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### **Paper:**

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**Original research article**

**Journal:** Agriculture, Ecosystems and Environment

**Title: Crop rotation and species-specific habitat preferences interact to drive the distribution and abundance of dominant carabid beetles in an agricultural landscape**

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## Abstract

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This study investigated how crop type and crop rotation influences the distribution and the dynamics of abundance of two dominant carabid beetle species (*Poecilus cupreus* and *Brachinus sclopeta*) at two critical stages of their life cycle: the spring reproductive and overwintering periods. The study was conducted over nine years in an agricultural landscape of western France using both pitfall and emergence traps located within the fields and in the field margins of the five dominant crops. The two species used crop and non-crop habitat types differently during the reproductive period and while overwintering, suggesting two different strategies of habitat use. Both species used within-field areas during the spring reproductive period, but *P. cupreus* was active in many crops while *B. sclopeta* was only active in oilseed rape. Our data suggested a beneficial role of oilseed rape for both species. *P. cupreus* overwintering emergences occurred in oilseed rape, suggesting active selection of this crop during autumn, and to a lesser extent in margins of fields which had been cropped with oilseed rape the previous year. *B. sclopeta* emergence from overwintering occurred predominantly in margins of fields cropped with oilseed rape the previous year. Overall results suggest that inter-field movements and active selection rather than differences in survival rates may explain distribution and abundance dynamics of these two carabid species in agricultural landscapes. This study provides valuable insights on the influence of crop type heterogeneity and the dynamics of cropped habitats on the population dynamics of species contributing to biological control. Such knowledge may help to manage their populations and improve ecosystem services.

## Keywords

Carabidae; *Brachinus sclopeta*; *Poecilus cupreus*; distribution shift; oilseed rape; winter habitat

## 1. Introduction

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5           Agricultural intensification in Europe has affected the dynamics (Benton et al., 2003)  
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7 and ecosystem services provided by biodiversity, such as biological control of agricultural  
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9 pests (Thies and Tschardtke, 1999). Species contributing to biological control are mainly  
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11 polyphagous predators (e.g. Costanza et al., 1997; Losey and Vaughan, 2006; Van Driesche et  
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13 al., 2008; Jonason et al., 2013). Among them, carabid beetles play an important role in  
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15 agriculture as natural enemies of pests or as elements of trophic chains sustaining biodiversity  
16  
17 (Thiele, 1977). Carabid beetle communities in crops are usually numerically dominated by a  
18  
19 few species, which may drive ecosystem functioning (Holland and Luff, 2000; Luff, 2002).  
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21 However, information on the basic ecology of individual species is relatively scant and  
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23 contradictory for even the most common species (Thomas et al., 2001). Indeed, most studies  
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25 on carabid beetles investigated the diversity and abundance of the whole community. Detailed  
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27 understanding of species distribution among habitats at the different life stages can provide  
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29 insights into their ecological requirements. It would allow us to better adapt crop protection  
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31 strategies and/or help design ecological strategies of management through environmental  
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33 engineering (Landis et al., 2000; Vasseur et al., 2013; Raymond et al., 2014).  
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41           Agricultural landscapes consist of a mosaic of habitat patches whose suitability may  
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43 be good, moderate or hostile to a given species (Fahrig et al., 2011). This functional  
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45 representation of patch suitability includes the heterogeneity of the cultivated mosaic which  
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47 results from the diversity of crops (Vasseur et al., 2013). Crops provide different  
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49 environmental conditions and food availability which are two of the most important factors  
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51 influencing carabid beetle distribution (Luff, 1987; Holland, 2002; Thomas et al., 2002). In  
52  
53 addition, crops also differ in the intensity and timing of management practices, such as soil  
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55 tillage and harvesting, which are determined by crop successions (Joannon et al., 2008).  
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1 Agricultural practices have been shown to influence carabid beetle abundance either directly,  
2 through mortality and emigration, or indirectly, by affecting local microhabitat conditions  
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4 (Kromp, 1999; Cole et al., 2002; Thorbek and Bilde, 2004; Hatten et al., 2007). Accordingly,  
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6 studies which investigated the effect of crop management practices on the species  
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8 composition of carabid beetle communities concluded that the crop type was one of the most  
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10 influential factors (Booij and Noorlander, 1992; Weibull and Östman, 2003; Eyre et al.,  
11  
12 2013). Altogether, the crops and their succession should be major determinants of habitat  
13  
14 suitability because they integrate both intrinsic characteristics of the cultivated plants and the  
15  
16 associated practices (Vasseur et al., 2013). In addition, many species use non-crop habitats at  
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18 critical moments of their annual life cycle. Adults of spring-summer breeding species often  
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20 overwinter in boundary structures or grassland habitats and re-colonize crop fields in spring  
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22 (Geiger et al., 2009; Lee and Landis, 2002). Hence, over their lifetime, individuals can use  
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24 different habitat types including both crop and non-crop habitats (Bommarco, 1998a) and may  
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26 therefore be particularly sensitive to the dynamics of cropped habitats within the landscape  
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28 (Thomas et al., 2002). While many studies have addressed the role of non-crop habitats as  
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30 alternative and overwintering habitats (Lys and Nentwig, 1992; Pfiffner and Luka, 2000;  
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32 Frank and Reichhart, 2004; Smith et al., 2008; Hof and Bright, 2010), few have taken into  
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34 account the crop type they were bordering (e.g. Eyre and Leifert, 2011; Eyre et al., 2013) to  
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36 explain species' spatial dynamics.  
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46 Here, we aimed to investigate how spring-breeding carabids use the different habitats  
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48 in the farmland landscape mosaic to complete their annual life cycle. Using two numerically  
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50 dominant carabid species of western France agroecosystems, *Poecilus cupreus* and *Brachinus*  
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52 *sclopeta* (Jeannel, 1942), we focused on two crucial life stages, i.e. overwintering and spring  
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54 reproductive periods. We postulated that crop types may influence the distribution and  
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56 activity-density (AD) of carabid species among habitats. It was hypothesized that the  
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1 influence of crop and succession may vary (i) between species (Thomas et al., 2001; Holland  
2 et al., 2005) and (ii) between stages of the life cycle (Holland and Luff, 2000; Geiger et al.,  
3 2009; Holland et al., 2009). We also hypothesized that (iii) field margin use may vary  
4 according to the crop in the field concerned, to the species and the life stage (Eyre and Leifert,  
5 2011; Eyre et al., 2013). As carabid beetle abundance fluctuates widely from year to year and  
6 can vary within and between fields (Thomas et al., 2001; Holland et al., 2004, 2005), any  
7 reliable knowledge of crop influence should be based on long-term observations carried out  
8 simultaneously in many fields of each crop. In the present study, data from surveys carried out  
9 over 9 years in 734 fields located in a 430 km<sup>2</sup> study area (including about five hundred  
10 farms) were analysed. To our knowledge, no study has been carried out on this scale.  
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## 26 **2. Materials and methods**

### 27 *2.1. Study area*

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36 The study was conducted in the LTER Zone-Atelier “*Plaine et Val de Sèvre*” covering  
37 an area of 430 km<sup>2</sup> in western France (46.11° N, 0.28° W) and containing *ca.* 12,500 fields  
38 (mean area  $\pm$  SD: 2.94 ha  $\pm$  3.15) mostly dedicated to cereal crop production. Since 1995,  
39 land use has been recorded annually for each field and mapped with a Geographical  
40 Information System (ArcGis 9.2 - ESRI Redlands, CA, USA). Perennial crops represented  
41 11.9%  $\pm$  0.3 of the total area of the study site (mean value  $\pm$  SE from 2005 to 2013) including  
42 grasslands (8.5%  $\pm$  0.4) and alfalfa (3.4%  $\pm$  0.3). From 2005 to 2013, annual crops were  
43 dominated by winter cereals (36.9%  $\pm$  0.4 of the total area), sunflower (10.8%  $\pm$  0.5) and  
44 oilseed rape (10.1%  $\pm$  0.7). Other main land uses were urban areas (9.3%  $\pm$  0.3) and wood  
45 (2.9%  $\pm$  0.1), the other crop types accounting for 18.2%  $\pm$  3.4 of the land use.  
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## 2.2. Experimental design and sampling technique

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5 First, in order to assess spring activity-density (AD) according to habitat and crop  
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7 type, carabid beetles were sampled using pitfall traps, the standard method to estimate AD  
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9 during their activity period (Thiele, 1977). The method is simple, cost-efficient, and produces  
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11 high capture rates (Luff, 1975; Spence and Niemelä, 1994). The five dominant crops (alfalfa,  
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13 grassland, oilseed rape, sunflower and winter cereal), accounting for almost 80% of the arable  
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15 land use, were sampled from 2005 to 2013 (Table 1). In our sample, oilseed rape (*WC/OSR*)  
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17 and sunflower (*WC/Sun*) were always preceded by winter cereals, and winter cereal by oilseed  
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19 rape (*OSR/WC*), sunflower (*Sun/WC*) or winter cereal (*WC/WC*). These 2-year crop  
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21 successions were dominant over the study site (Lazrak et al., 2010). Grassland and alfalfa  
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23 were classified according to their age deduced from the GIS database (from 1 to +4 years of  
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25 age). The number of fields sampled in each year and for each succession ranged from one to  
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27 61 (Table 1). Sampling design slightly varied from year to year, as detailed below. The  
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29 number of pitfall traps per field ranged from three to four according to the year. From 2005 to  
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31 2013, three pitfall traps were placed at less than 30 m from the field edge and at 10 m from  
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33 each other. From 2009 to 2013, one additional trap was placed in the grassy field margin.  
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35 Traps were filled with a 50% preservative solution of ethylene glycol (2005 to 2010),  
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37 monopropylene glycol (2009 and 2010) or ethanol (2011 to 2013). The number of sampling  
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39 sessions depended on the year and sampling occurred from late April to mid-July (Table 1).  
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41 Pitfall traps were left in place for five (2005-2010) or four (2011-2013) trapping-effective  
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43 days and, for a given year, were set up at the same location for all sessions.  
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53 Second, to determine overwintering location of carabid beetles, emergence traps were  
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55 set up within fields (one in 2012, two in 2013) and in field margins (one trap) to collect post-  
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57 overwintering emerging adults. As for the pitfall trap protocol, our aim was to investigate the  
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1 influence of habitat type. Thus, emergence traps were set up at the end of March (81 in 2012  
2 and 102 in 2013; see Table 1) in alfalfa, winter cereal (*OSR/WC*, *Sun/WC*, *WC/WC*), and  
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4 oilseed rape (*WC/OSR*) (Table 1). The emergence trap method consisted of hermetically  
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6 sealing a soil area to collect all emerging insects, while preventing both emigration and  
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8 immigration. Insects were caught in one collection bottle and one pitfall trap per emergence  
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10 trap, filled with a 70% preservative solution of ethanol. This sampling method has been  
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12 shown to be efficient to estimate absolute density of ground-dwelling arthropods (Sunderland  
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14 et al., 1995). The area of each trap was 0.36 m<sup>2</sup> (Soil Emergence trap 96x26 mesh, Black,  
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16 MegaView Science Co., Ltd, Taichung, Taiwan). Traps were emptied every fortnight from  
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18 early April to mid-July (Table 1), covering most of the adult emergence period. Carabid  
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20 beetles were stored in the lab in a 96° ethanol solution and identified at the species level.  
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26 < Table 1 >  
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### 31 2.3. Carabid beetle species 32 33 34 35

36 During the nine trapping years, two species accounted for more than 50% of the total  
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38 AD in pitfall traps (Appendix A): *Poecilus cupreus* (L.) (33%) and *Brachinus sclopeta*  
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40 (Fabricius) (19%). *P. cupreus* is a typical and beneficial predator on arable lands (e.g.  
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42 Langmaack et al., 2001) associated with many crops (e.g. cereals: Heydemann, 1955; Luik et  
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44 al., 2005; clover: Luik et al., 2005 ; oilseed rape: Hossfeld, 1963; Schlein and Büchs, 2004;  
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46 Veromann et al., 2005; pea: Holland et al., 2005). *B. sclopeta* is a Brachinini bombardier  
47  
48 beetle, a genus described as ectoparasitoid of other insects (Erwin, 1979). *B. sclopeta* is  
49  
50 characterized as an open habitat species (Zetto Brandmayr et al., 2006) but its ecology is  
51  
52 largely unknown. Both species overwinter as adults and reproduce in spring (Matalin, 2007;  
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54 Pilon et al., 2013). They are macropterous, with well-developed wing muscles (Bommarco,  
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1998b; Hendrickx et al., 2009; Pilon et al., 2013), but *P. cupreus* is more likely to disperse by walking (Wallin, 1985).

## 2.4. Statistical analyses

### 2.4.1. Spring activity-density (pitfall trap data)

To investigate habitat and crop succession influence on carabid AD, we used generalized linear mixed models (GLMM) with Poisson distribution and a log-link function. AD of *P. cupreus* and *B. sclopeta* was modelled separately as the response variable using the number of individuals caught in a pitfall trap. Several models were fitted to test our hypotheses (Table 2).

< Table 2 >

First, model 1 tested for the effect of pitfall trap location (*TL*) (within field vs. grassy field margin) on the spring dynamics of *P. cupreus* and *B. sclopeta* AD. *TL* was set as fixed effect and we included Julian date (*JD*) as a quadratic covariate, using a two-degree scaled polynomial (scaled with mean = 0) ( $date = JD + JD^2$ ). Interaction levels were restricted to two-way interactions between *TL* and the date.

Second, model 2 tested for the effect of the crop type on the dynamics of *P. cupreus* and *B. sclopeta* AD in field margins. We compared all crops (alfalfa, grassland, oilseed rape, sunflower, winter cereal) in the same statistical model because field margins are grassy margins and have the same vegetation structure whatever the crop in the field they belong to. In this model, the crop was included as a fixed effect factor and the date as a covariate. Interaction terms were added.

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Third, models 3 and 4 tested for the effect of the crop on the dynamics of *P. cupreus* and *B. sclopeta* AD within fields. Vegetation structure, e.g. plant density and cover, is known to affect ground dwelling invertebrate movements and therefore pitfall trap efficiency (Lang, 2000; Thomas et al., 2006). Since grasslands and alfalfa differ from annual crops in their vegetation structure, we analyzed the effect of the type of perennial and annual crops in two separate models. Model 3 tested for the effects of the perennial crop (alfalfa and grasslands) and its age. The crop was included as a fixed effect factor and the date and age as covariates. Three-way interaction terms were added. Model 4 tested for the effect of the type of annual crop (oilseed rape, sunflower, winter cereal) on the dynamics of species AD. In this model, the crop was included as a fixed effect factor and the date as a covariate. Two-way interaction terms were added.

Finally, models 5 and 6 tested for the influence of the previous crop (oilseed rape, sunflower or winter cereal) on the dynamics of *P. cupreus* and *B. sclopeta* AD in winter cereal field margins (Model 5) and within fields (Model 6). The previous crop was included as a fixed effect factor and the date as a covariate. Interaction terms were added.

To account for the sampling design, in all models we included the field identity (N = 660, 572, 299, 373, 290 and 296 levels respectively for models 1 to 6, see above) and a single factor combining the sampling year and preservative solution used (as it could influence catch probability, see Luff, 1975; Schmidt et al., 2006) (Model 1: N = 7 levels, Model 2 and 5: N = 5; Model 3, 4 and 6: N = 11) as random intercepts. Furthermore, we allowed the effect of seasonal variation, modelled as Julian date, to vary between years, by including it as a random slope. Finally, to account for differences in the number of trapping days between years we included it as an offset on a log scale in all models.

Analyses were made using the package *lme4* (Bates and Maechler, 2013) in R 3.0.2 (R Development Core team 2013). We used a backward stepwise selection procedure: the full

1 model was simplified step-by-step by removing the least non-significant interaction terms and  
2 explanatory variables, using Maximum Likelihood Ratio tests (Type II Wald chi square tests)  
3  
4 in the R package *car* (function *Anova*; Fox and Weisberg, 2011). *P* was set to 0.05 for  
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6 variable selection. Results of model selections are summarized in Table 2.  
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#### 10 11 2.4.2. Post overwintering emergences (emergence trap data) 12 13 14

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17 Emergences from early April to the beginning of June were pooled (i.e. sessions one to  
18 four), thus excluding data collected thereafter because many traps were destroyed in June  
19 2013 by violent thunderstorms. In the undamaged emergence traps, these four first sessions  
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21 included 88.9% and 83.3% of the total *P. cupreus* and *B. sclopeta* individuals respectively.  
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23 We used generalized linear mixed models to analyze the number of individuals caught in an  
24 emergence trap for each species separately. Two models were fitted to test our hypotheses  
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26 (Table 2).  
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34 Model 7 tested for the effect of the crop (alfalfa, oilseed rape and winter cereal) and  
35 TL on the emergence density. In this model, the year, crop and TL were included as fixed  
36 effect factors. Two-way interaction between crop and TL was added.  
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41 Model 8 tested for the influence of the previous crop (oilseed rape, sunflower or winter  
42 cereal) and TL on emergences in winter cereal fields. In this model, the year, previous crop  
43 and TL were included as fixed effect factors. Two-way interaction between previous crop and  
44 TL was added.  
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51 We used a Poisson distribution and log-link function for all of these GLMMs. The  
52 field identity was included as a random effect. We used the same methodology as in 2.4.1 for  
53 model selection and for parameter significance and estimations except that *P* was set to 0.10  
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2 for variable selection due to the low number of replicates in some cells. Results of model  
3 selections are summarized in Table 2.  
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### 6 7 **3. Results** 8 9

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11 A total of 18536 individuals of *P. cupreus* and 10765 of *B. sclopeta* were collected in  
12 pitfall traps between 2005 and 2013. The number of individuals caught per trap (observed  
13 mean  $\pm$  SE; all crop types combined) fluctuated between the years, with a minimum in 2013  
14 for both species (*P. cupreus*:  $1.07 \pm 0.19$ ; *B. sclopeta*:  $0.73 \pm 0.18$ ) and a maximum in 2008  
15 for *P. cupreus* ( $15.10 \pm 2.15$ ) and 2005 for *B. sclopeta* ( $16.12 \pm 6.04$ ), respectively. With the  
16 emergence traps, a total of 98 *P. cupreus* and 390 *B. sclopeta* were trapped between early  
17 April and early June in 2012 and 2013.  
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#### 31 *3.1. Effect of pitfall trap location on the dynamics of AD (Model 1)* 32 33 34 35

36 The activity density (AD) of the two species was significantly ( $P < 0.001$  – Table 2)  
37 higher in traps located within fields (observed mean  $\pm$  SE: *P. cupreus*  $6.08 \pm 0.27$ ; *B. sclopeta*  
38  $3.37 \pm 0.37$ ) than in traps located in field margins (*P. cupreus*  $1.97 \pm 0.20$ ; *B. sclopeta*  $0.81 \pm$   
39  $0.19$ ). In addition, the dynamics of AD for both species differed according to trap location  
40 (see Appendix B). Separate analyzes were hence made to investigate the dynamics of carabid  
41 AD within fields and in field margins.  
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#### 53 *3.2. Effect of current crop type on the dynamics of AD in field margins (Model 2)* 54 55 56 57 58 59 60 61 62 63 64 65

1 The temporal dynamics of *P. cupreus* AD had the same pattern in all crop margins  
2 and decreased significantly from the beginning of the trapping period to the end (Fig. 1a; JD  
3 effect:  $P < 0.001$  – Table 2). AD was low in all field margins but differed slightly between  
4 crops, being highest in sunflower margins and lowest in grassland margins (Fig. 1a; Crop  
5 effect:  $P < 0.001$  – Table 2). *B. sclopeta* AD in field margins was almost zero and varied  
6 slightly between crops (Fig. 1b; Crop effect:  $P = 0.03$  – Table 2).

14 < Fig. 1 >

### 19 3.3. Effect of current crop type on the dynamics of AD within fields (Models 3 and 4)

24 Among perennial crops, *P. cupreus* AD was higher in alfalfa than in grassland (Figs.  
25 1c and 1e) and the temporal dynamics of AD differed between the two crops (Crop effect:  $P <$   
26 0.001; JD effect:  $P < 0.001$ ; JD<sup>2</sup> effect:  $P = 0.39$ ; Crop\*JD effect:  $P < 0.001$ ; Crop\*JD<sup>2</sup> effect:  
27  $P < 0.001$  – Table 2). In alfalfa, AD was high at the beginning of the trapping period and then  
28 decreased while in grassland AD was low and decreased after the end of May (Figs. 1c and  
29 1e). *P. cupreus* AD varied with the age of alfalfa and grassland at the beginning of the  
30 trapping period; the younger the habitat, the higher the AD in early spring (Figs. 1c and 1e;  
31 Age effect:  $P = 0.89$ ; Age\*JD effect:  $P < 0.001$ ; Age\*JD<sup>2</sup> effect:  $P < 0.001$  – Table 2). *B.*  
32 *sclopeta* AD was low in perennial crops but was higher in alfalfa than in grassland and varied  
33 slightly with the date (Figs. 1d and 1f; Crop effect:  $P < 0.001$ ; JD effect:  $P = 0.95$ ; JD<sup>2</sup> effect:  
34  $P = 0.02$  – Table 2). In alfalfa, *B. sclopeta* AD increased with the date until June and then  
35 decreased, while in grassland it was almost zero at every date (Figs. 1d and 1f; Crop\*JD  
36 effect:  $P < 0.001$ ; Crop\*JD<sup>2</sup> effect:  $P < 0.001$  – Table 2). *B. sclopeta* AD varied with age only  
37 in alfalfa; the younger the habitat, the higher the peak of AD in June (Figs. 1d and 1f; Age  
38 effect:  $P < 0.001$ ; Age\*JD effect:  $P < 0.001$ ; Age\*JD<sup>2</sup> effect:  $P < 0.001$  – Table 2).

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2 effect:  $P = 0.76$ ; Age\*JD effect:  $P < 0.001$ ; Age\*JD<sup>2</sup> effect:  $P < 0.001$ ; Crop\*Age:  $P = 0.08$ ;  
3 JD\*Crop\*Age:  $P = 0.03$ ; JD<sup>2</sup>\*Crop\*Age:  $P < 0.001$  – Table 2).

4  
5 In annual crops, *P. cupreus* AD was high in oilseed rape during the whole sampling  
6 period and was much lower in sunflower and winter cereal (Fig. 1g; Crop effect:  $P < 0.001$  –  
7 Table 2). AD in the winter crops (oilseed rape and winter cereal) was at its highest at the  
8 beginning of the trapping period and then decreased after mid-May, while AD in sunflower  
9 was almost zero in late April, increased until June and then decreased (Fig. 1g; JD effect:  $P =$   
10  $0.07$ ; JD<sup>2</sup> effect:  $P = 0.34$ ; Crop\*JD effect:  $P < 0.001$ ; Crop\*JD<sup>2</sup> effect:  $P = 0.01$  – Table 2). *B.*  
11 *sclopeta* was almost exclusively trapped in oilseed rape fields. AD increased importantly with  
12 time until mid-June and then declined (Fig. 1h; Crop effect:  $P < 0.001$ ; JD effect:  $P = 0.52$ ;  
13 JD<sup>2</sup> effect:  $P < 0.001$ ; Crop\*JD effect:  $P < 0.001$ ; Crop\*JD<sup>2</sup> effect:  $P < 0.001$  – Table 2).

#### 24 25 26 27 28 29 3.4. Effect of previous crop type on the dynamics of AD in winter cereal (Models 5 and 6)

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34 *P. cupreus* AD in margins and within winter cereal fields was not influenced by the  
35 previous crop (Previous Crop effect:  $P = 0.56$  and  $0.31$  in field margins and within fields  
36 respectively – Table 2). A slight significant effect of the previous crop on the dynamics of AD  
37 was observed in both field margins and within fields, but trends were similar among previous  
38 crops (see Appendix B). Neither *B. sclopeta* AD nor its dynamics were affected by the  
39 previous crop in winter cereal fields (field margins and within fields) (Table 2).

#### 40 41 42 43 44 45 46 47 48 49 50 51 3.5. Effects of current crop type and trap location on post-overwintering emergence (Model 7)

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56 The distribution of overwintering *P. cupreus* in field margins vs. within fields varied  
57 with the crop (Crop effect:  $P = 0.40$ ; TL effect:  $P = 0.77$ ; Crop\*TL effect:  $P = 0.08$  – Table 2).

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*P. cupreus* emergence densities were the highest within oilseed rape fields while they were almost zero elsewhere (Fig. 2a). *B. sclopeta* emerged mainly in field margins (TL effect:  $P < 0.001$  – Table 2). These differences depended on the crop (Crop effect:  $P = 0.20$ ; Crop\*TL effect:  $P = 0.07$  – Table 2). In oilseed rape, emergence densities in field margins were only twice those observed within the fields. In alfalfa and winter cereals there were around five and 15 times more emergences in field margins than within fields respectively (Fig. 2b).

< Fig. 2 >

### 3.6. Effect of previous crop type and trap location on post-overwintering emergence in winter cereal (Model 8)

*P. cupreus* overwintering densities were low in winter cereals, both within the fields and their margins (Fig. 3a) irrespective of the previous crop type. The ratio of the distribution of overwintering *P. cupreus* in field margins to that within fields varied with the previous crop (Previous crop effect:  $P = 0.24$ ; TL effect:  $P = 0.76$ ; Previous crop\*TL effect:  $P = 0.006$  – Table 2). More *P. cupreus* individuals overwintered in field margins than within the fields when winter cereal was preceded by oilseed rape (*OSR/WC*) (Fig. 3a). The opposite pattern was observed in *Sun/WC* fields (Fig. 3a). Similar low emergences were observed in margins and within *WC/WC* fields (Fig. 3a). High densities of *B. sclopeta* emerged in *OSR/WC* field margins (Previous crop effect:  $P < 0.001$ ; TL effect:  $P < 0.001$ ; Previous crop\*TL effect:  $P < 0.001$  – Table 2), while almost no emergence occurred elsewhere (Fig. 3b).

< Fig. 3 >

## 4. Discussion

1 Crop type strongly influences spring activity density (AD) and overwintering  
2 emergence of both *P. cupreus* and *B. sclopeta*, the two dominant spring breeding carabid  
3 species in our study area, which confirms earlier suggestions. Using pitfall traps, some  
4 limitations can appear when comparing AD between crops, due to differences in catch  
5 probability (Lang, 2000; Thomas et al., 2006). Nevertheless, biases linked to variation in  
6 activity alone cannot explain differences between crops, which are confirmed by results  
7 obtained using the unbiased emergence trap method (Holland and Reynolds, 2003). Effect of  
8 crop type on carabid species distribution has only been suggested in previous studies (e.g.  
9 Thomas et al., 2002; Holland et al., 2005; Eyre et al., 2013). Importantly, contrary to these  
10 earlier studies, which involved one or few fields at small spatial and temporal scales, our  
11 results are based on a large dataset of different fields and crop types sampled and can hence  
12 overcome the uncertainties generated by the highly heterogeneous distribution of carabid  
13 beetles within fields, between fields and between years (e.g. Holland and Luff, 2000; Holland  
14 and Reynolds, 2003). Furthermore, we showed that the two species have different habitat use  
15 strategies to complete their life cycle, but that oilseed rape (OSR) has a highly beneficial role  
16 for both species.

#### 4.1. *Spatial and temporal distribution shifts among habitat types*

45 During the spring reproductive period, *P. cupreus* was abundant in all the crops except  
46 grassland and margins. This is consistent with previous studies that have shown its preference  
47 for arable lands (Langmaack et al., 2001; Holland et al., 2005). In addition, we found  
48 differences in AD and its dynamics among crops. First, AD was highest in OSR and alfalfa  
49 during the early spring. This suggests that these crops are major overwintering habitats for  
50 this species. Consistently, *P. cupreus* post-overwintering emergences were highest within



1 fields of OSR. Post-overwintering emergences in alfalfa were lower than expected according  
2 to pitfall trap data. This raises the difficulty of interpreting pitfall trap data which measure  
3 both activity and abundance (Thiele, 1977). By using emergence traps, more robust data are  
4 obtained because the influence of activity and redistribution is excluded (Holland and  
5 Reynolds, 2003). Here, the high and rapidly declining early spring AD in alfalfa may be  
6 explained by *P. cupreus* redistribution from alfalfa to annual crops. Then, AD peaked in late  
7 May, especially in OSR, suggesting that it may be the main reproductive habitat for *P.*  
8 *cupreus*. Since abundance and reproductive success in one crop may have an impact on the  
9 following crop type in a crop rotation (Holland and Reynolds, 2003), we could expect that  
10 adults of the new generation should overwinter within OSR/WC fields. However, in our study  
11 there was no positive influence of OSR in the previous year on overwintering emergences and  
12 spring AD in WC. This result suggests a complete distribution shift between spring and  
13 winter.

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31 Unlike the relative ubiquity of *P. cupreus*, *B. sclopeta* life cycle was strongly  
32 associated to a single crop (OSR). AD dynamics peaked in June within OSR fields while it  
33 remained almost zero elsewhere. Following the same rationale as for *P. cupreus*, a positive  
34 influence of OSR as previous crop was expected in WC. Our results partially support this  
35 hypothesis since post-overwintering emergences occurred mainly in the margins of OSR/WC.  
36 This suggests that *B. sclopeta* moves before winter from fields to their margins to overwinter,  
37 as reported for many carabid species (Holland and Luff, 2000). The combination of  
38 emergence and pitfall trap results also supports a complete changeover in spring of *B.*  
39 *sclopeta* from OSR/WC margins to WC/OSR fields, highlighting the complementarity of the  
40 two trapping methods.

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Changes in habitat suitability, due to crop rotation and associated agricultural  
practices, are likely to induce the observed distribution shifts (Holland and Luff, 2000). Such

1 distribution shifts have been reported in *P. cupreus* (Thomas et al., 2001) and other carabid  
2 species (Holland, 2002; Thorbek and Bilde, 2004; Holland et al., 2005), suggesting either  
3 inter-field movements or differences in survival rates. In the present study, inter-field  
4 movements were not directly addressed but might well explain the patterns found. Indeed, our  
5 results strongly suggest that fields sown with OSR in August may be rapidly colonized by *P.*  
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Patterns found using emergence and pitfall traps were mostly consistent for *P.*  
*cupreus*, but not for *B. sclopeta*. Surprisingly, early spring pitfall trap data did not show that  
*B. sclopeta* overwintered in OSR/WC field margins. Differences in species' dispersal ability  
may explain this paradox. Since *P. cupreus* disperse mainly by walking (Wallin 1985),  
moving individuals were caught in pitfall traps. On the other hand, colonization of new OSR  
fields in spring is likely to occur through long distance flight in *B. sclopeta*. Accordingly,  
most of *B. sclopeta* individuals were caught in the collection bottle at the top of the  
emergence traps while *P. cupreus* individuals were caught in the pitfall trap (data not shown).

#### 4.2. Oilseed rape: a highly beneficial crop for carabid beetles

Association with a particular crop has been previously suggested for carabid beetles,  
and for *P. cupreus* in particular (Heydemann, 1955; Thomas et al., 2001; Holland et al.,

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2005). Carabid beetle preference for OSR, despite the large quantity of chemical insecticides used on this crop, has been previously reported (Williams, 2010; Eyre et al., 2013).

First, species may select OSR according to the coincidence of their periods of emergence, activity and breeding with OSR phenology and timing of crop management practices (Thiele, 1977; Holland and Luff, 2000). In our study area, OSR is available all year round since new OSR fields are sown in August and OSR stubbles are ploughed in October while WC fields are sown in October and stubbles are ploughed in August-September. Hence, new OSR fields remain undisturbed in autumn and provide a larger vegetation cover in autumn and winter. Overwintering site selection is known to be linked to the absence of disturbance during autumn-winter and to vegetation density providing shelter (Sotherton, 1984; Pffiffner and Luka, 2000; Frank and Reichhart, 2004; Thorbek and Bilde, 2004). This might explain why *P. cupreus* has been found overwintering within new OSR fields.

Second, species distribution depends on availability of resources (Lövei and Sunderland, 1996). Because predatory carabids may be limited by prey availability (Bommarco, 1998b), *P. cupreus* preference for OSR can be related to the larger amount of preys found in OSR (Haschek et al., 2012), especially agricultural pests such as the pollen beetle *Meligethes aeneus* (Piper and Williams, 2004; Veromann et al., 2005, 2008), *Ceutorhynchus* weevils (Piper and Williams, 2004), the brassica pod midge *Dasineura brassicae* (Schlein and Büchs, 2004) or slug eggs (Oberholzer and Frank, 2003). Similarly, as an ectoparasitoid, *B. sclopeta* is limited by the presence of its hosts. Host species of European *Brachinus* remain unknown but are likely coleopterans (Erwin, 1979; Saska and Honek, 2004), like most OSR pests (Alford et al., 2003; Williams, 2010). Some of them, like the pollen beetles *Meligethes sp.* and the weevils *Ceuthorhynchus sp.*, pupate in the soil and are accessible to *Brachinus* larvae for parasitism. Moreover, Saska and Honek (2004) demonstrated that larvae of two closely-related species (*B. crepitans* and *B. explodens*) were

1 able to feed on pupae of *Amara* carabid beetles which are particularly abundant in OSR  
2 throughout Europe (Williams et al., 2010) and in our study site in particular (unpublished  
3 result). Association with OSR for reproduction may explain why *B. sclopeta* appears to  
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5 colonize OSR only in spring, the period of reproduction (Saska and Honek, 2008).  
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9 Finally, abiotic characteristics such as soil structure and microclimatic conditions  
10 affect carabid beetles and could influence the pattern of distribution observed (Thiele, 1977;  
11 Forsythe, 2000; Giglio et al., 2003). Habitat selection based on soil softness (Giglio et al.,  
12 2003) can partly explain the higher overwintering in OSR and winter cereal fields in annual  
13 crops that are ploughed in every year. The slight decreasing tendency of observed activity  
14 with age in alfalfa is consistent with an adverse effect of compacted soil. Moreover, the two  
15 studied species show preferences for moist environmental conditions (Forsythe, 2000; Pilon et  
16 al., 2013); OSR, providing a wet environment, supports the assumption that carabid beetle  
17 species select particular temperature and moisture conditions (Thiele, 1977; Forsythe, 2000;  
18 Williams et al., 2010).  
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### 34 35 36 *4.3. Conclusions* 37 38 39 40

41 The present study provides evidence that the heterogeneity of crops and the dynamics  
42 of cropped habitats influence carabid beetles' population dynamics in space and time. Long-  
43 term persistence of populations might not necessarily require permanent habitats, but  
44 complementary habitats that are spatially and/or temporally connected (Vasseur et al., 2013).  
45 We show that both of the dominant spring breeding species undergo major changes in their  
46 distribution, suggesting inter-field movements at the landscape scale to overwinter and  
47 reproduce. Due to their high abundance in OSR, the two species may have the potential to  
48 regulate OSR pests. Biological control from *P. cupreus* at the landscape scale may benefit  
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1 from the presence of OSR in the crop matrix. Detailed knowledge of *B. sclopeta* trophic  
2 ecology and its host(s) is required to assess its potential for pest control. Increased ecosystem  
3 services, mainly biological control of insect pests, are required from carabid beetles, either  
4 due to conversion to organic systems or because of the stresses imposed on agriculture by  
5 environmental, economic and legislative pressures (Power, 2010; Eyre et al., 2013). Although  
6 large scale management within agro-ecosystems must focus on whole assemblages (Stoner  
7 and Joern, 2004; Woodcock et al., 2010), understanding carabid beetle dynamics in relation  
8 with habitat appears essential to manage their populations and improve ecosystem services.  
9

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## Figure captions

**Fig. 1.** Predicted spring dynamics of *P. cupreus* and *B. sclopeta* activity-density (AD) per trap in field margins of five crops (a and b), within fields of alfalfa (c and d), grasslands (e and f) and annual crops (g and h). Predictions were made using parameters estimated in GLMM models 2, 3 and 4. Julian date courses from the 27<sup>th</sup> April to the 18<sup>th</sup> July. Width of ticks at the bottom of each plot represents the sampling effort.

**Fig. 2.** Effects of the crop (alfalfa, oilseed rape and winter cereal) and trap location (in field margin or within field) on *P. cupreus* (a) and *B. sclopeta* (b) emergence density per trap (Observed mean  $\pm$  SE).

**Fig. 3.** Effects of the previous crop (oilseed rape, sunflower and winter cereal) and trap location (in field margin or within field) on *P. cupreus* (a) and *B. sclopeta* (b) emergence density per trap in winter cereal fields (Observed mean  $\pm$  SE).

**Table 1**

Description of the dataset.

Year	Nb traps	Trap location	Sampling dates	NSes	Alfalfa	Grassland	Number of sampled fields per crop					
							WC/OSR	WC/Sun	OSR/WC	Sun/WC	WC/WC	
2005	3	F	13 <sup>th</sup> May-8 <sup>th</sup> July	5	4	1	2	3	1	1	1	0
2006	3	F	29 <sup>th</sup> April-28 <sup>th</sup> June	3	5	4	3	1	2	0	0	0
2007	3	F	31 <sup>st</sup> May-27 <sup>th</sup> June	2	6	3	4	1	2	1	0	0
2008	3	F	2 <sup>nd</sup> June-30 <sup>th</sup> June	2	5	5	4	2	1	1	0	0
2009	3/4	F/M	27 <sup>th</sup> April-18 <sup>th</sup> July	1/3	61	56	5	6	37	35	61	61
2010	3/4	F/M	7 <sup>th</sup> June-10 <sup>th</sup> July	1/2	67	44	5	2	25	34	49	49
2011	4	F/M	2 <sup>nd</sup> May-1 <sup>st</sup> July	3/4	15	5	10	13	3	6	4	4
2012	4	F/M	27 <sup>th</sup> April-6 <sup>th</sup> July	4/6	14	5	14	9	5	17	11	11
2013	4	F/M	7 <sup>th</sup> May-6 <sup>th</sup> July	3	11	0	10	3	10	10	10	10
<i>Pitfall traps</i>												
<i>Emergence</i>												
2012	2	F/M	10 <sup>th</sup> April-16 <sup>th</sup> July	6	4	-	8	-	5	14	10	10
2013	3	F/M	5 <sup>th</sup> April-5 <sup>th</sup> July	6	10	-	7	-	10	10	9	9

*Year*: trapping year; *Nb traps*: number of traps per field; *Trap location*: trap location within the field (*F*) or in field margin (*M*); *Sampling dates*;

*NSes*: number of trapping sessions per trap; *Number of sampled fields per crop*: perennial crops (*Alfalfa*, *Grassland*) and annual crops named

according to the previous crop (see section 2.2.1) (WC: winter cereal; Sun: sunflower, OSR: oilseed rape).

**Table 2**

GLMM statistical models (full and selected models) used to study *P. cupreus* and *B. sclopeta* AD (from pitfall traps; Models 1 to 6), and emergence density (from emergence traps; Models 7 and 8). Only fixed effects are shown.

Model	TL	Crops	Sampling years	Species	Full model	Selected model
<b>1</b>	F/M	All	2009-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$TL*(JD + JD^2)$	$TL*(JD + JD^2)$
<b>2</b>	M	All	2009-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Crop*(JD + JD^2)$	$Crop + JD$ $Crop*(JD + JD^2)$
<b>3</b>	F	Perennial	2005-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Crop*Age*(JD + JD^2)$	$(Crop + Age)*(JD + JD^2)$ $Crop*Age*(JD + JD^2)$
<b>4</b>	F	Annual	2005-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Crop*(JD + JD^2)$	$Crop*(JD + JD^2)$
<b>5</b>	M	WC	2009-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Previous\ crop*(JD + JD^2)$	$Previous\ crop*(JD + JD^2)$ <i>Null</i>
<b>6</b>	F	WC	2005-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Previous\ crop*(JD + JD^2)$	$Previous\ crop*(JD + JD^2)$ <i>Null</i>
<b>7</b>	F/M	All	2012-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Crop*TL + Year$	$Crop*TL + Year$
<b>8</b>	F/M	WC	2012-2013	<i>P. cupreus</i> <i>B. sclopeta</i>	$Previous\ crop*TL + Year$	$Previous\ crop*TL$

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*Crop*: sampled crop; *Previous crop*; *TL*: trap location within the field (*F*) or in field margin (*M*); *JD*: scaled Julian date;  $JD^2$ : squared *JD*; *Age*: age of perennial crops (in year); *Year*: sampling year.

## Appendix A. Supplementary data

**Table A.1**

Overall and per crop relative abundance of carabid beetle species in the study area. Are presented the 11 species over 133 accounting for at least 2% of the total activity-density during the 2005-2013 period.

	OSR	Sun	WC	Alfalfa	Grassland	All crops
<i>Poecilus cupreus</i>	27,4%	24,9%	35,9%	38,7%	33,3%	<b>33,1%</b>
<i>Brachinus sclopeta</i>	39,9%	5,8%	6,4%	19,5%	7,7%	<b>20,4%</b>
<i>Anchomenus dorsalis</i>	12,5%	1,8%	9,2%	8,8%	4,6%	<b>9,7%</b>
<i>Pterostichus melanarius</i>	1,2%	9,8%	9,5%	0,6%	2,6%	<b>4,6%</b>
<i>Pseudoophonus rufipes</i>	1,4%	27,0%	2,8%	4,1%	7,3%	<b>4,1%</b>
<i>Brachinus crepitans</i>	0,6%	3,4%	8,5%	1,7%	7,6%	<b>4,1%</b>
<i>Calathus fuscipes</i>	0,9%	11,9%	3,7%	3,5%	2,6%	<b>3,2%</b>
<i>Nebria salina</i>	2,0%	2,9%	2,7%	5,2%	0,8%	<b>3,0%</b>
<i>Amara similata</i>	7,2%	0,2%	0,2%	0,7%	0,3%	<b>2,6%</b>
<i>Trechus quadristriatus</i>	0,2%	0,8%	6,0%	0,7%	1,2%	<b>2,4%</b>
<i>Harpalus dimidiatus</i>	0,8%	2,4%	2,3%	2,5%	6,8%	<b>2,0%</b>
<b>Total</b>	<b>94,0%</b>	<b>91,0%</b>	<b>87,4%</b>	<b>86,0%</b>	<b>74,7%</b>	<b>89,1%</b>

## Appendix B. Supplementary data

### Table B.1

Values and significance of Type II Wald chi square tests realized on fixed effects selected in each of the final tested models after the backward stepwise selection procedure (see Table 2).

*P* was set to 0.05 for variable selection for models 1 to 6 and to 0.10 for models 7 and 8.

Fixed effects	<i>P. cupreus</i>		<i>B. sclopeta</i>		
	Chisq	P (>Chisq)	Chisq	P (>Chisq)	
<b>Model 1</b>	JD	2.57	0.11	<b>8.63</b>	<b>0.003</b>
	JD <sup>2</sup>	0.21	0.65	<b>8.97</b>	<b>0.003</b>
	TL	<b>0.46</b>	<b>&lt; 0.001</b>	<b>87.54</b>	<b>&lt; 0.001</b>
	JD*TL	1.30	0.25	<b>19.58</b>	<b>&lt; 0.001</b>
	JD <sup>2</sup> *TL	<b>52.57</b>	<b>&lt; 0.001</b>	<b>206.40</b>	<b>&lt; 0.001</b>
<b>Model 2</b>	JD	<b>31.45</b>	<b>&lt; 0.001</b>	3.71	0.05
	JD <sup>2</sup>	-	-	<b>5.52</b>	<b>0.02</b>
	Crop	<b>30.80</b>	<b>&lt; 0.001</b>	<b>10.84</b>	<b>0.03</b>
	JD*Crop	-	-	<b>10.14</b>	<b>0.04</b>
	JD <sup>2</sup> *Crop	-	-	9.48	0.05
<b>Model 3</b>	JD	<b>19.01</b>	<b>&lt; 0.001</b>	0.01	0.95
	JD <sup>2</sup>	0.72	0.39	<b>5.15</b>	<b>0.02</b>
	Crop	<b>55.37</b>	<b>&lt; 0.001</b>	<b>27.33</b>	<b>&lt; 0.001</b>
	Age	0.02	0.89	0.09	0.76
	JD*Crop	<b>51.12</b>	<b>&lt; 0.001</b>	<b>44.00</b>	<b>&lt; 0.001</b>
	JD <sup>2</sup> *Crop	<b>85.21</b>	<b>&lt; 0.001</b>	<b>36.37</b>	<b>&lt; 0.001</b>
	JD*Age	<b>21.07</b>	<b>&lt; 0.001</b>	<b>46.36</b>	<b>&lt; 0.001</b>
	JD <sup>2</sup> *Age	<b>22.00</b>	<b>&lt; 0.001</b>	<b>22.24</b>	<b>&lt; 0.001</b>
	Crop*Age	-	-	3.12	0.08
	JD*Crop:Age	-	-	<b>4.90</b>	<b>0.03</b>
JD <sup>2</sup> *Crop:Age	-	-	<b>28.55</b>	<b>&lt; 0.001</b>	
<b>Model 4</b>	JD	3.24	0.07	0.42	0.52
	JD <sup>2</sup>	0.91	0.34	<b>17.11</b>	<b>&lt; 0.001</b>
	Crop	<b>37.79</b>	<b>&lt; 0.001</b>	<b>140.23</b>	<b>&lt; 0.001</b>
	JD*Crop	<b>67.36</b>	<b>&lt; 0.001</b>	<b>29.04</b>	<b>&lt; 0.001</b>
	JD <sup>2</sup> *Crop	<b>9.08</b>	<b>0.01</b>	<b>22.19</b>	<b>&lt; 0.001</b>
<b>Model 5</b>	JD	2.94	0.09	-	-
	JD <sup>2</sup>	1.03	0.31	-	-
	Past Crop	1.17	0.56	-	-
	JD*Past Crop	3.35	0.19	-	-
	JD <sup>2</sup> *Past Crop	<b>6.33</b>	<b>0.04</b>	-	-
<b>Model 6</b>	JD	<b>18.94</b>	<b>&lt; 0.001</b>	-	-
	JD <sup>2</sup>	2.56	0.11	-	-



	Past Crop	2.37	0.31	-	-
	JD*Past Crop	<b>9.53</b>	<b>0.009</b>	-	-
	JD <sup>2</sup> *Past Crop	<b>10.61</b>	<b>0.005</b>	-	-
<b>Model 7</b>	Crop	1.85	0.40	3.18	0.20
	TL	0.09	0.77	181.97	< <b>0.001</b>
	Crop*TL	<b>7.30</b>	<b>0.007</b>	<b>5.46</b>	<b>0.07</b>
	Year	<b>5.03</b>	<b>0.08</b>	<b>5.35</b>	<b>0.02</b>
<b>Model 8</b>	Past Crop	2.84	0.24	<b>20.07</b>	< <b>0.001</b>
	TL	0.09	0.76	<b>16.85</b>	< <b>0.001</b>
	Past Crop*TL	<b>10.37</b>	<b>0.006</b>	<b>34.45</b>	< <b>0.001</b>

Figure 1

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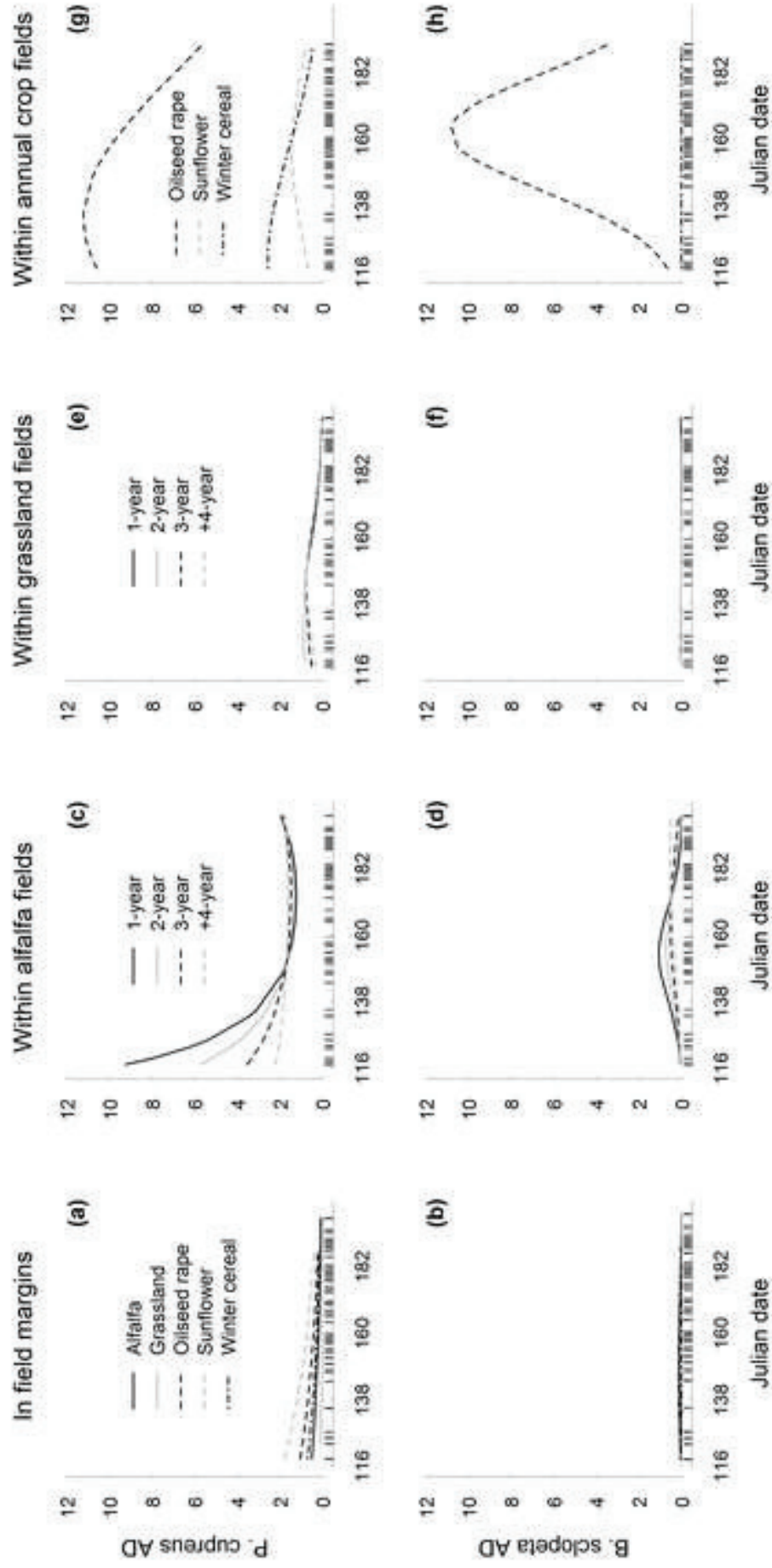


Figure 2  
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