Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape

Ronan Marrec [a,b,*], Isabelle Badenhausser [a,b,c], Vincent Bretagnolle [a,b],
Luca Börger [a,b,d,e], Marilyn Roncoroni [a,b,c], Nadine Guillon [a], Bertrand Gauffre [a,b,c]

[a] CEBC, UMR 7372CNRS – Université de La Rochelle, F-79360 Villiers en Bois, France
[b] LTER, ZA Plaine & Val de Sèvre, CNRS-CEBC, F-79360 Villiers en Bois, France
[c] INRA, USC 1339CEBC, F-79360 Villiers en Bois, France
[d] IGEPP, UMR 1349 INRA – Agrocampus Ouest, F-35653 Le Rheu, France
[e] Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK

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ABSTRACT

This study investigated how crop type and crop succession influence 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 9 years in an agricultural landscape of western France using both pitfall and emergence traps located within and in the margins of fields of the five dominant crops in the study area. The two carabid 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. However, *B. sclopeta* was only active in oilseed rape while *P. cupreus* was also active in the other crops. Overall, data suggested a beneficial role of oilseed rape for both species. *B. sclopeta* emergence from overwintering occurred predominantly in the margins of fields cropped with oilseed rape the previous year. *P. cupreus* used both margins and within field areas as overwintering habitats. 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.

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1. Introduction

Carabid beetles play an important role in agriculture as natural enemies of pests or as elements of trophic chains sustaining biodiversity (Thiele, 1977). Carabid communities in crops are usually numerically dominated by a few species, which may drive ecosystem functioning (Holland and Luff, 2000; Luff, 2002). However, information on the basic ecology of individual species is relatively scant and contradictory for even the most common species (Thomas et al., 2001). Indeed, most studies on carabid beetles investigated the diversity and abundance of the whole community. Detailed understanding of species distribution among habitats at the different life stages can provide insights into their ecological requirements, possibly allowing to better adapt crop protection strategies and/or help design ecological strategies of

management through environmental engineering (Landis et al., 2000; Vasseur et al., 2013; Raymond et al., 2014).

Agricultural landscapes consist of a mosaic of habitat patches whose suitability may be good, moderate or hostile to a given species (Fahrig et al., 2011). This functional representation of patch suitability includes the heterogeneity of the cultivated mosaic which results from the diversity of crops (Vasseur et al., 2013). Crops provide different environmental conditions and food availability which are two of the most important factors influencing carabid beetle distribution (Luff, 1987; Holland, 2002; Thomas et al., 2002). In addition, crops also differ in the intensity and timing of management practices, such as soil tillage and harvesting, which are determined by crop successions (Joannon et al., 2008). Agricultural practices have been shown to influence carabid beetle abundance either directly, through mortality and emigration, or indirectly, by affecting local microhabitat conditions (Kromp, 1999; Cole et al., 2002; Thorbek and Bilde, 2004; Hatten et al., 2007). Accordingly, studies which investigated the effect of crop management practices on the species composition of carabid communities concluded that the

crop type was one of the most influential factors (Booij and Noorlander, 1992; Weibull and Östman, 2003; Eyre et al., 2013). In addition, many species use non-crop habitats at critical moments of their annual life cycle. Adults of spring-summer breeding species often overwinter in boundary structures or grassland habitats and re-colonize crop fields in spring (Lee and Landis, 2002; Geiger et al., 2009). Hence, over their lifetime, individuals can use different habitat types including both crop and non-crop habitats (Bommarco, 1998a) and the dynamics of cropped habitats within the landscape may induce distribution shifts among habitat patches (Thomas et al., 2002; Holland et al., 2005). While many studies have addressed the role of non-crop habitats as alternative and overwintering habitats (*e.g.*, Lys and Nentwig, 1992; Pfiffner and Luka, 2000; Hof and Bright, 2010), few have taken into account the influence of the crop type they were bordering (*e.g.*, Eyre and Leifert, 2011; Eyre et al., 2013) nor the role of annual crops as transient habitats (Vandermeer et al., 2010; Vasseur et al., 2013) to explain species' spatial dynamics.

The aim of the present study was to investigate how spring-breeding carabids use different habitats in the farmland landscape mosaic to complete their annual life cycle. Focusing on two numerically dominant carabid species of agroecosystems in western France, *Poecilus cupreus* (L.) and *Brachinus sclopeta* (Fabricius) (Jeannel, 1942) two crucial life stages were considered, *i.e.*, overwintering and spring reproductive periods. *P. cupreus* is a typical polyphagous predator in arable lands (*e.g.*, Langmaack et al., 2001) associated with many crops (*e.g.*, winter cereals: Heydemann, 1955; Luik et al., 2005 clover: Luik et al., 2005 oilseed rape: Hossfeld, 1963; Schlein and Büchs, 2004; Veromann et al., 2005 pea: Holland et al., 2005). *B. sclopeta* is a bombardier beetle, a genus described as ectoparasitoid of other insects (Erwin, 1979). *B. sclopeta* is characterized as an open habitat species (Zetto Brandmayr et al., 2006) but its ecology is largely unknown. Both species overwinter as adults and reproduce in spring (Matalin, 2007; Pilon et al., 2013). *P. cupreus* overwinters in the soil of crop and non-crop habitats (Wallin, 1985; Holland and Reynolds, 2003),

while *B. sclopeta* was reported to overwinter over ground, forming aggregates under heavy stones in open lands with sparse vegetation (Bonacci et al., 2004). They are macropterous, with well-developed wing muscles (Bommarco, 1998b; Hendrickx et al., 2009; Pilon et al., 2013), although *P. cupreus* is more likely to disperse by walking (Wallin, 1985). We assessed the distribution and abundance of the different stages of the species within cropped fields and their immediate environment (field margins) according to (i) the current crop type and (ii) the crop type in the previous year. It was hypothesized that carabid abundance in a crop type in a given year will impact the distribution and abundance of species in the crop type of the following year along the crop succession (Holland and Reynolds, 2003). Crop rotation and associated agricultural practices, however, may induce rapid distribution shifts and thus are expected to mitigate the influence of previous crop type. As carabid beetle abundance fluctuates widely from year to year and can vary within and between fields (Thomas et al., 2001; Holland et al., 2004, 2005), any reliable knowledge of crop influence should be based on long-term observations carried out simultaneously in many fields of each crop. In the present study, data from surveys carried out over 9 years in 734 fields located in a 430 km^2 study area (including about five hundred farms) were analysed.

2. Materials and methods

The study was conducted in the LTER Zone-Atelier "*Plaine et Val de Sèvre*" covering an area of 430 km^2 in western France (46.23°N, 0.41°W) and dedicated to cereal crop production. Since 1995, land use has been recorded annually for each field and mapped with a geographical information system (ArcGis 9.2 – ESRI Redlands, CA, USA). Perennial crops represented 11.9% ± 0.3 of the total area of the study site (mean value ± SE from 2005 to 2013) including grasslands (8.5% ± 0.4) and alfalfa (3.4% ± 0.3). From 2005 to 2013, annual crops were dominated by winter cereals (36.9% ± 0.4 of the total area), sunflower (10.8% ± 0.5) and oilseed rape (10.1% ± 0.7).

Table 1
Description of the dataset.

	Year	Nb traps	Trap location	Sampling dates	NSes	Number of sampled fields per crop						
						Alfalfa	Grassland	WC/OSR	WC/Sun	OSR/WC	Sun/WC	WC/WC
Pitfall traps	2005	3	F	13th May–8th July	5	4	1	2	3	1	1	0
	2006	3	F	29th April–28th June	3	5	4	3	1	2	0	0
	2007	3	F	31st May–28th June	2	6	3	4	1	2	1	0
	2008	3	F	2nd June–30th June	2	5	5	4	2	1	1	0
	2009	03-Apr	F/M	27th April–18th July	01-Mar	61	56	5	6	37	35	61
	2010	03-Apr	F/M	7th June–10th July	01-Feb	67	44	5	2	25	34	49
	2011	4	F/M	2nd May–1st July	03-Apr	15	5	10	13	3	6	4
	2012	4	F/M	27th April–6th July	04-Jun	14	5	14	9	5	17	11
	2013	4	F/M	7th May–6th July	3	11	0	10	3	10	10	10
			Total number of traps (margin/field)			197/804	117/457	91/316	51/247	102/307	173/434	171/491
Emergence traps	2012	2	F/M	10th April–16th July	6	4	–	8	–	5	14	10
	2013	3	F/M	5th April–5th July	6	10	–	7	–	10	10	9
			Total number of traps (margin/field)			Nov-20		13/16		13/21	23/29	16/21

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 2.1) (WC: winter cereal; Sun: sunflower, OSR: oilseed rape).
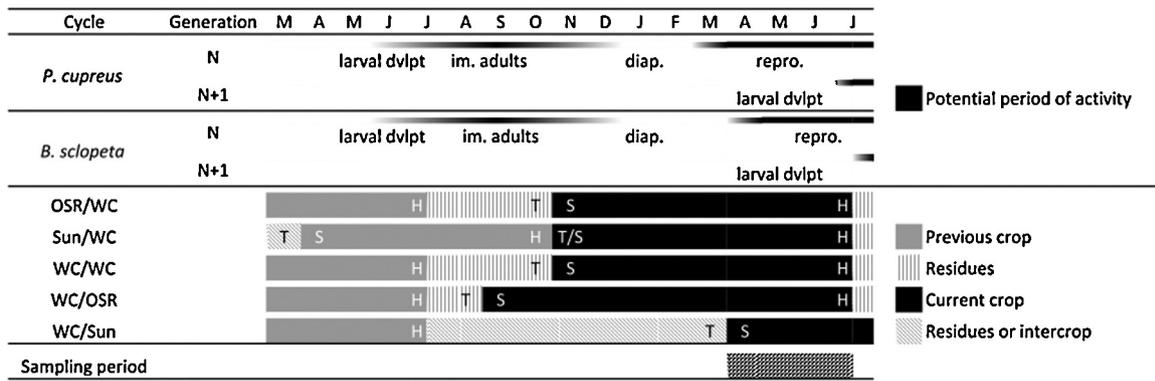
Fig. 1. Timeline summarizing the life cycle of *P. cupreus* and *B. sclopeta*, and the phenology of the two-year crop successions investigated. For carabid species: im. adults: immature adults; diap.: winter diapause; repro.: reproductive period; larval dvlpt: larval development period. For crop successions: T: tillage; S: sowing; H: harvesting.

Other main land uses were urban areas (9.3% ± 0.3) and woodland (2.9% ± 0.1), with other crop types accounting for 18.2% ± 3.4 of the land use.

2.1. Experimental design and sampling technique

First, in order to assess spring activity–density (AD) according to habitat and crop type, carabid beetles were sampled using pitfall traps, the standard method to estimate AD during their activity period (Thiele, 1977). The five dominant crops (alfalfa, grassland, oilseed rape, sunflower and winter cereal), accounting for almost 80% of the arable land use, were sampled from 2005 to 2013 (Table 1). In our sample of fields, oilseed rape and sunflower were always preceded by winter cereals (WC/OSR and WC/Sun respectively), and winter cereal by oilseed rape (OSR/WC), sunflower (Sun/WC) or winter cereal (WC/WC) (Fig. 1). These 2-year crop successions were dominant over the study site (Lazrak et al., 2010). Grassland and alfalfa were classified according to their age deduced from the GIS database (from 1 to +4 years of age). The number of fields sampled in each year and for each succession ranged from 1 to 61 (Table 1). The sampling design varied slightly from year to year, as detailed below. The number of pitfall traps per field ranged from 3 to 4 according to the year. From 2005 to 2013, three pitfall traps were placed between 10 and 30 m from the field margin and at 10 m from each other. From 2009 to 2013, one additional trap was placed in the grassy field margin. Traps were filled with a 50% preservative solution of ethylene glycol (2005–

2010), monopropylene glycol (2009 and 2010) or ethanol (2011–2013). Change in preservative solution was reported to affect catch probability (Luff, 1975; Schmidt et al., 2006). Here, the different preservative solutions used impacted AD but the differences among crops were robust for this bias (data not shown). The number of sampling sessions depended on the year and sampling occurred from late April to mid-July (Table 1). Pitfall traps were left in place for five (2005–2010) or four (2011–2013) trapping-effective days and, for a given year, were set up at the same location for all sessions.

Second, to determine overwintering location of carabid beetles, emergence traps were set up within fields (1 in 2012, 2 in 2013) and in field margins (one trap) to collect post-overwintering emerging adults. Emergence traps were set up at the end of March (81 in 2012 and 102 in 2013; see Table 1) in alfalfa, winter cereal (OSR/WC, Sun/WC, WC/WC), and oilseed rape (WC/OSR) (Table 1) to investigate the influence of habitat type. The emergence trap method consisted of hermetically sealing a soil area to collect all emerging insects, while preventing both emigration and immigration. Insects were caught in one collection bottle and one pitfall trap per emergence trap, both filled with a 70% preservative solution of ethanol. This sampling method has been shown to be efficient to estimate absolute density of ground-dwelling arthropods (Sunderland et al., 1995). The area of each trap was 0.36 m^2 (Soil Emergence trap 96 × 26 mesh, Black, MegaView Science Co., Ltd., Taichung, Taiwan). Traps were emptied every fortnight from early April to mid-July (Table 1), covering most of the adult

Table 2

GLMM statistical models (full and selected models) used to study *P. cupreus* and *B. sclopeta* AD (from pitfall traps; Models 1–6) 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
1	F/M	WC, OSR, Sun, Alf, Grass	2009–2013	*P. cupreus* *B. sclopeta*	TL × (JD + JD^2)	TL × (JD + JD^2)
2	M	WC, OSR, Sun, Alf, Grass	2009–2013	*P. cupreus* *B. sclopeta*	Crop × (JD + JD^2)	Crop + JD Crop × (JD + D^2)
3	F	WC, OSR, Sun, Alf, Grass	2005–2013	*P. cupreus* *B. sclopeta*	Crop × (JD + JD^2)	Crop × (JD + JD^2)
4	F	Alf, Grass	2005–2013	*P. cupreus* *B. sclopeta*	Crop × age × (JD + JD^2)	(Crop + age) × (JD + JD^2) Crop × Age × (JD + JD^2)
5	M	WC	2009–2013	*P. cupreus* *B. sclopeta*	Previous crop × (JD + JD^2)	Previous crop × (JD + JD^2) Null
6	F	WC	2005–2013	*P. cupreus* *B. sclopeta*	Previous crop × (JD + JD^2)	Previo + JD^2) Null
7	F/M	WC, OSR, Alf	2012–2013	*P. cupreus* *B. sclopeta*	Crop × TL + year	Crop × TL + year
8	F/M	WC	2012–2013	*P. cupreus* *B. sclopeta*	Previous crop × TL + year	Previous crop × TL

TL: trap location (within the field (F) or in field margin (M)); crops: sampled crop used in given model (WC: winter cereal; OSR: oilseed rape; Sun: sunflower; Alf: alfalfa; Grass: grassland). In model formulae: crop: sampled crop; previous crop; TL: trap location; JD: scaled Julian date; JD^2: squared JD; age: age of perennial crops (in year); year: sampling year.

emergence period. Carabid beetles were stored in the lab in a 96° ethanol solution and identified at the species level.

2.2. Statistical analyses

Habitat and crop succession influence on carabid AD was analyzed using generalized linear mixed effect models (GLMM) with Poisson distribution and a log-link function, using the package *lme4* (Bates and Maechler, 2013) in R 3.0.2 (R Core Team, 2013). AD of *P. cupreus* and *B. sclopeta* were modeled separately as the response variable using the number of individuals caught in a pitfall trap. Six models were fitted to test our hypotheses (Models 1 to 6 – Table 2). Three random intercepts were included in all models to account for the sampling design: the field identity (N = 660, 572, 672,299, 290 and 296 levels respectively for Models 1–6), 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), and an observation level factor (to account for overdispersion). Furthermore, to account for changes in the consistency of the pattern across years, a random slope for the seasonal variation was included in all models. Seasonal variation was considered as the Julian date (JD) as a quadratic covariate, using a two-degree scaled polynomial (scaled with mean = 0) (date = JD + JD^2). Finally, to account for differences in the number of trapping days between years, sampling effort was included as an offset on a log scale in all models. In all models, the date was included as a quadratic covariate. Two-way interactions were systematically added between the date and all other fixed effects in all models.

The effect of pitfall trap location (TL) (within field *vs.* grassy field margin) on the spring dynamics of *P. cupreus* and *B. sclopeta* AD was first tested using the whole dataset (Model 1). In a second step, crop type effect on the dynamics of *P. cupreus* and *B. sclopeta* AD was tested, (i) in field margins (Model 2), and (ii) within fields (Model 3) of all crops pooled. Finally, the effect of crop succession was modeled separately for perennial and annual crops. In Model 4 the age effect of perennial crops was tested within field and included as an interacting covariate with crop and date effects. Models 5 and 6 tested for the influence of the previous crop (oilseed rape, sunflower or winter cereal) on the dynamics of carabid AD in field margins and within fields of winter cereal, respectively. The effect of the previous crop was only tested in winter cereal because the other annual crops were always preceded by winter cereal in the dataset (see Section 2.1).

A backward stepwise selection procedure was used for all models: the full model was simplified step-by-step by removing the most non-significant interaction terms and explanatory variables, using maximum likelihood ratio tests (Type II Wald chi square tests) in the R package *car* (function *Anova*; Fox and Weisberg, 2011). *P* was set to 0.10 for variable selection (in order to include marginally significant variables in the selected models) and to 0.05 for variable significance (Table 2).

To investigate the influence of habitat and crop succession on carabid emergences, GLMM models with a Poisson distribution and log-link function were also used. Emergences from early April to the beginning of June were pooled (*i.e.*, sessions one to four), thus excluding data collected thereafter because many traps were destroyed in June 2013 by violent thunderstorms. In the undamaged emergence traps, these four first sessions included 88.9% and 83.3% of the total *P. cupreus* and *B. sclopeta* individuals respectively. Data considered were the number of individuals caught in an emergence trap for each species separately. For each species, two models were fitted to test our hypotheses (Table 2). The field identity and observation level factor were included as random effects in all models. The sampling year was included as a

fixed additive factor in all models. Crop type (alfalfa, oilseed rape and winter cereal) and trap location (TL) (two-way interaction included) were first tested (Model 7). Secondly, Model 8 tested for the influence of the previous crop (oilseed rape, sunflower or winter cereal) and TL (two-way interaction included) on emergences in winter cereal fields. As for pitfall trap data, the effect of the previous crop was only tested in winter cereal because the other annual crops were always preceded by winter cereal in the dataset (see Section 2.1). The same methodology as for pitfall trap data was used for variable selection and for parameter significance (Table 2).

Table 3
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 0.10 for variable selection.

		P. cupreus		B. sclopeta	
	Fixed effects	Chisq	P (>Chisq)	Chisq	P (>Chisq)
Model 1	JD	2.57	0.11	8.63	0.003
	JD^2	0.21	0.65	8.97	0.003
	TL	0.46	<0.001	87.54	<0.001
	JD:TL	1.3	0.25	19.58	<0.001
	JD^2:TL	52.57	<0.001	206.4	<0.001
Model 2	JD	31.45	<0.001	3.71	0.05
	JD^2	–	–	5.52	0.02
	Crop	30.8	<0.001	10.84	0.03
	JD:crop	–	–	10.14	0.04
	JD^2:crop	–	–	9.48	0.05
Model 3	JD	2.4	0.12	7.66	0.006
	JD^2	0.58	0.44	8.92	0.003
	Crop	63.66	<0.001	112.35	<0.001
	JD:crop	116.46	<0.001	25.77	<0.001
	JD^2:crop	120.23	<0.001	21.89	<0.001
Model 4	JD	19.01	<0.001	0.01	0.95
	JD^2	0.72	0.39	5.15	0.02
	Crop	55.37	<0.001	27.33	<0.001
	Age	0.02	0.89	0.09	0.76
	JD:crop	51.12	<0.001	44	<0.001
	JD^2:crop	85.21	<0.001	36.37	<0.001
	JD × age	21.07	<0.001	46.36	<0.001
	JD^2 × age	22	<0.001	22.24	<0.001
	Crop × age	–	–	3.12	0.08
	JD × crop:age	–	–	4.9	0.03
	JD^2 × crop:age	–	–	28.55	<0.001
Model 5	JD	2.94	0.09	–	–
	JD^2	1.03	0.31	–	–
	Previous crop	1.17	0.56	–	–
	JD × previous Crop	3.35	0.19	–	–
	JD^2 × previous Crop	6.33	0.04	–	–
Model 6	JD	18.94	<0.001	–	–
	JD^2	2.56	0.11	–	–
	Previous crop	2.37	0.31	–	–
	JD × previous Crop	9.53	0.009	–	–
	JD^2 × Previous Crop	10.61	0.005	–	–
Model 7	Crop	1.85	0.4	3.18	0.2
	TL	0.09	0.77	181.97	<0.001
	Crop × TL	7.3	0.007	5.46	0.07
	Year	5.03	0.08	5.35	0.02
Model 8	Previous crop	2.84	0.24	20.07	<0.001
	TL	0.09	0.76	16.85	<0.001
	Previous crop × TL	10.37	0.006	34.45	<0.001

In model formulae: crop: sampled crop; Previous crop; TL: trap location; JD: scaled Julian date; JD^2: squared JD; age: age of perennial crops (in year); year: sampling year.

3. Results

A total of 18536 individuals of *P. cupreus* and 10,765 of *B. sclopeta* were collected in pitfall traps between 2005 and 2013. The two species accounted for more than 50% of the total activity density (AD) in pitfall traps (Appendix A). The number of individuals caught per trap (observed mean ± SE; all crop types combined) fluctuated among years, with a minimum in 2013 for both species (*P. cupreus*: 1.07 ± 0.19; *B. sclopeta*: 0.73 ± 0.18) and a maximum in 2008 for *P. cupreus* (15.10 ± 2.15) and 2005 for *B. sclopeta* (16.12 ± 6.04) respectively. With the emergence traps, a total of 98 *P. cupreus* and 390 *B. sclopeta* were trapped between early April and early June in 2012 and 2013.

The AD of *P. cupreus* was significantly higher in traps located within fields than in traps located in field margins (observed mean ± SE: 6.08 ± 0.27 and 1.97 ± 0.20 within fields and in margins, respectively – Model 1, Tables 2 and 3). In addition, the dynamics of *P. cupreus* AD differed according to trap location (Table 3). For *B. sclopeta* instead, there was no overall significant AD difference between trap locations (Model 1, Tables 2 and 3), but the temporal dynamics of AD differed between locations with steeper increases within fields than in field margins during the spring. Analyzes were performed to further investigate the dynamics of AD of both carabid species within fields and in field margins separately.

The temporal dynamics of *P. cupreus* AD had the same pattern in all crop margins and decreased significantly from the beginning of the trapping period to the end (Fig. 2a – Model 2, Tables 2 and 3). AD differed significantly between crops, being highest in sunflower margins and lowest in grassland margins (Fig. 2a; Table 3). *B.*

sclopeta AD in field margins was almost zero and did not vary among crops (Model 2, Tables 2 and 3)

Within fields, *P. cupreus* AD and its dynamics varied significantly among crops (Model 3, Tables 2 and 3). The highest AD was in oilseed rape during the whole trapping period and was more than twice higher than in all other crops (Fig. 2b). Among the other crops, *P. cupreus* AD was maximal in alfalfa and was null in grassland fields (Fig. 2b). In alfalfa and winter cereal, the highest AD was at the beginning of the trapping period. Then, AD decreased continuously in alfalfa while the decrease started from mid-May in winter cereal. In oilseed rape and sunflower, *P. cupreus* AD increased during spring, peaked from the end of May to mid-June and then decreased. As for *P. cupreus*, *B. sclopeta* AD and its dynamics varied significantly among crops (Model 3, Tables 2 and 3). *B. sclopeta* individuals were almost exclusively trapped in oilseed rape fields (Fig. 2c) where AD increased importantly until mid-June and then declined.

P. cupreus AD and its dynamics did not vary with the age of alfalfa and grassland (Model 4, Tables 2 and 3). *B. sclopeta* AD tended to decrease with age of perennial crops (Model 4, Table 3). Neither Tables 2 and 3).

Distribution of overwintering *P. cupreus* was influenced neither by the crop nor by the trap location (Model 7, Tables 2 and 3). *B. sclopeta* emerged mainly in field margins (Model 7, Tables 2 and 3), whatever the crop (Table 3).

P. cupreus overwintering densities were low in winter cereals, both within the fields and in their margins and irrespective of the previous crop type. High densities of *B. sclopeta* emerged in OSR/ WC field margins (Model 8, Table 2 and 3), while almost no emergence occurred elsewhere (Fig. 3).
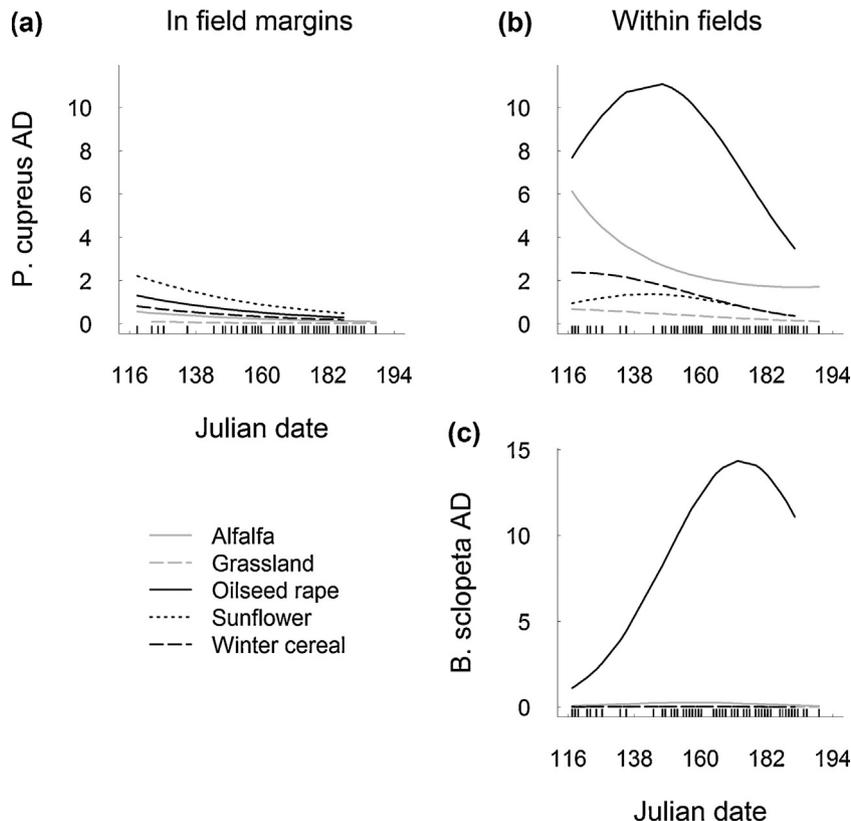

Fig. 2. Spring dynamics of *P. cupreus* activity-density (AD) per trap in field margins (a) and of *P. cupreus* and *B. sclopeta* AD within fields (b and c) of alfalfa, grassland, oilseed rape, sunflower and winter cereal. Predictions were made over all years using parameters estimated in GLMM Models 2 and 3. Julian date courses from the 27th April to the 18th July. Width of ticks at the bottom of each plot represents the sampling effort.
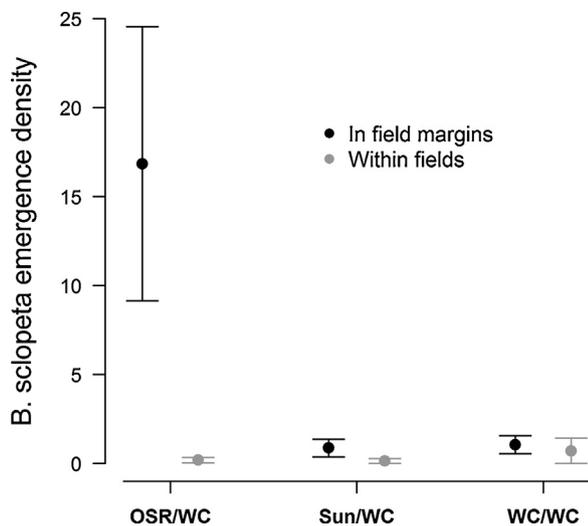
Fig. 3. Effects of the previous crop (oilseed rape, sunflower and winter cereal) and trap location (in field margin or within field) on *B. sclopeta* emergence density per trap in winter cereal fields (observed mean ± SE over all years).

4. Discussion

Crop type strongly influenced spring activity density (AD) and overwintering emergence of both *P. cupreus* and *B. sclopeta*, the two dominant spring breeding carabid species in the study area. Oilseed rape had a highly beneficial role for both species which, however, showed different strategies of habitat use to complete their life cycle. Using pitfall traps, some limitations can appear when comparing AD among crops, due to differences in catch probability (Lang, 2000; Thomas et al., 2006). Nevertheless, biases linked to variation in activity alone cannot explain observed differences among crops. Furthermore, differences among crops were supported by results obtained using the unbiased emergence trap method (Holland and Reynolds, 2003). Effect of crop type on carabid species distribution had only been suggested in previous studies (*e.g.*, Thomas et al., 2002; Holland et al., 2005; Eyre et al., 2013). Importantly, contrary to these earlier studies which involved one or few fields at small spatial and temporal scales, our results are based on a large dataset of different fields and crop types. The present design overcomes the uncertainties generated by the highly heterogeneous distribution of carabid beetles within fields, between fields and between years (*e.g.*, Holland and Luff, 2000; Holland and Reynolds, 2003).

4.1. Spatial and temporal distribution shifts among habitat types

During the spring reproductive period, *P. cupreus* AD was high in every crop except grassland. This is consistent with previous studies that have shown its preference for arable lands (Langmaack et al., 2001; Holland et al., 2005). In addition, differences were found in AD and its dynamics among crops. First, AD was highest in oilseed rape and alfalfa during the early spring. This suggests that these crops were major overwintering habitats for this species. Consistently, *P. cupreus* post-overwintering emergences tended to be highest within fields of oilseed rape. Post-overwintering emergences in alfalfa were lower than expected according to pitfall trap data. This raises the difficulty of interpreting pitfall trap data, which measure both activity and abundance (Thiele, 1977). Overwintering in field margins, especially in those bordering sunflower and oilseed rape fields, was also suggested by pitfall and emergence data. By using emergence traps, more robust data were obtained because the confounding influence of activity and redistribution was excluded (Holland and Reynolds, 2003). Here,

the high and rapidly declining early spring AD in alfalfa and margins may be explained by *P. cupreus* redistribution from perennial habitats to annual crops. Then, AD peaked in late May especially in oilseed rape, suggesting that it may be the main reproductive habitat for *P. cupreus*. Since abundance and reproductive success in one crop may have an impact on the following crop type in a crop succession (Holland and Reynolds, 2003), adults of the new generation should be expected to overwinter within OSR/WC fields. However, in our study there was no positive influence of oilseed rape in the previous year on overwintering emergences and spring AD in winter cereal. This result suggests a complete distribution shift between spring and winter.

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

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 distribution shifts have been reported in *P. cupreus* (Thomas et al., 2001) and other carabid species (Holland, 2002; Thorbek and Bilde, 2004; Holland et al., 2005), suggesting either inter-field movements or differences in survival rates. Rapid colonization of fields sown with oilseed rape in August by *P. cupreus* adults of the new generation was strongly suggested by the present study. Conversely, in *B. sclopeta* inter-field movements to reach new oilseed rape fields are likely to occur in spring since it was found to overwinter in OSR/WC margins. In the present study, inter-field movements were not directly addressed but might well explain the patterns observed. Further studies are needed to investigate the effect of landscape configuration and composition on carabid movements since landscape structure has been shown to affect carabid communities (Maisonhaute et al., 2010; Trichard et al., 2013).

Patterns found using emergence and pitfall traps were consistent for *P. cupreus*, but not for *B. sclopeta* which was absent from early spring pitfall traps in OSR/WC field margins. Differences in species' dispersal ability may explain this paradox. *P. cupreus* is reported to disperse mainly by walking (Wallin 1985). Consistently, moving individuals were caught in pitfall traps. On the other hand, colonization of new oilseed rape 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 traps of the emergence traps (data not shown).

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

Association with a particular crop had been previously suggested for carabid beetles, and for *P. cupreus* in particular (Heydemann, 1955; Thomas et al., 2001; Holland et al., 2005). Carabid beetle preference for oilseed rape, despite the large quantity of chemical insecticides used on this crop, had been previously reported (Williams, 2010; Eyre et al., 2013).

First, species may select oilseed rape according to the coincidence of their periods of emergence, activity and breeding with oilseed rape phenology and timing of crop management practices (Thiele, 1977; Holland and Luff, 2000). In the study area,

oilseed rape is available all year round since new oilseed rape fields are sown in August and oilseed rape stubbles are ploughed in October (Fig. 1). Hence, new oilseed rape fields provide an undisturbed habitat in autumn with a large vegetation cover. This may explain why *P. cupreus* has been found overwintering within new oilseed rape fields. Second, species distribution depends on availability of resources (Lövei and Sunderland, 1996). *P. cupreus* preference for oilseed rape can be related to the larger amount of prey items found in oilseed rape (Haschek et al., 2012), especially agricultural pests such as the pollen beetle *Meligethes aeneus* (Stephens) (Veromann et al., 2008), *Ceutorhynchus* Germar weevils (Piper and Williams, 2004), the brassica pod midge *Dasineura brassicae* (Winnertz) (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), as most oilseed rape pests (Alford et al., 2003; Williams, 2010). Moreover, Saska and Honek (2004) demonstrated that larvae of two closely-related species (*B. crepitans* and *B. explodens*) were able to feed on pupae of *Amara* Bonelli carabid beetles which are particularly abundant in oilseed rape throughout Europe (Williams et al., 2010) and in our study site in particular (unpublished result). Association with oilseed rape for reproduction may explain why *B. sclopeta* colonized oilseed rape only in spring, when its reproductive period start (Saska and Honek, 2008). Finally, abiotic characteristics such as soil structure and microclimatic conditions affect carabid beetles and could influence the observed distribution pattern (Thiele, 1977; Forsythe, 2000; Giglio et al., 2003). Habitat selection based on soil softness (Giglio et al., 2003) may partly explain the higher density of individuals overwintering within fields of annual crops which are ploughed annually. Moreover, oilseed rape provides moist environmental conditions that are preferred by the two studied species (Forsythe, 2000; Pilon et al., 2013).

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2014.10.005.

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