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RESEARCH ARTICLE

Spatiotemporal dynamics of the agricultural landscape mosaic drives distribution and abundance of dominant carabid beetles

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Abstract

Context Agroecosystems are dynamic, with yearly changing proportions of crops. Explicit consideration of this temporal heterogeneity is required to decipher population and community patterns but remains poorly studied.

Objectives We evaluated the impact on the activity-density of two dominant carabid species (*Poecilus cupreus* and *Anchomenus dorsalis*) of (1) local crop, current year landscape composition, and their interaction, and (2) inter-annual changes in landscape composition due to crop rotations.

Methods Carabids were sampled using pitfall-traps in 188 fields of winter cereals and oilseed rape in three agricultural areas of western France contrasting in their spatial heterogeneity. We summarized landscape composition in the current and previous years in a multi-scale perspective, using buffers of increasing size around sampling locations.

Results Both species were more abundant in oilseed rape, and in landscapes with a higher proportion of oilseed rape in the previous year. *P. cupreus* abundance was negatively influenced by oilseed rape

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proportion in the current year landscape in winter cereals and positively by winter cereal proportion in oilseed rape. *A. dorsalis* was globally impacted at finer scales than *P. cupreus*.

Conclusions Resource concentration and dilution-concentration processes jointly appear to cause transient dynamics of population abundance and distribution among habitat patches. Inter-patch movements across years appear to be key drivers of carabids' survival and distribution, in response to crop rotation. Therefore, the explicit consideration of the spatiotemporal dynamics of landscape composition can allow future studies to better evidence ecological processes behind observed species patterns and help developing new management strategies.

Keywords Crop rotation · Landscape dynamics · Landscape composition · Temporal redistribution · Oilseed rape · Resource concentration · Dilution-concentration processes · Multi-scale framework · *Poecilus cupreus* · *Anchomenus dorsalis*

Introduction

To better manage ecosystem services such as biological control, it is important to increase our knowledge on factors influencing the distribution and abundance of agricultural pests and their natural enemies in agricultural landscapes (Rusch et al. 2012; Vinatier et al. 2012). However, the interacting effects of local (i.e., patch level) and landscape factors on pests or natural enemies are still poorly understood (Martin et al. 2013; Caro et al. 2016).

Agricultural landscapes consist of a mosaic of patches that provide a range of habitats varying in their suitability depending on the organism under study (Fahrig et al. 2011). For many studies on the landscape ecology of agroecosystems, the patch-matrix paradigm (sensu Forman 1995) that stipulates habitat patches are distributed in an inhospitable landscape matrix has been the prevailing conceptual framework (Vasseur et al. 2013; Bertrand et al. 2016b). However, this neglects the fact that many species accomplish most of their life cycle in the matrix and their population sizes are likely to be shaped by the heterogeneity and structure of the crop mosaic. In addition, most studies have considered agricultural landscapes as static and only their characteristics during the sampling period are usually taken into account (Fahrig et al. 2011; Vasseur et al. 2013; Bertrand et al. 2016b). While this is relevant when investigating the role of permanent landscape elements, such as grasslands, hedgerows, and woodlots, it precludes assessing the influence of the different crop types and rotation dynamics of annual crops (Vasseur et al. 2013; Marrec et al. 2015). Therefore, more concern should be given to the role of the dynamics of the crop mosaic for biodiversity management (Bertrand et al. 2016b), to provide a more realistic representation of the ecological functionality of spatially and temporally varying cropped systems.

Population spatial dynamics in heterogeneous landscapes

The amount of habitat in a landscape can affect animal populations in two opposite ways (Schneider et al. 2015). At larger scales, the *resource concentration hypothesis* predicts that landscapes with high proportions of host habitat should be more attractive, resulting in higher abundance of individuals due to long-distance dispersal (i.e., increase of local abundance with increasing proportion of host habitat in the landscape; Schneider et al. 2015). On the other hand, at smaller spatial scales, *dilution and concentration effects* may lead to either lower or higher local abundance depending on the proportion of available host habitat in the surrounding landscape, which defines the area over which individuals can distribute (Tscharntke et al. 2012). This theoretical framework has been suggested for the simple case of habitat-specialist pest species (Schneider et al. 2015). However, many pests and most of their natural enemies are not strictly associated with a single crop type but rather may exploit other crop types and semi-natural habitats with different levels of suitability (e.g., Alignier et al. 2014; Marrec et al. 2015). This suitability may also vary according to the season (crop phenology) and stage of the organism life cycle. Alternative habitats may provide either lower quality substitutable resources or non-substitutable resources (*landscape complementation* and *landscape supplementation*; Dunning et al. 1992). An expected consequence is an increase of local population abundance with increasing proportion of different complementary or supplementary habitats in the landscape, as they make the landscape globally more suitable (Dunning et al. 1992), as predicted by the resource concentration hypothesis. In addition, extending the number of alternative habitat types is likely to increase the global amount of habitat and thus strengthen the role of dilution-concentration processes, in particular between habitat types of different suitability. The effect of alternative habitat proportion in the landscape is however complex to predict and is likely to vary among crop types and species, especially depending on the strength of association to the different crop types and individual ability to move between patches of different habitat types.

Influence of temporal landscape changes on population spatial dynamics

Crop rotation is a major source of structural changes in agroecosystems, modifying constantly the landscape composition across time. The ephemeral nature of annual crops is thus likely to induce further redistributions of individuals in the landscape from year to year (Vandermeer et al. 2010). Consequently, dilution and concentration effects may therefore be expected across time, as individuals are frequently forced to move from former habitats destroyed by crop rotation to more suitable ones (Fig. 1a; Schneider et al. 2015). For example, an increase in a suitable crop proportion in a landscape from one year to another can lead to inter-annual dilution effects (Fig. 1b; e.g., Thies et al. 2008; Holzschuh et al. 2011) due to migration into a larger amount of newly available habitat. On the other hand, a high proportion of a suitable crop in the previous year landscape is likely to result in a larger population in the next generation the following year (i.e., increase of local abundance in the current year with increasing proportion of a source, suitable habitat in the previous year landscape; Fig. 1b). The effects of spatiotemporal changes of the crop mosaic on biodiversity patterns depending on these processes operating at different spatial and temporal scales remain poorly investigated, especially on beneficial generalist species.

Carabid populations in spatiotemporally dynamic agricultural landscapes

In this study, we aimed at identifying the factors driving the distribution and abundance of carabid beetles in agroecosystems facing high structural changes. Carabid beetles are a major component of agricultural biodiversity and have an important functional role in providing biocontrol services and as preys for birds and mammals (Kromp 1999; Holland 2002). At field level, crop type has been recognized as a major determinant of carabid distribution and abundance (e.g., Holland et al. 2005; Marrec et al. 2015). Carabid beetles are also strongly affected by management intensity (Vanbergen et al. 2005; Caro et al. 2016) and practices, particularly by crop rotation and associated practices (Kromp 1999; Thorbek and Bilde 2004; Hatten et al. 2007).

Landscape was shown to affect carabid abundance and/or community structure through composition in crop and non-crop patches (Vanbergen et al. 2010; Labruyere et al. 2015; Duflot et al. 2016). At the farm scale, based on the survey of five adjacent fields over 3 years, Holland et al. (2005) showed that carabid abundance and distribution shift among adjacent fields to follow inter-annual redistribution of crop types, and suggested the strong role of landscape-scale movements. Species distribution shifts are though likely to occur in response to crop rotation at scales larger than adjacent fields, through the movement of individuals across landscapes in search for a new habitat (Dunning et al. 1992; Marrec et al. 2015).

In agricultural landscapes, carabid communities are usually numerically dominated by a few species (Holland and Luff 2000; Luff 2002; Vanbergen et al. 2005). Recent studies established a significant effect of temporal heterogeneity of crops on the abundance of dominant carabid species both at the field (Marrec et al. 2015) and landscape levels (Bertrand et al. 2016b), which suggested inter-annual redistribution of carabid beetles in the landscape due to crop rotation. However, how local crop type interacts with landscape composition to shape carabid abundance and distribution in space and time remains largely unknown.

In this paper we investigated how inter-annual changes in the composition of the crop mosaic influenced the distribution and abundance of common carabid beetles in two major winter crops: winter cereals and oilseed rape. We analyzed a dataset

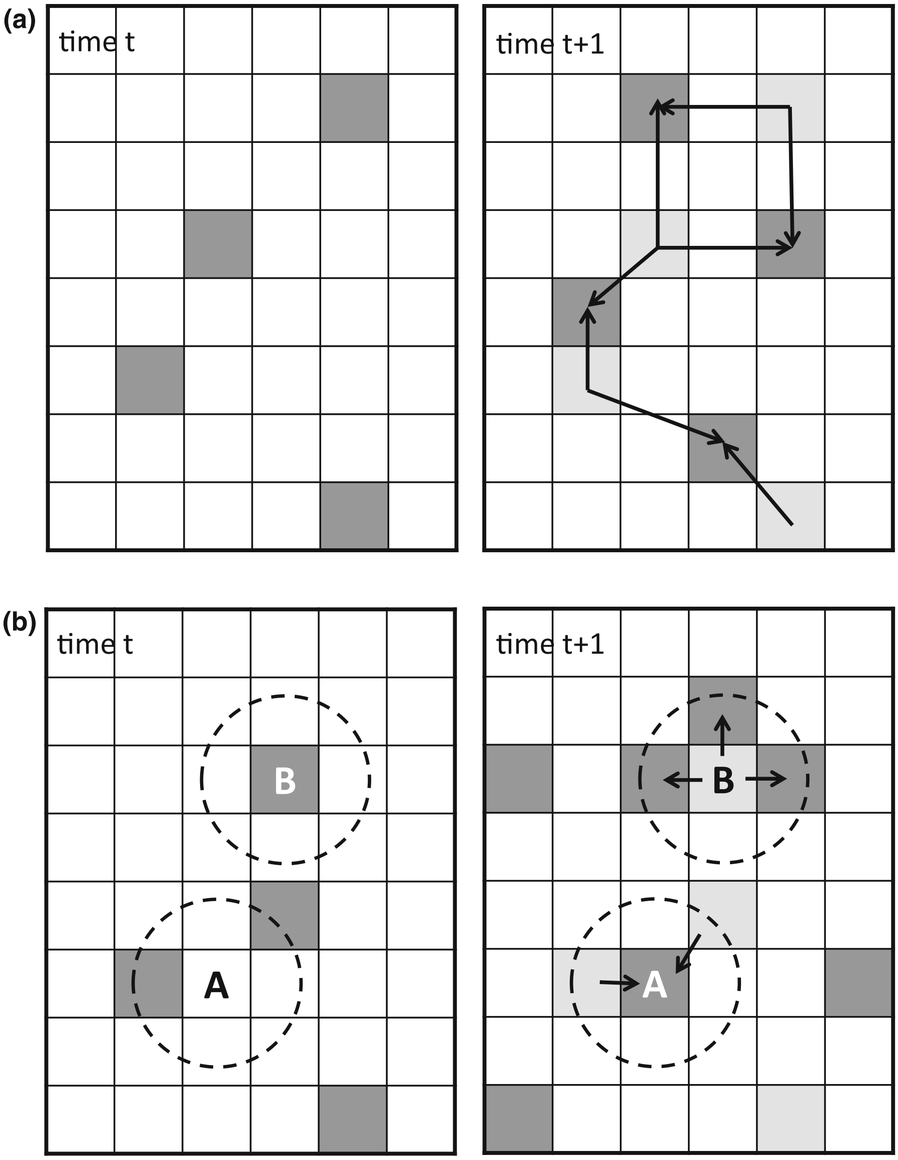

Fig. 1 Transient dynamics of landscape moderation on populations. First, temporal inter-habitat movements may be expected in situations of habitat destruction (e.g., following crop ploughing) between time t and time t + 1 **(a)**. Organisms which survived destruction of suitable habitat patches (dark gray, left panel) at time t are likely to move out to escape newly unsuitable conditions at time t + 1 (light gray, right panel), and search for new suitable habitat in the surrounding landscape (dark gray, right panel). In this case, sources of individuals are ephemeral (Vandermeer et al. 2010) and 'hidden' at time t + 1 because of their destruction due to crop rotation (Vasseur et al. 2013). Landscape dynamics due to crop rotation is also expected to create spatial transient concentration or dilution effects **(b)**. In situations of habitat restoration (patch A) or destruction (patch B), between time t and time t + 1, transient increases in abundance may locally occur in remnant habitat patches. Individuals emigrating from newly destroyed habitats (unsuitable habitat; light gray) may concentrate (e.g., in patch A) or dilute (e.g., in patches surrounding patch B), depending on the quantity of available suitable habitat at time t + 1 (dark gray). This process will involve an increase of abundance in patch A and a decrease in patch B. Dashed circles represent area accessible by individual movements. In all four panels, white patches are considered as always unsuitable

collected over 3 years in three study areas of western France and used generalized linear mixed models (GLMM) to test for the influence of local and landscape components on the spring activity-density of two dominant carabid species with contrasted life history traits, *Poecilus cupreus* (L.) and *Anchomenus* *dorsalis* (Pontoppidan). As oilseed rape is expected to be the most favorable spring habitat for the two species (Marrec 2014; Marrec et al. 2015), we specifically tested the following predictions:

(1) Considering the current-year landscape, our first aim was to decipher the role of resource concentration and dilution-concentration hypotheses on carabid distribution and abundance by investigating the effect of oilseed rape proportion in the landscape. With resource concentration effects, oilseed rape proportion in the landscape is expected to increase local abundance, whereas the opposite pattern is expected with dilution-concentration effects (Schneider et al. 2015). In addition, resource concentration effects are expected to occur at larger spatial scales. We tested the same hypotheses for the effect of winter cereals, another suitable, but less favorable crop type. Lastly, we investigated the effect of the proportion of permanent elements (grasslands and hedgerows) in the landscape and expected a positive impact considering their potential role as complementary or supplementary habitats.

(2) At the temporal level, because oilseed rape is expected to be a major inter-annual source of carabid beetles, we tested the prediction that a high proportion of oilseed rape in the previous year influences positively the abundance of carabid beetles the following year through temporal redistribution of individuals at the landscape level (Fig. 1).

Methods

Study sites and data collection

Carabid beetles were trapped during spring in three French long-term ecological research sites (LTER) located in western France (Fig. 2) that comprise a large gradient in landscape structure. The study sites differ in their level of agricultural intensification, defined by the proportion of perennial habitats such as permanent grasslands, low in intensively managed sites. *Armorique* study site (ARM, ca. 130 km^2; 48°36′N, 1°32′W) is composed of hedged farmlands, characterized by a mixture of cultivated crops [mainly winter wheat (17.08 ± 7.33; Mean % ± SD of the total buffer surface at 1000 m radius around sampled points) and maize (23.11 ± 6.19)] and permanent grasslands (30.66 ± 12.56) with a dense network of hedgerows. *Vallées et Coteaux de Gascogne* study site (VCG, ca. 45 km^2; 43°17′N, 0°54′E) is a hilly farmland, composed of crop-livestock fields and a high proportion of permanent grasslands (37.61 ± 12.05). Finally, *Plaine & Val de Sèvre* study site (PVS, ca. 430 km^2; 46°23′N, 0°41′W) is a lowland intensive farmland area strongly dominated by annual crops, mainly winter cereals (38.43 ± 10.69).

In the three study sites, sampling was carried out in conventionally managed fields of winter oilseed rape and winter cereals. ARM was monitored in 2010 and 2011 (41 fields), VCG from 2010 to 2012 (48 fields) and PVS from 2011 to 2013 (99 fields; Table 1, Fig. 2). Data were collected from late April to early July using three 8-cm diameter pitfall traps randomly located within fields for four effective days (i.e., 96 h) and half-filled with a 50% conservative solution of ethanol and a few drops of detergent. The number of trapping sessions per year ranged from two to nine depending on site and year (Table 1). Carabid beetles were stored in the lab in a 96° ethanol solution and identified to species level following Jeannel (1941, 1942) and Hurka (1996). Data from the three pitfall traps were kept separate and used as the statistical unit in the following analyses.

Carabid species

P. cupreus and *A. dorsalis* were among the most common and abundant species over the three study sites (see ESM Appendix 1). These species are omnivorous and are widely spread over European arable lands, especially on winter annual crops (Langmaack et al. 2001; Büchi 2002; Schlein and Büchs 2004; Thorbek and Bilde 2004; Luik et al. 2005; Zaller et al. 2009). Both species overwinter as adults and reproduce in spring (Matalin 2007; Pilon et al. 2013). *P. cupreus* has been shown to overwinter both within cultivated fields and perennial habitats (Marrec et al. 2015) whereas *A. dorsalis* overwinters mostly in perennial habitats such as field margins (Marrec 2014). They are macropterous, with well-developed wing muscles (Bommarco 1998; Pilon et al. 2013), although *P. cupreus* is more likely to disperse by walking (Wallin 1985).

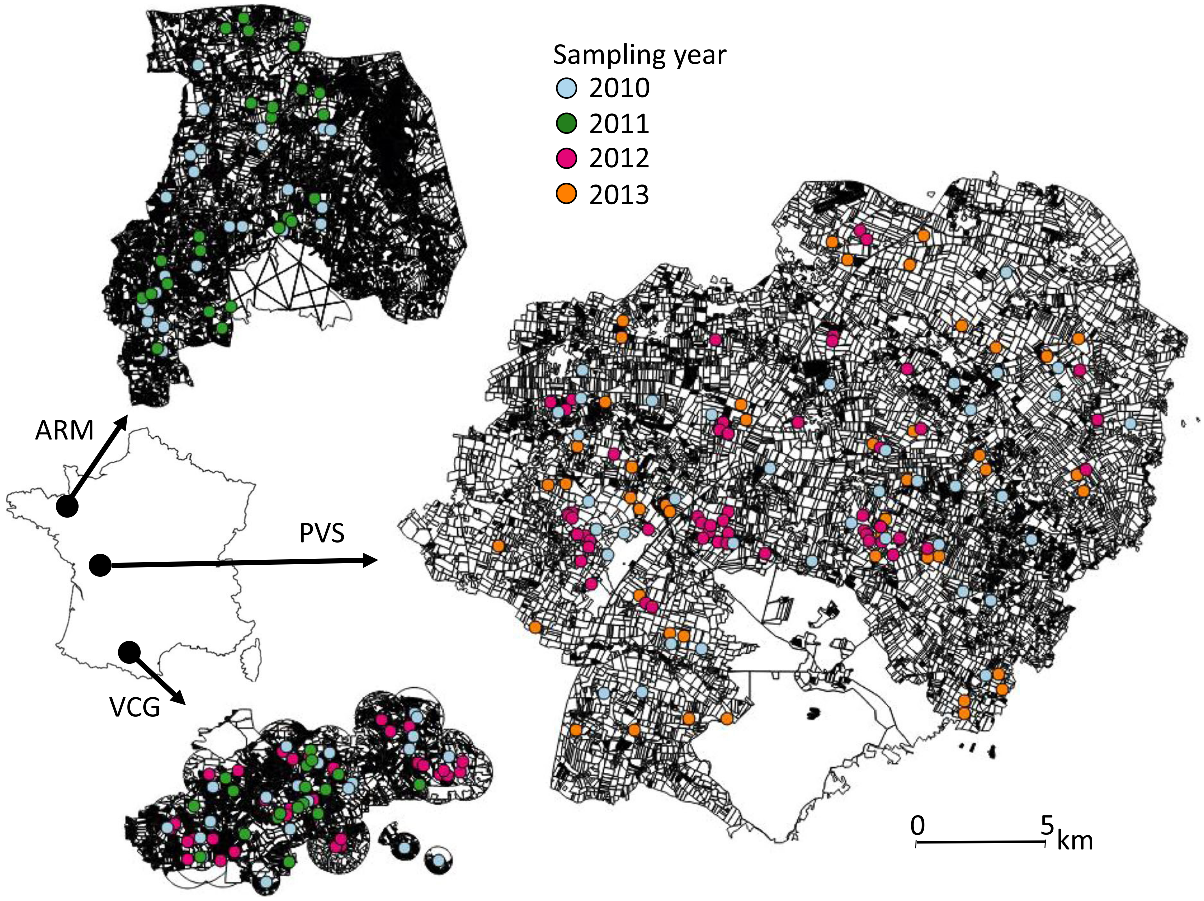

Fig. 2 Maps of the three study areas showing the location of sampled fields in each year (color dots) and the proportion of grassland (black areas). From north to south, ARM, PVS and VCG study sites. (Color figure online)

Table 1 Description of the dataset. For each site: range of the sampling dates (Range), number of times fields were sampled per year (Nb sessions), and number of sampled fields per year and crop type (*OSR* oilseed rape, *WC* winter cereal)

Year	Range	Nb sessions	OSR	WC
Arm site				
2010	From 6th May to 8th July	9	6	11
2011	From 22nd April to 24th June	5	8	16
2012	–	–	–	–
2013	–	–	–	–
VCG site				
2010	From 26th April to 2nd July	5	–	6
2011	From 22nd April to 17th June	5	6	8
2012	From 29th April to 24th June	5	10	18
2013	–	–	–	–
PVS site				
2010	–	–	–	–
2011	From 2nd May to 21st June	2/4	9	10
2012	From 12th April to 28th June	6	8	33
2013	From 7th May to 5th July	2/3	9	30

Landscape descriptors

Landscape descriptors were quantified in nine concentric buffers of increasing radius around each pitfall trap. Buffer radii examined were set every 100 m from 200 m up to 1000 m radius. The maximal distance was set to 1000 m, which is much greater than usually considered in such studies on carabid beetles, often up to 500 m (e.g., Weibull and Östman 2003; Aviron et al. 2005; Maisonhaute et al. 2010). Geoprocessing and buffer extraction were undertaken using QUANTUMGIS 2.14 (QGIS Development Team 2016).

Moreover, as suggested by Martin and Fahrig (2012) and Fahrig (2013), we preferred considering composition-based measurements of patch isolation rather than distance and configuration-based measurements to study species' responses to landscape. Composition was summarized within each buffer as (1) the proportion of each of the three most abundant annual crop types (winter cereals, WC_{Land}; oilseed rape, OSR_{Land}; and spring crops, including sunflower and maize, SC_{Land}), both in the current and previous year ($n = 6$ variables); (2) the proportion of grasslands, $Grass_{Land}$ ($n = 1$); and (3) the hedgerow density ($n = 1$), calculated as the ratio of total hedgerow length over buffer area (km/km^2). Hedgerow density was considered as it may influence the dispersal of carabid beetles throughout the landscape, either as a corridor or a barrier (Petit and Usher 1998; García et al. 2000; Marchi et al. 2013), and as hedges can act as a potential complementary habitat. $Grass_{Land}$ and hedgerow density were only considered in the current year as they did not vary significantly between years.

To address possible confounding effects due to correlations between landscape descriptors, we computed pairwise Pearson correlation tests between landscape descriptors for each buffer radius. Considering a threshold of 0.70 (Dormann et al. 2013), we found high, negative correlation coefficients between $Grass_{Land}$ and WC_{Land} in the current year at 700, 900, and 1000 m, and high, positive correlation coefficients between WC_{Land} in the current and previous year at 1000 m (correlation matrices provided in ESM Appendix 2). These correlations were taken into account in the interpretation of our results.

Statistical analyses

Because the number of explanatory variables was large, we used a stepwise selection procedure based on an information-theoretic approach (AIC-based; Burnham and Anderson 2004) to reduce the number of variables within three models of increasing complexity. Generalized linear models with mixed effects (GLMM), with Poisson distribution and log-link function, were used (R package LME4; Bates and Maechler 2013). The pitfall trap identity ($n = 521$ pitfall trap locations) and a year*study site combined factor ($n = 8$) were included as random intercepts in models. Activity-density of *P. cupreus* and *A. dorsalis* were modeled separately as the response variable using the number of individuals caught in a pitfall trap at one trapping session. The model suite is described below.

Step 1 Influences of the sampled crop type and trapping date In the first step, we tested for the influences of the sampled crop (WC and OSR) and trapping date, included in the model as explanatory variables. Trapping dates were considered as the Julian dates of the trapping sessions (JD, day 0 corresponding to the first day of the sampled year), as a scaled covariate (scaled with mean = 0). We considered the first (JD) and second (JD^2) order to allow for non-linear seasonal variation. Complete model formula was:

$$\begin{aligned} AD \sim & (1|TrapID) + (1|Year \times Site) \\ & + Sampled\_Crop + JD + JD^2 \end{aligned} \qquad (1)$$

The best sub-model was selected by comparing AIC values between all possible sub-models (R package *MuMIn*; Barton 2013), and the combination of variables for this model was retained for the next step. The significance of selected variables was evaluated using Type II Wald Chi square tests.

Step 2 Influence of the current year landscape composition In the second step, we tested for the influence of the composition-based descriptors of the current landscape. We used a scale-by-scale and descriptor-by-descriptor procedure; one landscape descriptor considered at one scale was added to the model selected at step 1. All landscape descriptors were considered as scaled covariates (scaled with mean = 0). Based on our hypotheses, the influence of the landscape annual crop composition in the current year is expected to be different depending on sampled crop (i.e., oilseed rape or winter cereals). However, landscape influence of perennial elements (i.e., grasslands and hedges) is not likely to differ depending on sampled habitat. Consequently, a two-way interaction between sampled crop and the landscape descriptor was included only when the proportion of an annual crop was considered (i.e., oilseed rape, winter cereals, and spring crops). The complete model formulae (including by default all variables tested at step 1) for annual and perennial landscape descriptors were, respectively:

$$\begin{aligned} AD \sim\ & (1|TrapID) + (1|Year \times Site) \\ & + Sampled\_Crop * \%Annual_{CropX(N)_{scaleY}} \\ & + JD + JD^2 \end{aligned} \tag{2}$$

$$\begin{aligned} AD \sim\ & (1|TrapID) + (1|Year \times Site) \\ & + Sampled\_Crop + \%Perennial_{ElementX(N)_{scaleY}} \\ & + JD + JD^2 \end{aligned} \tag{3}$$

where $\%Annual_{CropX}$ is the proportion of one of the three annual crops, $\%Perennial_{ElementX}$ is the proportion of grassland or the hedgerow density, and *scaleY*, the spatial scale (buffer radius) at which they are considered in the model. To analyze the influence of landscape descriptors, estimated slopes for each sampled crop (annual descriptors) or all sampled crops combined (perennial descriptors) were extracted from descriptor-scale models and their significance was evaluated using a Wald test. To evaluate the importance of the influence of each landscape descriptor at each scale, ΔAIC were calculated between the resulting model of step 2 and that resulting of step 1. We used a threshold of $\Delta AIC \leq -2$ to consider the resulting model of step 2 as significantly more explicative than that resulting of step 1.

Step 3: Influence of the previous year landscape composition In the third step, we tested for the influence of composition-based descriptors of the previous landscape. For this step, only annual crops were considered as the distribution and proportion of perennial elements did not change significantly between consecutive years. One previous year landscape descriptor considered at one scale was added to the model from step 2 which considered the same descriptor at the same scale in the current year:

$$\begin{aligned} AD \sim\ & (1|TrapID) + (1|Year \times Site) \\ & + Sampled\_Crop * \%Annual_{CropX(N)_{scaleY}} \\ & + \%Annual_{CropX(N-1)_{scaleY}} + JD + JD^2 \end{aligned} \tag{4}$$

All variables tested at steps 1 and 2 are included by default in the formula. As for step 2, estimated slope of the influence of considered previous landscape descriptor was extracted from the models for all sampled crops combined and its significance was evaluated using a Wald test. We used the same procedure as in step 2 to evaluate the importance of the influence of each landscape descriptor at each scale.

Results

A total of 14 629 *P. cupreus* and 2663 *A. dorsalis* were sampled from our 188 sampled fields. On average, 13.00 ± 1.15 *P. cupreus* (observed mean ± SE) were caught per trap on ARM area, 3.69 ± 0.40 on VCG area, and 1.41 ± 0.11 on PVS area; while 1.53 ± 0.19 *A. dorsalis* were caught per trap on ARM area, 1.36 ± 0.18 on VCG area, and 0.45 ± 0.09 on PVS area. Significantly more individuals of *P. cupreus* (Crop effect: $P = 0.002$) and *A. dorsalis* (Crop effect: $P < 0.001$) were collected per trap in oilseed rape fields than in winter cereal fields (0.46 and 1.09 times more, respectively; step 1; Table 2). For both species, the sampling date (JD, JD^2) showed highly significant effect (step 1; Table 2). Consequently, all the variables tested in step 1 were maintained in following steps.

Table 2 Values and significance of Type II Wald Chi square tests realized on fixed effects selected in each of the final tested local models after the selection procedure (step 1). All variables of the initial model are presented

Fixed effects	*P. cupreus*		*A. dorsalis*	
	Chisq	*P* (> Chisq)	Chisq	*P* (> Chisq)
Crop	9.32	0.002**	50.37	< 0.001***
JD	20.85	< 0.001***	107.91	< 0.001***
JD^2	385.21	< 0.001***	523.20	< 0.001***

P was set to 0.05 for variable significance

Significance of *** < 0.001; ** < 0.01, * < 0.05

Landscape effect of perennial elements on carabid activity-density

Activity-densities of both *P. cupreus* and *A. dorsalis* were positively influenced by $\text{Grass}_{\text{Land}}$ at the largest landscape scales, from 800 m (highest influence at 1000 m, $\Delta\text{AIC} = -3.06$; bar plots in Fig. 3g) and 600 m (highest influence at 900 m, $\Delta\text{AIC} = -6.28$; bar plots in Fig. 4g), respectively. The hedgerow density did not influence *P. cupreus* and *A. dorsalis* activity-densities in sampled crops at any of the considered scales (Fig. 3h, 4h).

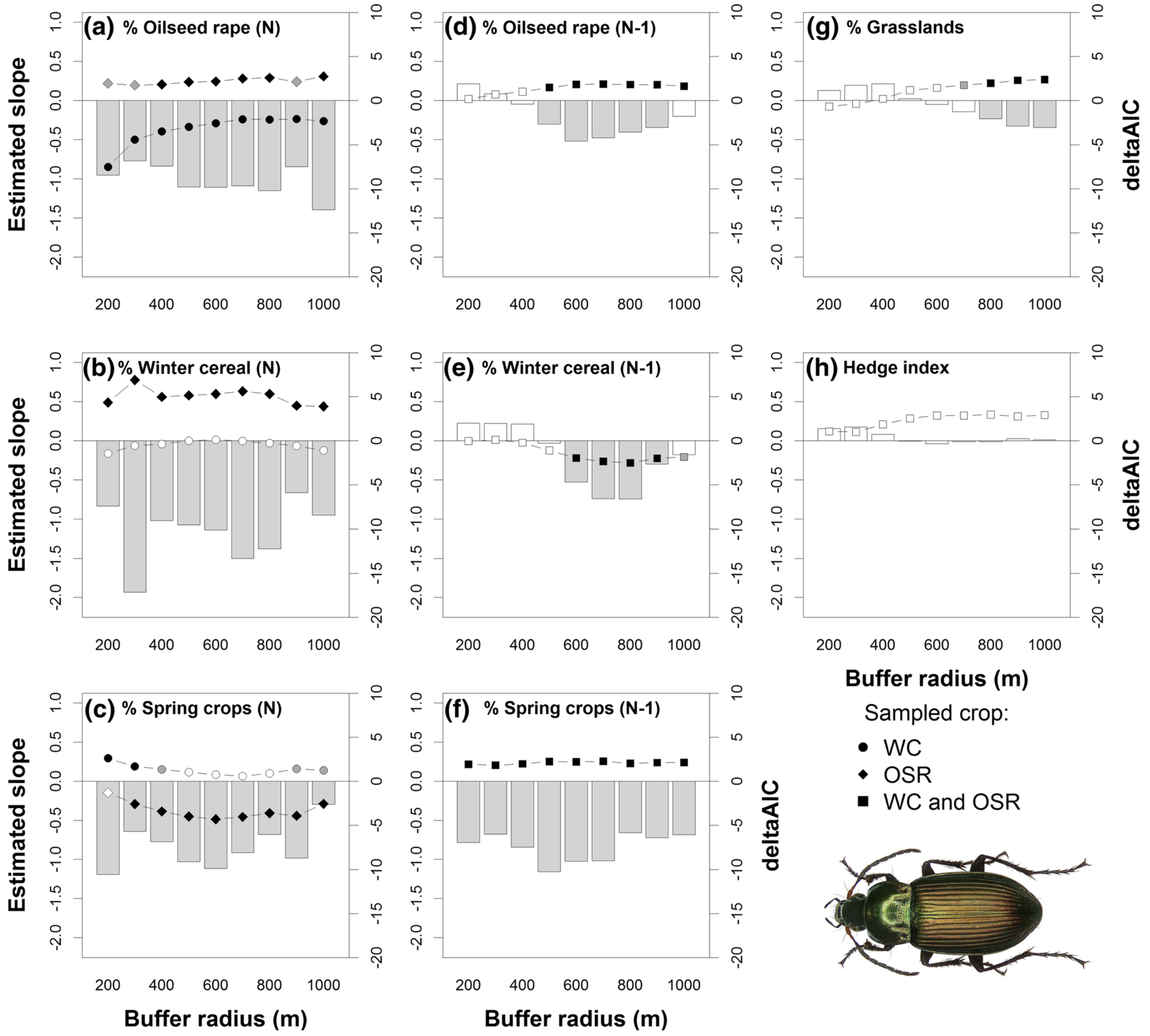

Fig. 3 Influence of the proportion of landscape descriptors on *P. cupreus* AD. Are represented (1) the estimated slopes of the influence of each descriptor at each scale (dots and lines), and (2) the difference in the Akaike information criterion (ΔAIC; bar plots) between the model considering a considered landscape descriptor and the previous step model (**a**–**c**, **g**–**h**, step 2–step 1; **d**–**f**, step 3–step 2). When considering the proportion of annual crops in the current year, N (**a**–**c**), values are given for sampled winter cereal (circle) and oilseed rape (diamond) separately. This separation was not considered for the percentages of annual crops in the previous year, N-1 (**d**–**f**), or of perennial elements (**g**–**h**). Black dots indicate significant influences ($P < 0.05$), following the Wald tests; gray dots indicate marginally significant influences ($P < 0.10$); white dots indicate non-significant influences. For ΔAIC bar plots, gray bars indicate $\Delta\text{AIC} < -2$, set as a threshold

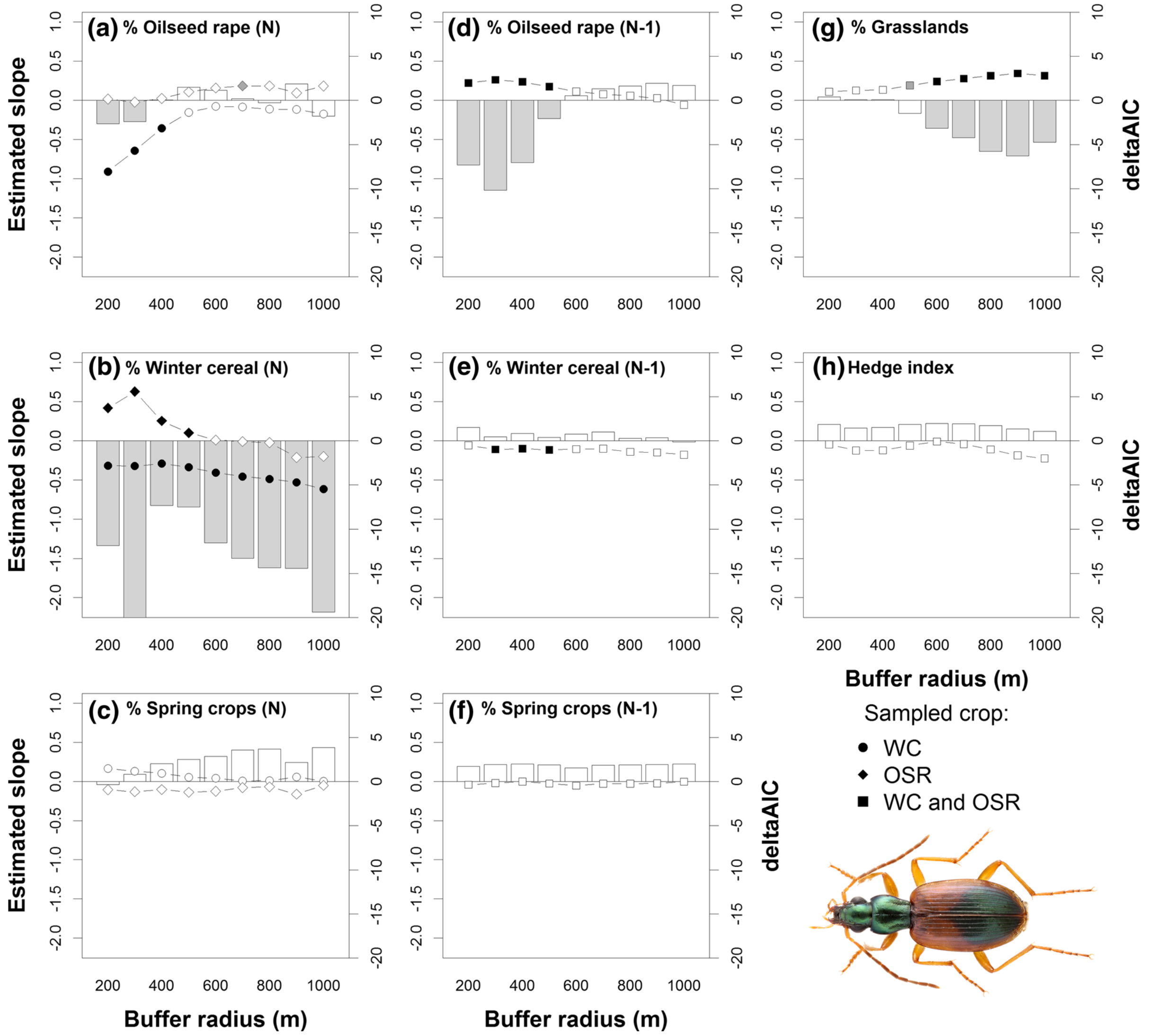

Fig. 4 Influence of the proportion of landscape descriptors on *A. dorsalis* AD. See Fig. 3 for details

Current year landscape effect of annual crops on carabid activity-density

The current arable landscape context had a major influence on *P. cupreus* activity-density in both sampled crops (bar plots in Fig. 3a–c). In oilseed rape, *P. cupreus* activity-density was influenced positively by OSR_{Land} from 400 m (highest influence at 1000 m, $\Delta AIC = -12.38$) and WC_{Land} at all scales (highest influence at 300 m, $\Delta AIC = -17.15$), and negatively by SC_{Land} from 300 m (highest influence at 600 m, $\Delta AIC = -9.88$) (diamonds in Fig. 3a–c). In winter cereals, *P. cupreus* activity-density was influenced negatively by OSR_{Land} in the landscape at all scales (highest influence at 200 m, $\Delta AIC = -8.46$) and positively by local SC_{Land} (200–300 m; highest influence at 200 m, $\Delta AIC = -10.57$), and not influenced by WC_{Land} (circles in Fig. 3a–c).

The current arable landscape context had a slighter and lower-scale influence on *A. dorsalis* activity-density in both sampled crops (bar plots in Fig. 4a–c). In oilseed rape, *A. dorsalis* activity-density was influenced positively by WC_{Land} (200–500 m; highest influence at 300 m, $\Delta AIC = -20.00$), but not by OSR_{Land} and SC_{Land} (diamonds in Fig. 4a–c). In winter cereals, *A. dorsalis* activity-density was influenced negatively by $\mathrm{OSR}_{\mathrm{Land}}$ (200–400 m; highest influence at 200 m, $\Delta\mathrm{AIC} = -2.64$) and $\mathrm{WC}_{\mathrm{Land}}$ (at all scales; highest influence at 1000 m, $\Delta\mathrm{AIC} = -19.36$), but not by $\mathrm{SC}_{\mathrm{Land}}$ (circles in Fig. 4a–c).

Previous year landscape effect of annual crops on carabid activity-density

The previous arable landscape context had a large influence on *P. cupreus* activity-density, even if less important compared with current landscape's (bar plots in Fig. 3d–f). *P. cupreus* activity-density was influenced positively by $\mathrm{OSR}_{\mathrm{Land}}$ at larger scales (500–1000 m; highest influence at 700 m, $\Delta\mathrm{AIC} = -4.22$) and $\mathrm{SC}_{\mathrm{Land}}$ at all scales (highest influence at 700 m, $\Delta\mathrm{AIC} = -9.03$), and negatively by $\mathrm{WC}_{\mathrm{Land}}$ at larger scales (600–1000 m; highest influence at 800 m, $\Delta\mathrm{AIC} = -6.59$) (squares in Fig. 3d–f).

The previous arable landscape context had a large influence on *A. dorsalis* activity-density only when considering $\mathrm{OSR}_{\mathrm{Land}}$ (bar plot in Fig. 4d). This influence was higher than that of $\mathrm{OSR}_{\mathrm{Land}}$ in the current landscape. *A. dorsalis* activity-density was influenced positively by $\mathrm{OSR}_{\mathrm{Land}}$ at finest scales (200–500 m; highest influence at 300 m, $\Delta\mathrm{AIC} = -10.19$) and not by $\mathrm{WC}_{\mathrm{Land}}$ and $\mathrm{SC}_{\mathrm{Land}}$ (squares in Fig. 4d–f).

Discussion

To our knowledge, this study is the first to compare the influence of current and previous year landscape composition to understand the spatial dynamics of carabid populations. As expected, the effects of current and previous year landscape compositions on *P. cupreus* and *A. dorsalis* activity-densities in the spring period were found to vary depending on the sampled crop type and carabid species. The combined investigation of multiple temporal and spatial scales allowed us to consider the different ecological processes behind the observed carabid population distributions and activity-density, and found that most of them could not be deduced from the sole consideration of the current landscape composition.

At the field level, we confirmed differences in crop preference for both carabid species (Williams et al. 2010; Eyre et al. 2013; Marrec 2014; Marrec et al. 2015). Oilseed rape appeared more favorable than winter cereals, and this effect was stronger for *A. dorsalis* than for *P. cupreus*. It is often advocated that there are some limitations when comparing activity-density among crops as the pitfall trap sampling could be biased due to differences in catch probability (Lang 2000; Thomas et al. 2006). However, biases linked to variation in activity alone cannot explain observed differences among crops. Indeed, this difference was supported by the unbiased emergence trap method in a previous study (Marrec et al. 2015) and, importantly, the influence of oilseed rape at the landscape level in the current and previous year identified in the present study is consistent with differences in activity-density observed between these crops. Preference for oilseed rape can be related to the larger amount of prey items found in this crop (Haschek et al. 2012) and its availability all year round since new oilseed rape fields are sown in August and oilseed rape stubbles and volunteers (i.e., recruited from the seeds fallen after harvesting) from previous cropping are ploughed in October in western France.

Landscape moderation of carabid abundance and distribution

The first aim of this study was to test whether resource concentration or dilution-concentration processes influence the distribution and abundance of two dominant carabid species. The resource concentration hypothesis predicts that landscapes with high proportion of host crop should be more attractive, resulting in higher local abundance in globally more favorable surrounding landscapes (Root 1973). Consistently, *P. cupreus* activity-density in oilseed rape was positively impacted by current $\mathrm{OSR}_{\mathrm{Land}}$ at all considered spatial scales. However, contrary to the resource concentration prediction, $\mathrm{OSR}_{\mathrm{Land}}$ had a negative impact on *P. cupreus* activity-density in winter cereal, suggesting dilution-concentration effects (sensu Tscharntke et al. 2012) at play when considering crops with different levels of attractiveness. Conversely, *P. cupreus*, we found no evidence supporting the resource concentration hypothesis for *A. dorsalis*. $\mathrm{OSR}_{\mathrm{Land}}$ did not have any significant effect on activity-density in oilseed rape. However, up to 400 m buffer size, there was a negative effect of OSR_{Land} on *A. dorsalis* activity-density in winter cereal suggesting redistribution of individuals between crops and dilution-concentration processes as for *P. cupreus*. This hypothesis of landscape-scale redistributions to explain observed patterns is in accordance with previous studies (e.g., Holland et al. 2005). The scale of landscape effects was smaller for *A. dorsalis* suggesting that no important long-distance movement is likely to occur in this species which may explain the absence of resource concentration effect. Considering the influence of WC_{Land}, results were consistent with dilution-concentration effects for both species: the more winter cereals in the landscape, the highest the activity-density in oilseed rape. As for OSR_{Land}, the effect of WC_{Land} was only detected at the smallest spatial scales for *A. dorsalis*.

Regarding semi-natural permanent habitats, for both carabid species, our results suggest that complementation and/or supplementation processes occur between grasslands and annual crops. We observed a positive, large-scale (from 500–700 to 1000 m) effect of $Grass_{Land}$ in the landscape surrounding sampled crops. Grassy areas are well known winter shelters and overwintering reservoirs for carabid beetles in agricultural landscapes (French and Elliott 1999; Kromp 1999) and allow to increase carabid richness and diversity in surrounding annual crops (Purtauf et al. 2005; Duflot et al. 2015).

Previous landscape composition influences on carabid abundance and distribution

Our results suggest that landscape-scale movements occur between annual crops from one year to another. This temporal cross-habitat redistribution could be seen as a response of carabid beetles to the inter-annual redistribution of resources caused by crop rotation at landscape level as previously suggested (Thomas et al. 2002; Russon and Woltz 2015). Local *P. cupreus* and *A. dorsalis* activity-density were both positively influenced by OSR_{Land} (squares in Figs. 3d, 4d) in the previous year. This result advocates the role of oilseed rape as breeding habitat for these species and as an important inter-annual source of individuals at the landscape level.

P. cupreus activity-density was also positively influenced by SC_{Land} in the previous year (squares in Fig. 3f), suggesting an important role of these crops in the annual cycle of this species. It may be due to a distribution shift at the landscape scale during the summer-fall period of the previous year, from oilseed rape to spring crops that are the most favorable annual crops in the landscape after cereals and oilseed rape are harvested (i.e., temporal landscape complementation). While oilseed rape stubbles and volunteers from the previous cropping should still provide resources and shelter for carabid beetles after harvesting, the carrying capacity of harvested fields is likely to decrease. Hence, individuals may redistribute in the landscape in other habitats including spring crops which are at their maximum growth in summer, as already suggested in carabids or aphids (Thomas et al. 2001; Vialatte et al. 2006). Consequently, during the main dispersal phase before winter, individuals could mainly come from fields previously cropped with spring crops and not oilseed rape. To validate such a scenario, sampling should be done during summer-fall period in spring crops and winter crops stubbles.

The role of spring crops for *A. dorsalis* remains unclear. SC_{Land} has no influence on *A. dorsalis* activity-density, either in the current or previous year. Bonacci et al. (2004) and Marrec (2014) suggested that *A. dorsalis* individuals mainly overwinter in perennial elements, and particularly fields margins. Consequently, individuals are more likely to move from previous oilseed rape fields to perennial grassy habitats during the summer-fall period, rather than to an alternate annual crop such as spring crops. From there, they can colonize current oilseed rape fields in the early spring.

Surprisingly, winter cereals do not seem to be an inter-annual source of *P. cupreus* and *A. dorsalis* individuals. This result was more unexpected for *P. cupreus* as this crop is an alternative habitat in spring for this species. Because of high differences in spring activities-densities, it is likely that reproduction rate is proportionally lower in winter cereals than in oilseed rape, resulting in fewer individuals in the next generation. In addition, it is also likely that the suitability of winter cereals after harvesting is much lower than oilseed rape's, and do not provide enough resources for *P. cupreus*. Consequently, most *P. cupreus* individuals have to migrate from winter cereals to another suitable habitat including especially spring crops fields at this period.

Considering a temporal landscape perspective when managing agroecosystems

From year to year, crop rotations largely modify landscape composition. For most species which use annual crops, individuals have to face crop rotations and their effect on habitat quality and distribution, leading them to either die, tolerate the new environment, or move. In spite of its importance, temporal environmental heterogeneity has been poorly investigated to explain population dynamics and to propose key landscape management options (Wu and Loucks 1995; Burel and Baudry 2005; Wimberly 2006; Vasseur et al. 2013). To face the transient dynamics of habitat distribution, availability, and suitability, landscape-level movement appears to be a major process allowing species to survive in ephemeral systems as agroecosystems (Ronce 2007).

The important influence of the previous landscape composition we observed here may explain why some studies considering only current landscape composition did not find any influence of landscape context on carabid activity-density (Jeanneret et al. 2003; Weibull and Östman 2003; Aviron et al. 2005). Previous landscape composition determines the availability of reproductive habitats for the previous generation, and thus the origin and size of the pool of individuals present in the landscape the following year.

To corroborate our results on the supposed (1) role of agricultural practices to induce landscape-level movements and (2) directionality of these movements between particular habitat types, it would be interesting to study directly the movements of carabid beetles using interception traps placed at the edges of crop fields (for example following the method proposed by Russon and Woltz 2015). Contrary to mark-recapture experiments (e.g., Griffiths et al. 2005), this type of protocol does not allow to estimate dispersal distances. However, it perfectly suits to the evaluation of direction and period of movements among different habitat types.

Based on our correlative study, some preliminary recommendations may be made to improve agroecosystem management and enhance biocontrol potential of carabid beetles. The suggested role of movements and complementary habitat use through and between years supports the idea that strengthening spatiotemporal stability of key landscape-level habitats has the potential to influence the success of inter-patch movement and hence increase the abundance of beneficial carabid populations. Indeed, strengthened stability in landscape mosaic between successive years would allow enhancing transient landscape connectivity and availability of habitats for most species (Schellhorn et al. 2015). Furthermore, spatially disconnected patches may thus be connected through temporal stepping stones (Wimberly 2006). In addition, high spatial heterogeneity of the crop mosaic in a given year, especially of complementary and supplementary habitats for within-year redistributions (e.g., winter crops, spring crops, and grasslands) is also likely to improve the sustainability of populations and communities in time. Our results suggest that a first option is to increase the proportion of grassy elements (field margins, grasslands) in the landscape, which can provide more alternative shelters, for species to complement or supplement their resources, especially during winter.

Landscape features influenced carabid abundance and distribution mostly at scales below 1000 m. To enhance temporal stability of key landscape-level habitat and spatial heterogeneity of the crop mosaic at this scale, m the management scale should be the farm level. Two further options may be favored: first, increasing crop succession diversity would help increasing landscape heterogeneity and availability of different habitat types and improve beneficial organisms and crop protection services (e.g., Bosem Baillod et al. 2017). In addition, it would allow to strengthen temporal resource stability, which has also been shown to increase beneficial organism populations and therefore stabilize ecosystem services (Schellhorn et al. 2015). Agri-environmental measures already include such type of management. However, fields are currently increasing in size in intensive agrosystems, farmers cultivating large blocks of a single crop. Therefore, a second alternative may be to try to reduce field units, either by decreasing field size or by cultivating complementary crops in alternate strips. Such smaller-grained landscapes have already been shown to benefit spider and carabid assemblages (e.g., Bertrand et al. 2016a). The way to achieve this second option is however unclear, especially in terms of financial support, if needed.

Conclusion

Altogether, considering landscape level in a spatial and temporal multi-scale approach allowed us to demonstrate the complementarity of current and previous year landscapes to understand population processes. The consequences of the ephemerality of source habitats, and their replacement by unfavorable, sink habitats which percolate in the landscape mosaic was theoretically developed by Vandermeer et al. (2010). In this study, we showed that the inter-annual destruction and redistribution of habitats in the landscape due to crop rotations may drive the spatiotemporal dynamics of carabid \ distribution in the landscape. Our results emphasized then the importance of the inter-annual temporal variation of the landscape mosaic in shaping observed population patterns. Indeed, we were able to deduce processes that occurred at different periods of time to shape current population abundance and distribution. Finally, our findings established that landscape characteristics impacted carabid activity-density at different scales depending on the species. These highlights support that multi-scale studies can outperform single-scale studies (Graf et al. 2005; Boscolo and Metzger 2009; Kuhn et al. 2011).

The framework developed in this study can be used to better understand the dynamics of biodiversity associated to crops and their interplay with the crop mosaic own temporal dynamics. It is particularly relevant for species that can be associated with different degrees to several crop types like most carabid beetles, pollinators, and some pest species such as polyphagous aphids. An interesting perspective to this work would be to assess whether biocontrol by carabid beetles and other natural enemies is also responding to previous crop composition in the landscape. This issue would help for a better management of agricultural systems considering explicitly their temporal variation.

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