** Co-variation of ground beetles' morphological traits along the three first PCA axes  
821 (eigenvalue > 1). Morphological traits are in bold red, species are in blue. Trait abbreviations:  
822 *Bs*, body surface (mm<sup>2</sup>); *Lg*, leg length (mm); *Fm*, femur volume (mm<sup>3</sup>); *Wg*, membranous  
823 wing surface (mm<sup>2</sup>); *Bl:Bw*, body length vs. body width ratio (mm.mm<sup>-1</sup>); *Wg:Bs*,  
824 membranous wing surface vs. body surface ratio (mm<sup>2</sup>.mm<sup>-2</sup>); *Fm:Tb*, femur volume vs. tibia  
825 length ratio (mm<sup>3</sup>.mm<sup>-1</sup>); *Fm:Bs*, femur volume vs. body surface ratio (mm<sup>3</sup>.mm<sup>-2</sup>); *Md:Hd*,  
826 mandible length vs. head surface ratio (mm.mm<sup>-2</sup>); *Md:Lb*, mandible length vs. labrum length  
827 ratio (mm.mm<sup>-1</sup>); *Hl:Hw*, head length vs. head width (mm.mm<sup>-1</sup>). Species abbreviations are:  
828 *Ac*, *Amara consularis* ; *Ad*, *Anchomenus dorsalis* ; *Bc*, *Brachinus crepitans* ; *Bs*, *Brachinus*  
829 *sclopetata* ; *Cf*, *Calathus fuscipes*; *Hdim*, *Harpalus dimidiatus*; *Hdis*, *Harpalus distinguendus*;  
830 *Mmi*, *Microlestes minutulus*; *Mma*, *Microlestes maurus*; *Ns*, *Nebria salina*; *Pc*, *Poecilus*  
831 *cupreus*; *Pr*, *Pseudoophonus rufipes*; *Pm*, *Pterostichus melanarius*. M indicated male, F,  
832 female.

833

834 **Fig 3.** Change in community-weighted mean (CWM) through time (Julian days) for PCA axis  
835 1, 2 and 3. We indicated model prediction for each crop (see Table 3 for model selection and  
836 parameters). In panels A, C and E we show model prediction for perennial crop, i.e. alfalfa  
837 (pink line) and grasslands (green line). In panels B, D and F we indicated model prediction for

838 annual crops, i.e. wheat (blue line), oilseed rape (yellow line) and sunflower (orange line).

839 Dots are raw data for each crop.

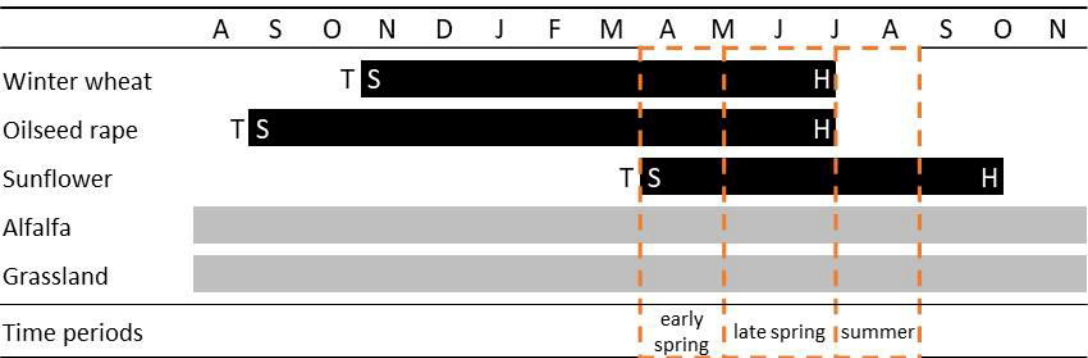
840




841 **Fig 4.** Change in community-weighted variance (log transformed, CWV) through time (Julian  
842 days) for PCA axis 1, 2 and 3. We indicated model prediction for each crop (see Table 3 for  
843 model selection and parameters). In panels A, C and E we show model prediction for  
844 perennial crop, i.e. alfalfa (pink line) and grasslands (green line). In panels B, D and F we  
845 indicated model prediction for annual crops, i.e. wheat (blue line), oilseed rape (yellow line)  
846 and sunflower (orange line). Dots are raw data. Predictions and dots were centered on the null  
847 model envelop (dash grey lines are the 95% confidence intervals).

848

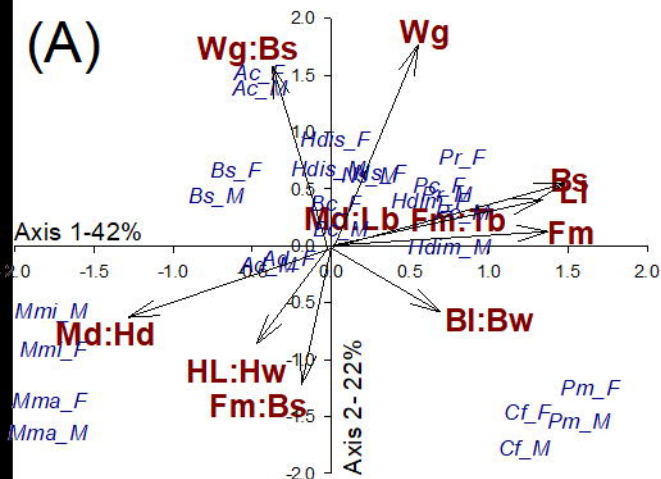
849 **Fig 5.** Community weighted variance (CWV) deviation from null prediction for traits 1, 2,  
850 and 3 in three successive time periods (early spring, April 1 to May 15; late spring, May15 to  
851 July 10); and summer July 10 to August 30). Each dot represents the observed CWV and  
852 associated standard error. Crops are: alfalfa (purple dots), grasslands (green dots), oilseed rape  
853 (yellow dots), sunflower (orange dots), and winter cereals (blue dots). Grey dashed lines are  
854 the 95% confidence interval of the null model envelop. We indicated for each CWV and  
855 periods model P values in each panel. Letters are *post hoc* Tukey HDS. For each panel,  
856 different letter indicated significant differences between crops.

857



-  Intercropping, residues or other crop in the succession
-  Annual crops
-  Permanent crops

(A)



(B)

