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

2 annual crops

3

4 **Authors:** Ronan Marrec[1,2*†], Nicolas Gross[2,3,4,5*], Isabelle Badenhausser[2,3,5,6], Aurélie

5 Dupeyron[2], Gaël Caro[2,7], Vincent Bretagnolle[2,3], Marilyn Roncoroni[2,3,4,5] and Bertrand

6 Gauffre[2,3,5,8*]

7

8 **Affiliations:**

9 [1] UMR CNRS 7058 EDYSAN, Université de Picardie Jules Verne, F-80039 Amiens, France

10 [2] CEBC UMR CNRS 7372, Université de La Rochelle, F-79360 Villiers-en-Bois, France

11 [3] LTSER « Zone Atelier Plaine & Val de Sèvre », F-79360 Villiers-en-Bois, France

12 [4] UMR INRAE 0874 Ecosystème Prairial, Université Clermont-Auvergne, VetAgro Sup, F-

13 63000 Clermont-Ferrand, France

14 [5] INRAE, USC 1339 CEBC, Villiers-en-Bois, F-79360 Niort, France

15 [6] URP3F, INRAE, F-86600 Lusignan, France

16 [7] UMR INRAE 1121 LAE, Université de Lorraine, F-54518 Vandœuvre, France

17 [8] 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

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

1. INTRODUCTION

55

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 breath (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 km²

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 km² 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*; mm²), 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*; mm.mm^{-1}); head length *vs.* head width

197   ratio (*Hl:Hw*; mm.mm^{-1});

198   (ii) *Mobility-related traits:* membranous wing surface (*Wg*; mm²); posterior leg length

199   (*Lg*; mm); femur volume of the posterior leg (*Fm*; mm^{3}); femur volume of the posterior leg *vs.*

200   body surface ratio (*Fm:Bs*; mm^{3}.mm^{-2}); femur volume *vs.* tibia length of the posterior leg ratio

201   (*Fm:Tb*; mm^{3}.mm^{-1}); membranous wing surface *vs.* body surface ratio (*Wg:Bs*; mm².mm^{-2});

202   (iii) *Resource acquisition-related traits:* mandible length *vs.* head surface ratio (*Md:Hd*;

203   mm.mm^{-2}); mandible length *vs.* labrum length ratio (*Md:Lb*; mm.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

Functional characterization of communities

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

232   axis separately:

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

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

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

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_{PCA}s and CWV_{PCA}s 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:

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

$$* Crop \qquad Eq. 3$$

256   The best sub-model was selected by comparing AIC values (ΔAIC < 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 felt 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:

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

303   All statistical analyses were performed using the R environment (R. Core Team, 2018)

304 and JMP11 (The SAS Institute, Cary, NC, USA).

305

3. RESULTS

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_{PCA}s 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 than 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

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

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, Badenhausser, 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

5. CONCLUSIONS

Most studies on carabid beetles functional traits have focused on size-related traits or

literature-based information. Recent studies have proposed that morphological diversification

of carabid beetles strongly respond to environmental heterogeneity and help to identify

contrasted functional specialization (other than size) axes by determining their response to

increasing environmental pressure (Le Provost, Badenhausser, Le Bagousse-Pinguet, et al.,

2020). Combining various morphological traits related to different ecological functions, we

found support to our second hypothesis: each crop type acts as a filter on carabid communities

for body size and resource-acquisition traits, and functional differentiation between crops

increases with time during crop growing season. Such variations seem to be mainly related to

crop type and phenology. However, other drivers such as disturbances involved by

agricultural practices associated with crop types may also explain the observed patterns. As

highly mobile organisms, carabid beetles are able to follow high temporal fluctuations of crop

distribution and resources. As such, mobility traits were not selected by crop types, but more

likely at the landscape scale. Indeed, intensive agricultural landscapes are dominated by crops

with short rotation times even in the case of grasslands which are mainly temporary

grasslands included in crop rotations. Consequently, because of the strong functional

specialisation to habitat type, maintaining high diversity of crops and non-crop habitats seems

crucial to sustain carabid communities in agroecosystems.

540

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

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801

802   **Table 1.** Effect of interspecific differences and sexual dimorphism on trait variability. We

803   indicated model parameter and proportion (%) of explained variance (%r²) 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. r²	Species			Sex		
		Df	*Fratio*	*%r²*	*Df*	*Fratio*	*%r²*
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 ΔAIC) 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)
CWM1	Year	15.6	< 0.001	**CWV1**	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^2	10.16	0.001		JD^2	42.2013	< 0.001
	JD^3	20.49	< 0.001		JD^3	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^2:Crop	31.15	< 0.001		JD^2:Crop	-	-
	JD^3:Crop	-	-		JD^3:Crop	19.882	< 0.001
CWM2	Year	2.11	0.146	**CWV2**	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^2	64.6	< 0.001		JD^2	29.081	< 0.001
	JD^3	4.26	0.039		JD^3	19.787	< 0.001
	Crop	29.27	< 0.001		Crop	61.103	< 0.001
	JD:Crop	-	-		JD:Crop	20.486	< 0.001
	JD^2:Crop	27.58	< 0.001		JD^2:Crop	18.572	< 0.001
	JD^3:Crop	-	-		JD^3:Crop	13.132	0.0107
CWM3	Year	0.05	0.826	**CWV3**	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^2	5.11	0.024		JD^2	1.6	0.205
	JD^3	2.51	0.113		JD^3	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^2:Crop	20.7	< 0.001		JD^2:Crop	-	-
	JD^3:Crop	21.26	< 0.001		JD^3: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 (mm²); *Lg*, leg length (mm); *Fm*, femur volume (mm^3); *Wg*, membranous

823   wing surface (mm²); *Bl:Bw*, body length *vs.* body width ratio (mm.mm^{-1}); *Wg:Bs*,

824   membranous wing surface *vs.* body surface ratio (mm².mm^{-2}); *Fm:Tb*, femur volume vs. tibia

825   length ratio (mm^3.mm^{-1}); *Fm:Bs*, femur volume *vs.* body surface ratio (mm^3.mm^{-2}); *Md:Hd*,

826   mandible length *vs.* head surface ratio (mm.mm^{-2}); *Md:Lb*, mandible length *vs.* labrum length

827   ratio (mm.mm^{-1}); *Hl:Hw*, head length *vs.* head width (mm.mm^{-1}). Species abbreviations are:

828   Ac, *Amara consularis* ; Ad, *Anchomenus dorsalis* ; Bc, *Brachinus crepitans* ; Bs, *Brachinus*

829   *sclopeta* ; 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).

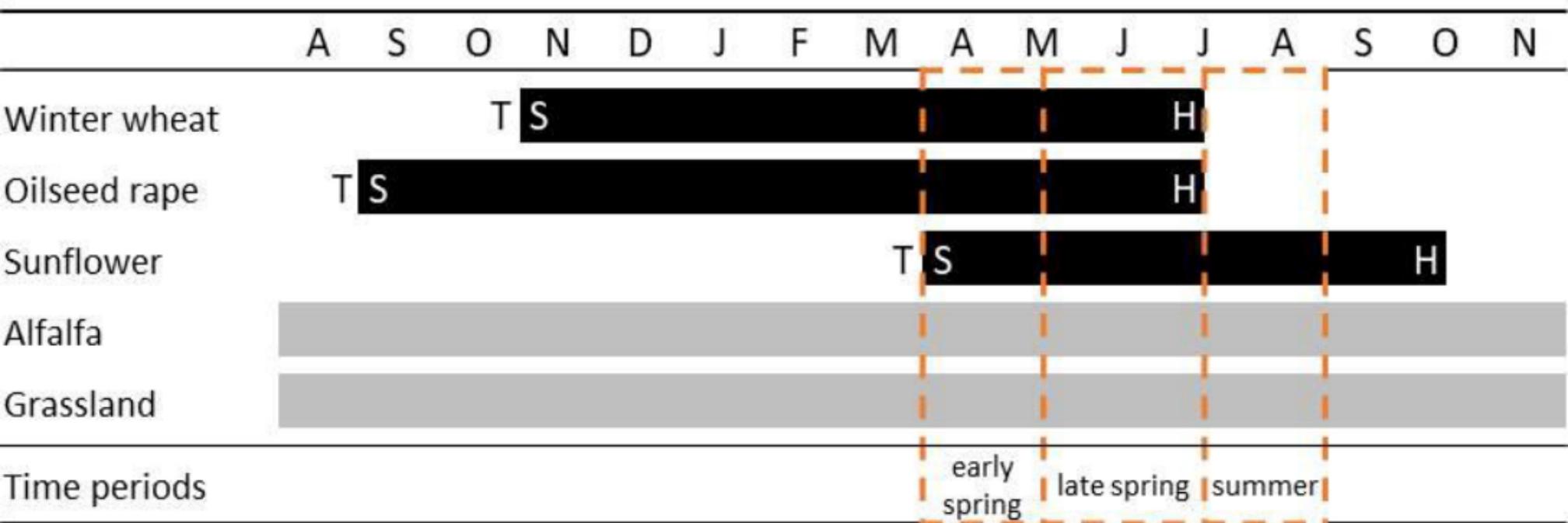839   Dots are raw data for each crop.

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

	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N
Winter wheat			T	S								H				
Oilseed rape		T	S									H				
Sunflower								T	S						H	
Alfalfa																
Grassland																
Time periods									early spring	late spring	summer					

□ Intercropping, residues or other crop in the succession

■ Annual crops

▨ Permanent crops

(A)

Wg:Bs
Ac_F
Ac_M
Hdis_F
Bs_F   Hdis_M Ns_F
Bs_M   Bc_M
Md:Lb Fm:Tb
Ald_F
Ac_F Ac_M
Mmi_M
Md:Hd
Mml_F
HL:Hw
Fm:Bs
Mma_F
Mma_M

Wg
Pr_F
Pc_F
Hdim_M
Hdim_M
Bs
Li
Fm
Bl:Bw
Pm_F
Cf_F Pm_M
Cf_M

Axis 1-42%
Axis 2 - 22%

(B)

HL:Hw Md:Lb
Bc_F
Bc_M
Bs_M
Bs_F   Ald_F
Wg:Bs
Fm:Bs
Ns_M
Ns_F
Md:Hd
Mmi_M
Mma_M
Mma_M
Hdis_M
Hdis_F
Ac_M
Ac_F

Pc_M
Wg:Tb
Bl:Bw
Ns_M
Pc_F
Pm_M
Hdim_M
Cf_F
Li Axis 1
Bs_M
Pm_F

Axis 3 - 10%

Early Spring · **Late Spring** · **Summer**

CWV PCA axis 1

Early Spring:
Crop: P = 0.01
Year ns
Liq ns

Late Spring:
Crop: P = 0.03
Year: P < 0.0001(-)
Liq: P = 0.004

Summer:
Crop: P = 0.0001
Year ns
Liq ns

CWV PCA axis 2

Early Spring:
Crop ns
Year: P = 0.01(-)
Liq: P = 0.01

Late Spring:
Crop: P < 0.0001
Year ns
Liq = 0.0003

Summer:
Crop ns
Year ns
Liq = 0.01

CWV PCA axis 3

Early Spring:
Crop ns
Year ns
Liq ns

Late Spring:
Crop ns
Year ns
Liq ns

Summer:
Crop: P = 0.03
Year ns
Liq ns