

# Spatial organisation of habitats in agricultural plots affects per-capita predator effect on conservation biological control: An individual based modelling study



B. Collard<sup>a,b,c,\*</sup>, P. Tixier<sup>b,c</sup>, D. Carval<sup>b,c</sup>, C. Lavigne<sup>a</sup>, T. Delattre<sup>a</sup>

<sup>a</sup> INRA, UR 1115 PSH, 84000, Avignon, France

<sup>b</sup> CIRAD, UPR GECO, F-34398, Montpellier, France

<sup>c</sup> GECO, Univ Montpellier, CIRAD, Montpellier, France

## ARTICLE INFO

### Keywords:

*Euborellia caraibea*  
Generalist predators  
Spatially explicit modelling  
Correlated random walk  
Banana fields  
Edge length

## ABSTRACT

A highly advocated approach to enhance pest control by indigenous predators is to add or maintain appropriate non-crop plant habitats in agrosystems. Although the addition of non-crop plant habitats can enhance the number of predators in crop by increasing their food resources or shelter, the effect is often insufficient to reduce pest abundance or damage. A number of explanations were identified in previous studies; the ability of such habitats to enhance predators, in particular, is affected by the spatial organisation of the habitats at the landscape level. Here, we explore how intra-plot spatial patterns of non-crop habitats affect the per-capita predator effect on pest control. We use a spatially explicit and individual-based model to simulate the foraging movements of an earwig-like predator in a banana field. Predator movements within a day were based on a simple non-specific behavioural assumption: movement is a correlated random walk affected by habitats and edges. Population dynamic processes occurring at larger time or spatial scales, such as reproduction and immigration, were not considered. In this model, non-crop habitats added to plots were considered favourable to predators: movements were slower and more sinuous in non-crop habitat than in unfavourable habitats. The intra-plot spatial patterns of the non-crop habitat were built and characterised using landscape ecology concepts and metrics. We found that the per-capita predator effect was strongly affected by a spatial dilution of predators, induced by non-crop habitat addition, but this negative effect could be partially or fully mitigated by the spatial organisation of the non-crop habitat. At the banana plant level, a long edge length between the crop and non-crop habitat can compensate for this dilution effect by reducing the duration of the periods between predator visits to the banana plant. At the plot level, the best plots (i.e., those in which all banana plants were often visited by predators) were those with non-crop strips in the banana plant rows. Overall, the results support the idea that the spatial organisation of non-crop habitats at the plot level, characterised by the metric edge length in particular, can be managed to minimise the negative impact of the dilution effect.

## 1. Introduction

The improvement of crop pest control by promoting indigenous predators has received substantial attention in the last 40 years (Altieri and Letourneau, 1982; Jonsson et al., 2008; Begg et al., 2017). This strategy is known as conservation biological control (CBC) (Eilenberg et al., 2001). A highly advocated CBC approach is to add or maintain appropriate non-crop plant habitats in agrosystems to provide alternative shelter or food for predators (Landis et al., 2000). The aim is to

support long-term increases in the abundance of predators resulting from an increase in habitat resources that support predator population growth (Holt, 1977) or an increase in habitat attractiveness that supports an increase in predator immigration (Schellhorn et al., 2014). Although adding non-crop habitats can help maintain or enhance predators locally, it often fails to reduce pest abundance or damage (Letourneau et al., 2011; Begg et al., 2017). Former studies indicate that the effects of non-crop habitats may greatly depend on their spatial organisation at the crop, farm, or landscape level (Landis et al., 2000;

*Abbreviations:* CBC, Conservation biological control

\* Corresponding author at: INRA, UR 1115 INRA, Unité PSH, Domaine St Paul, Site Agroparc, 228 Route Aérodrome, F-84914 Avignon 9, France.

*E-mail addresses:* [blanche.collard@gmail.com](mailto:blanche.collard@gmail.com) (B. Collard), [tixier@cirad.fr](mailto:tixier@cirad.fr) (P. Tixier), [dominique.carval@cirad.fr](mailto:dominique.carval@cirad.fr) (D. Carval), [claire.lavigne@inra.fr](mailto:claire.lavigne@inra.fr) (C. Lavigne), [thomas.delattre@inra.fr](mailto:thomas.delattre@inra.fr) (T. Delattre).

<https://doi.org/10.1016/j.ecolmodel.2018.09.026>

Received 3 May 2018; Received in revised form 28 September 2018; Accepted 28 September 2018

0304-3800/© 2018 Elsevier B.V. All rights reserved.

Tscharntke et al., 2016). Tscharntke et al. (2016), in particular, stressed that non-crop habitats at the landscape level must be large and close enough to crops to enhance pest control.

In the context of changing agricultural practices towards agroecology, the addition of non-crop habitats in agricultural plots has recently seen a renewed interest (FAO, 2017). The presence of other trophic resources within the plot may, however, divert predators from the crops and pests (Corbett and Plant, 1993; Rand et al., 2006; Holland et al., 2009). This approach may, then, reduce the per-capita predator effect on pests and, in turn, decrease the CBC. At the landscape scale, the potential effect of other trophic resources on a species was termed the ‘landscape-moderated dilution hypothesis’ by Tscharntke et al. (2012). At the plot scale, we will refer to it as the ‘dilution effect’. The per-capita predator effect should, furthermore, be affected by the spatial organisation of the non-crop habitats. Several field studies indeed have shown that increasing the distance from the non-crop habitat to the crop decreased the ground-dwelling predator efficiency to control pests (Collins et al., 2002; Thomson and Hoffmann, 2013; Penn, 2018). Therefore, our working hypothesis is that intra-plot spatial patterns of non-crop habitats could influence the per-capita predator effect and thereby limit the dilution effect on foraging behaviour.

Anticipating the effects of the spatial organisation and quantity of non-crop habitats on CBC or the spatial scale at which their variations will matter is not straightforward. For instance, predator abundance and diversity could be affected by non-crop habitat at different landscape levels (Tscharntke et al., 2007; Martin et al., 2016), depending on predator dispersal ability (Jackson and Fahrig, 2012; Henri et al., 2015) or predator diet (specialist or generalist) (Symondson et al., 2002; Chaplin-Kramer et al., 2011).

The effects of spatial patterns on biological processes have long been studied by landscape ecologists. Hence, spatial concepts such as proximity, edge length, connectivity, and aggregation, and associated metrics were developed mainly at the landscape level, which commonly refers to areas ranging from hectares to many square kilometres (Turner, 1989) and to long-term population dynamics (Kruess and Tscharntke, 1994; Tscharntke et al., 2007; Bianchi et al., 2010). In the field of biological control, these concepts and metrics have facilitated the use of spatially explicit models to investigate how prey and predator temporal dynamics are linked to the prey resource (Bianchi et al., 2009a, 2010) or to habitat distribution (Bianchi and Van Der Werf, 2003). Bianchi et al. (2010), for instance, showed that the nearest-neighbour distance between pest and predator patches explained pest abundance during the early colonisation of aphid patches by ladybird beetles.

These same spatial concepts, however, have not been directly used at the plot level (areas of a few hundred square metres, as can be found in intermediately intensive agricultural landscapes) for considering routine movements within a day, such as the foraging movements of arthropod predators. We argue that the use of spatial concepts at the plot level could be useful given the current social enthusiasm for habitat diversification in agriculture because plot-level foraging behaviour directly influences the per-capita predator effect and because foraging behaviours are influenced by the spatial distribution of resources. To our knowledge, only two models have been built at the plot level to explore the effects of the spatial pattern of habitats on predator movements (Corbett and Plant, 1993; Westerberg et al., 2005). Only one of them (Corbett and Plant, 1993) specifically investigated how non-crop spatial organisation altered the dilution effect relative to CBC, but that study considered only simple, non-crop strips at a daily scale. To build on this earlier work, we assume that the use of landscape ecology concepts such as proximity, edge length or aggregation at the plot level could improve our understanding of how spatial organisation of non-crop habitats may alter the per-capita predator effect.

The assessment of the per-capita predator effect is not simple and depends on the relation between the predator and the pest under consideration. Both the residence time of predators on crops (Arrignon

et al., 2007; Wajnberg et al., 2016) and the timing of the predator’s presence (Mailleret and Grognaud, 2006; Bianchi et al., 2009b; Pei et al., 2018) are important for pest control. Longer residence time on pest patches allows predators to consume more pests and, thus, should improve the predator efficiency to reduce the level of pest infestation on a crop. The timing of predator presence, on the other hand, is more critical for preventing pest establishment, and the timing especially matters for pests that have a rapid population growth rate, such as aphids (Snyder and Ives, 2003), or for pests that have a stage that is especially sensitive to predation, such as the egg of the banana weevil *Cosmopolites sordidus* (Germar), a serious pest of banana plants (Gold et al., 2001).

In the present study, we used a spatially explicit model named *Foragescape* to investigate how intra-plot spatial patterns of non-crop habitats alter the per-capita predator effect and, thus, the potential for CBC. We built and characterised the intra-plot spatial patterns by using spatial metrics at the landscape scale. We focus on generalist predators, whose behaviours are modified by the availability of alternative prey (Symondson et al., 2002), and on ground-dwelling arthropod predators because the foraging movements of such predators are affected by non-crop habitat localisation at the plot level. Because *Foragescape* is an individual-based model, we could use it to simulate individual adaptive decisions within heterogeneous environments and to understand which aspects of individual behaviour lead to particular results (Grimm et al., 2005). We used metrics of cultivated plant visits by predators (duration, frequency of visits, and duration of absence of predators) as proxies for the per-capita predator effect on pest control. Here, absence duration was used to evaluate predator efficiency in preventing pest establishment, and the duration and frequency of cultivated plant visits were used to evaluate predator efficiency in reducing established pests. We considered the timing of predator visits because generalist predators are usually assumed to be more efficient at preventing pest establishment since they are present before the arrival of the pest (Landis et al., 2000; Symondson et al., 2002; Snyder and Ives, 2003).

The present study is a theoretical contribution; however, we focused on an existing case of pest control to specify the quantitative boundaries of the model and to ensure that our conclusions were not too disconnected from a real situation in terms of CBC. We focused on banana fields, where plant cover is already used for weed control (Lavigne et al., 2012). Fine-grained spatial heterogeneity is particularly relevant for orchard crops in which growers can manage areas of bare soil, plant cover, or other habitats under crops (Lys et al., 1994). In addition, evidence exists that plant cover in banana fields may alter the food web (Duyck et al., 2011) and increase rates of egg predation of the banana weevil (Mollot et al., 2012). The eggs are laid on the corm of the banana plant and last 4 to 7 days before larva dig into and hide in the corm (Gold et al., 2001); therefore, an absence duration shorter than this period could help prevent pest establishment. Among the several potential predators of *C. sordidus*, the earwigs *Euborellia caribeana* (Hebard) and *Euborellia stali* (Dohrn) (Anisolabidae) are generalist predators and good candidates for CBC of *C. sordidus* (Mollot et al., 2014; Carval et al., 2016).

We used the model to answer the following questions: i) how are the duration, frequency and absence duration of banana plant visits by predators affected by the edge length between the plant and the non-crop habitats or by its proximity to such habitats; ii) are the duration, frequency and absence duration of banana plant visits by predators affected by the quantity and the organisation of non-crop habitats at the plot level; and iii) can the spatial organisation of non-crop habitats at the plot level enhance the per-capita predator effect and compensate for dilution effects?

## 2. Materials and methods

To explore how the spatial pattern of added favourable habitats affects the cultivated plant visits by predators and thereby affects the

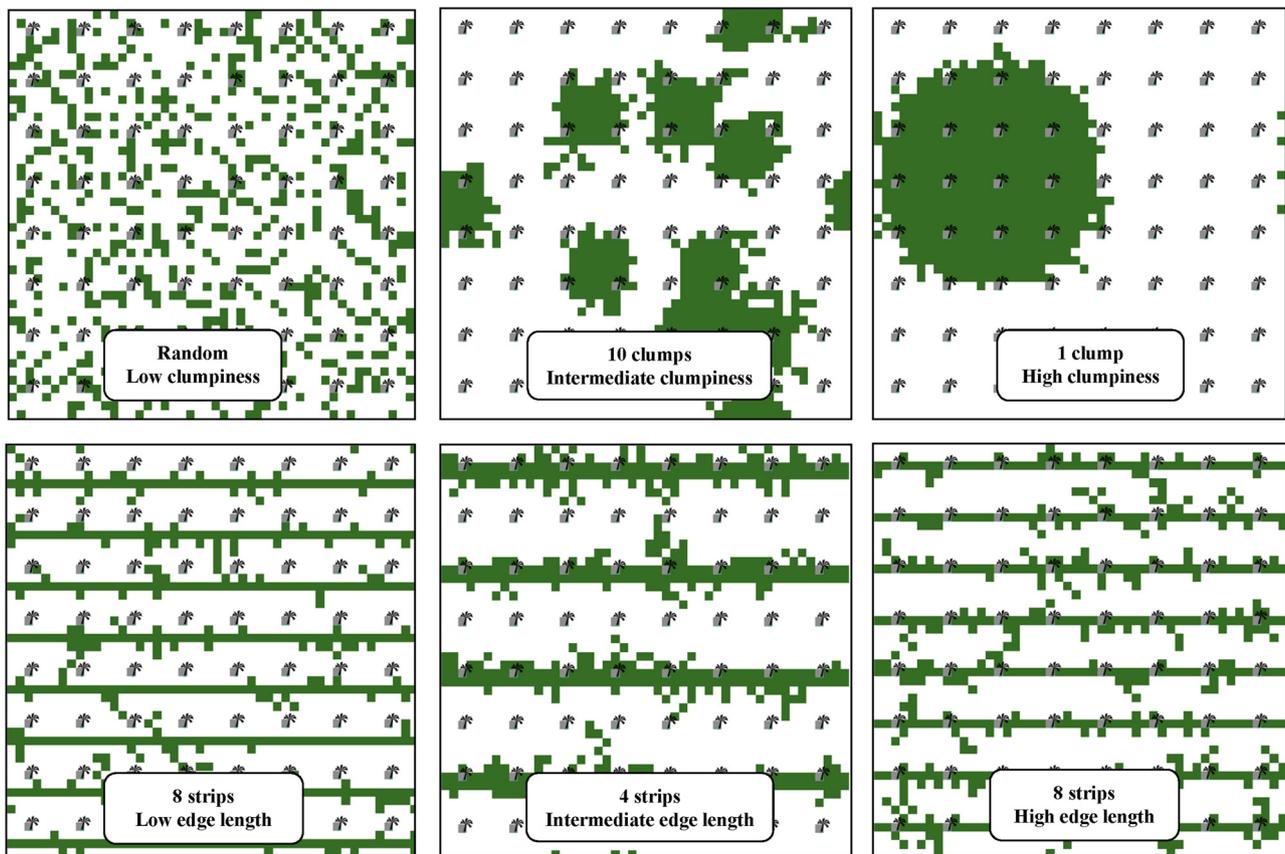


Fig. 1. Example of plots generated with 25% alternative favourable habitats and diverse input shapes leading to variation of Clumpiness and crop edge length. Unfavourable habitats are white, and favourable habitats are green (alternative favourable) and grey (crop). Each panel represents one plot (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

potential of pest control, we simulated the foraging movements of an earwig-like predator in diversified banana fields. The individual-based *Foragescape* model was implemented in NetLogo (Wilensky, 1999), and its description is detailed using the ODD protocol (Grimm et al., 2006, 2010) in the supplementary materials (A).

### 2.1. Plots simulation

The experimental plots were generated in Netlogo and consisted of plots of 19.2 x 19.2 m treated as a torus and modelled as squared grids of  $48 \times 48$  cells with a grain of  $0.4 \times 0.4$  m (Fig. 1). We kept the grain small to account for differences in habitat configuration in close vicinity to the banana plants. All plots comprised 8 rows of 8 banana plants (six cells apart from each other) and were characterised by a percentage of alternative favourable habitats ( $p_A$ ) and three structural metrics shaping the configuration of the alternative favourable habitats. Each cell of the plot is defined by a habitat type: the crop habitat (i.e. banana plants), the alternative habitats that are favourable for predators (i.e. non-crop habitats with alternative trophic resources or shelters), and the habitats that are unfavourable for predators (i.e. bare soil). Both the crop and alternative favourable habitats are considered favourable and have equal effects on the predators. The three structural metrics at the plot level were chosen from among a diversity of spatial metrics that have subtle differences and are often highly correlated (Wang et al., 2014). These metrics account for plot variation in the edge length, proximity, and aggregation of favourable habitats (Supplementary material A.6.1.2) (Table 1, Fig. 1):

- the crop edge length,
- the standard deviation of distances of banana plants to the nearest favourable habitat, and

- the *Clumpiness*, which is an aggregation metric known to be weakly correlated to the percentage of habitats (Wang et al., 2014).

The first two structural metrics at the plot level were calculated from two spatial metrics defined for each banana plant: the edge length ( $e_L$ ), which is the number of alternative favourable neighbours around the banana plant, and the distance to the nearest favourable habitat ( $d_r$ ) (Table 1).

The processes of generating and selecting plots with different spatial organisation of alternative favourable habitats are detailed in Supplementary materials (A.6.1). We generated 10,890 different random plots with Netlogo by systematically varying the percentage of alternative favourable habitats (25, 50 and 75%), the type of shapes (clump, 4 strips or 8 strips), the size (radius or width) and the number of shapes. The type of shapes, clump, one strip per row of banana plants (8 strips) and one strip every two rows (4 strips), were chosen to mimic vegetation patterns observed in banana fields or in other orchards and to produce contrasting values for structural metrics at the plot level. We then selected 1704 plots for simulations by sampling across the entire range of the three structural metrics. Ten plots with  $p_A = 0\%$  and 10 plots with  $p_A = 100\%$  were also included to study limit cases (resulting in a total of 1724 plots).

### 2.2. Model processes

The processes of the simulation model are described in the flow-chart (Fig. 2) and are detailed with the ODD protocol provided in the supplementary materials (A). For each selected plot, all predators were randomly distributed, and we ran the model for 360 min ( $\sim 1$  day) to avoid the influence of initial locations. We then ran the model for 10,800-minute time steps (representing 30 daily activity periods of *E.*

**Table 1**  
Overview and definitions of spatial metrics.

Name	Description	Range	Unit
<b>Banana plant level</b>			
$e_L$	Edge length: number of alternative favourable neighbouring cells (8 neighbours) around a banana plant	0 to 8	cells
$d_n$	Proximity: distance to the nearest favourable habitat (calculated from the centre of the cells)	0 to 2.4	m
<b>Plot level</b>			
$p_A$	Percentage of alternative favourable habitats among non-crop habitats	0 to 100	%
Crop edge length	Average edge lengths between banana plants and the alternative favourable habitats	0 to 8	cells
Standard deviation of $d_n$	Standard deviation of distances of banana plants to the nearest favourable habitat	0 to 0.9	m
Clumpiness	Proportional deviation of the proportion of like adjacencies involving favourable habitats from that expected under a spatially random distribution (See fragstat documentation 4.2)	-1 to 1	

caribea; Table 2). At each time step, all predators were moving (Forage) and the absence or presence of predators was recorded on all banana plants in banana plant numeric lists (Banana plant observation).

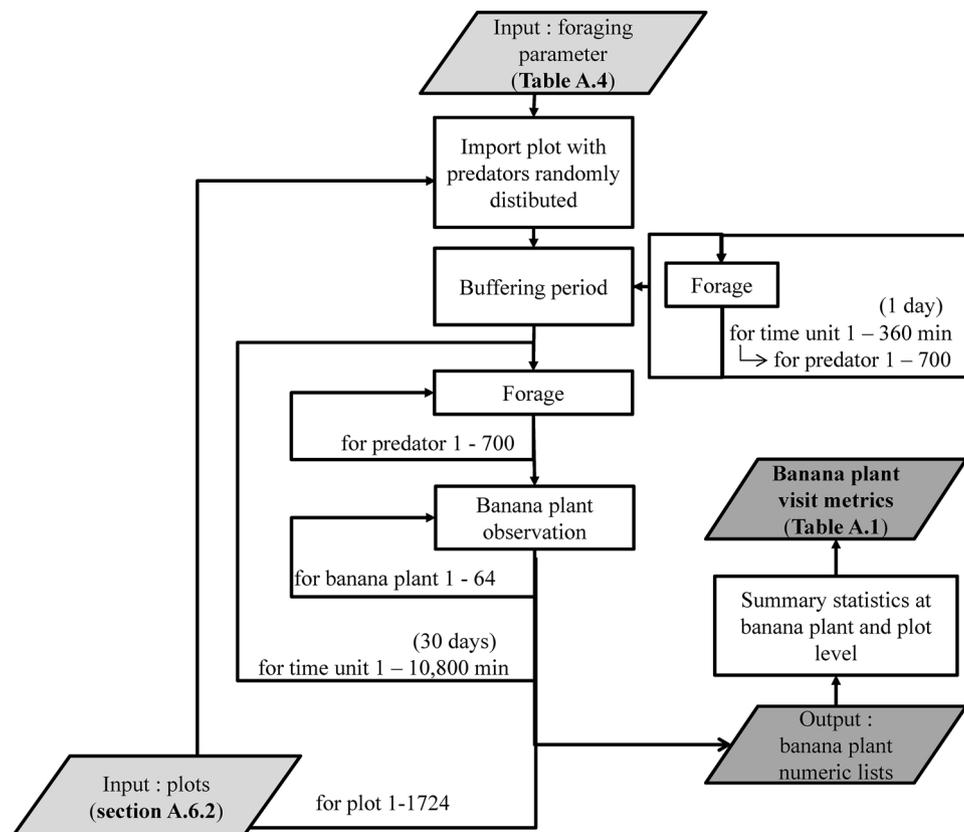
Based on the literature on ‘habitat selection’ and ‘movement ecology’, the predator movements are a correlated random walk that is affected by habitats and edges (Bell, 1991; Zollner and Lima, 1999; Barraquand and Benhamou, 2008). The step lengths of the predators during movements follow a truncated normal distribution characterised by means, standard deviations, and minimum and maximum values (Table 2). Turning angles follow a Cauchy distribution characterised by concentration parameters (Martin and Fahrig, 2015) (Table 2). In a favourable habitat, we assumed that predators can rest or search for resources while remaining protected from higher trophic level predators; as a result, their movements are slower and more sinuous than in an unfavourable habitat. Consequently, in the model, movement step lengths are shorter (mean and standard deviation), and the concentration parameter of turning angles is smaller in a favourable habitat than an unfavourable habitat (Table 2). Apart from movement changes, we also assume that the probability that predators cross an edge to enter an

unfavourable habitat is lower than 1 (Table 2). Indeed, leaving a profitable place and searching for a potentially better place with a chance of being exposed to predation, referred to as habitat selection, is a key decision faced by any forager (Morris, 1987).

We assumed that all movement characteristics are similar for each individual and constant over time. Because we focus on daily foraging movements, we have neglected mechanisms associated with population dynamics (mortality and reproduction) and with landscape scale movements (immigration and emigration). Because we expect the numerical response of a generalist predator to be either slow or independent of pest numbers, the change in pest number should not greatly influence predator abundance for the time considered (Landis et al., 2000).

2.3. Model parameters

The values used in our case study for each model parameter are given in Table 2 and were based on the published literature and on our personal observations. In particular, movement parameters were set



**Fig. 2.** Flow chart for the simulation model examining the relation between spatial organisation of alternative favourable habitat and visits by predators to the banana plant.

**Table 2**  
Overview of foraging parameters and values for the model.

Description	Value	Unit	References
Number of predators	700		According to the adult density of <i>E. carai-bea</i> found in a field experiment (unpublished data).
Daily activity period	360	min	Daily activity period (6 h) based on activity observation of Forficulidae (Joachim and Weisser, 2015) and on <i>E. carai-bea</i> (for 2 days, 10 adults were observed each 30 min; mean activity of 5:45, unpublished data).
<b>Movement parameters</b>			
- Minimum length step on favourable habitat:	0.001	cells/min	No negative step length
- Average length step	0.1	cells/min	Order of magnitude based on mark-and-recapture experiments on <i>Forficula auricularia</i> [L.] (Lamb, 1975) in quadrats with shelters. Mean net displacement between 1.2 m/day (0.008 cells/min) and 4.1 m/day (0.028 cells/min) with many 0 displacements.
- Standard deviation of length step	0.05	cells/min	
- Maximum length step	1	cells/min	maximum of net displacement observed of 8 m/day (0.056 cells/min)
- Concentration of turning angle on unfavourable habitat:	0.5		Movements are sinuous
- Average length step	3	cells/min	based on the known speed capacity for <i>F. auricularia</i> (3 cm/s; Van Heerd 1946 in Lamb, 1975) and observation of <i>E. carai-bea</i> (unpublished data).
- Standard deviation of length step	1	cells/min	
- Maximum length step	5	cells/min	
- Concentration of turning angle	0.8		Movements are almost straight
<i>Probability of crossing edges:</i>			
- favourable toward unfavourable	0.05		
- unfavourable toward favourable	1		

using published data from field and laboratory experiments on the European earwig (*Forficula auricularia* [L.]) and personal observations on *E. carai-bea*; data for the latter species were used to establish the order of magnitude for movements (Table 2). Predator maximal running speed was used to set the limit for step length in unfavourable habitats and the order of magnitude for other step length parameters. Step length in favourable habitats was difficult to find in the literature and to estimate from predator maximal running speed because step length can be reduced by multiple behaviours such as resting, searching, feeding, etc. In addition, most studies on ground-dwelling arthropods consider daily movement (Lamb, 1975; Corbett and Plant, 1993; Charrier et al., 1997; Vinatier et al., 2011), and those that considered finer time scales used remote sensing techniques that may have stressed the insects (Wallin and Ekbohm, 1988). We hypothesise that speed measured as the net displacement per minute in a favourable habitat will be substantially less than the maximal running speed but also greater than the average daily speed in favourable habitats, which was determined by a mark-and-recapture experiment with *F. auricularia* (see Table 2). We set the movement in favourable habitats as 30 times lower than in the unfavourable habitats. Standard deviations of step lengths were set lower but near the mean values to account for potential noise in the movements.

2.4. Model outputs

Summary statistics of the banana plant visits by predators were computed via R (R Core Team, 2018) while accounting for visit duration, visit frequency, and mean absence duration in-between visits

**Table 3**  
Summary statistics of banana plant visits by predators and proportion of time spent by predators on habitats for the duration of a simulation.

Name	Description	Range of output values	Unit
<b>banana plant level</b>			
Visit duration	proportion of total time with visits	0 to 1	
Visit frequency	number of visits	1 to 550	
Absence duration	mean duration of periods in between visits	0 to 856.2	min
<b>Plot level</b>			
Crop < output >	< output > averaged over banana plants within a plot, i.e. crop visit duration, crop visit frequency and crop absence duration	–	
Time spent on alternative favourable habitats	proportion of time spent by predators on alternative favourable habitats averaged over all predators in a plot	0 to 0.97	
Time spent on unfavourable habitats	proportion of time spent by predators on unfavourable habitats averaged over all predators in a plot	0 to 0.08	
Time spent on banana plants	proportion of time spent by predators on banana plants averaged over all predators in a plot	0.03 to 0.92	

(absence duration) and their means at the plot level (see detailed definition of parameters in Table 3). Means at the plot level will be referred to as crop visit duration, crop visit frequency and crop absence duration, respectively. Because arthropod predators should have the necessary chemical information to detect herbivores when they reach a host plant (Vet and Dicke, 1992), we assumed that a single predator is capable of finding and catching pests when it visits the crop and that the effect of several predators present simultaneously on the crop are negligible. Therefore, we define a visit as a continuous period of time when at least one predator is in a banana plant cell.

2.5. Model analysis

Model analysis was carried out on model outputs for each of the 1724 plots. We analysed the model outputs independently at the banana plant level and at the plot level because the banana plant level is relevant to examine how predators visit banana plants, and because properties might emerge at a higher level in individual-based models (Grimm and Railsback, 2005). We assessed relations between the banana plant visit metrics at the banana plant level and the spatial metrics at two levels: the banana plant level ( $e_L, d_n$ ), and the plot level ( $p_A$ , crop edge length, *Clumpiness*, standard deviation of  $d_n$ ). We checked pairwise interaction effects between plot level and banana plant level metrics. We further assessed relations between the banana plant visit metrics at the plot level and the spatial organisation variables at the plot level: the spatial metrics at the plot level and the presence and number of strips (random, 4 or 8 strips).

When needed to evaluate the strength of an effect, the percentage of

variation explained by an effect was quantified with a linear model (see Supplementary material C). Hence, we quantified the interaction effect of  $p_A$  and  $e_L$  on the visit frequency by analysing the variation in visit frequency with a linear model that included  $p_A$ ,  $e_L$  and their interaction as independent variables (R Core Team, 2018). Furthermore, at the plot level, we quantified the effect of proportion of time in crop habitat (Table 3) on the crop visit duration with a linear model including crop visit duration as the dependent variable and proportion of time on the crop habitat as the independent variable.

## 2.6. Qualitative analysis of parameter value choices

To explore how parameter values affected the response of the banana plant visits to spatial organisation, the model was run for all the 1724 plots, and the following set of parameters were explored one at a time:

- Predator number (135, 350 and 1400)
- Global speed: shorter step lengths on both favourable and unfavourable habitats (divided by 2, 4 and 10)
- Speed difference: higher and lower ratio of step lengths in favourable versus unfavourable habitats (15 and 60 times lower)

The outputs of those simulations are presented in the supplementary materials (D). We found that parameter values affected some values of the banana visit metrics. Visit duration was increased by a higher number of predators, but little changed with global speed (up to step lengths divided by 4) and speed differences. Visit frequency was increased and absence duration was decreased by a higher number of predators, higher global speed and lower speed differences. However, overall, we found that patterns of results were qualitatively similar for most parameter values and started to diverge only when the global speed was reduced 10 times.

## 3. Results

### 3.1. Banana plant level

Banana plant visits by predators were affected by both the spatial organisation in their close environment and the percentage of alternative favourable habitats at the plot level ( $p_A$ ) (Fig. 3). However, the effects of the spatial organisation and  $p_A$  differed for visit duration, visit frequency, and absence duration. Visit duration ranged from 9.4 to 100% and was reduced by an increase in  $p_A$ , regardless of the values of local spatial metrics (edge length ( $e_L$ ) and distance to the nearest favourable habitat ( $d_n$ ); Fig. 3a & b). In contrast, visit frequency was more strongly affected by those spatial metrics than by  $p_A$ . Visit frequency remained low and almost constant (visit frequency =  $27 \pm 7$ ) when the banana plants were isolated ( $d_n \geq 2$ ; Fig. 3c) and increased with the number of favourable neighbours when the banana plants were not isolated ( $e_L \geq 1$ ; Fig. 3d). We also observed a small reduction of visit frequency with  $p_A$  when  $e_L$  increased, but this explained only a small percentage of the variation in the visit frequency (2.35% of the total variation;  $p_A : e_L$  effect:  $-0.42 \pm 0.03$  visits; supplementary material C).

As a result, absence duration ranged from 4.8 min to 864 min and was affected by both  $p_A$  and local spatial metrics (Fig. 3e & f). When banana plants were isolated from alternative favourable habitats ( $d_n \geq 2$ ;  $e_L = 0$ ), the visit frequency was constant; as a result, as  $p_A$  increased, the absence duration increased concomitantly with the decrease in visit duration such that the absence duration was able to more than double (Fig. 3e). When banana plants were in contact with some alternative favourable habitats ( $d_n = 1$ ;  $e_L \geq 1$ ), the visit duration was not affected by  $e_L$ , and therefore as  $e_L$  increased, the absence duration decreased concomitantly with the increase in visit frequency (Fig. 3f). This decrease was exponential and could result in a 20-fold difference in absence duration between an isolated banana plant in a plot with a

$p_A$  of 75% ( $360 \pm 100$  min) and a banana plant surrounded by eight favourable neighbours ( $19 \pm 5$  min). The direct contact with the alternative favourable habitat ( $d_n = 1$ ) led to a maximum visit frequency of  $292 \pm 102$  visits and to a minimum absence duration of  $38 \pm 8$  min (Fig. 3c & e).

Aside from  $p_A$ , we found no links between predator presence at the banana plant level and spatial organisation at the plot scale described by the spatial metrics *Clumpiness*, crop edge length, or standard deviation of  $d_n$ , even when we investigated outputs for banana plants with the same local spatial organisations and in plots of similar  $p_A$  (see Fig. 4 and Supplementary material E). For example, the effects of  $e_L$ ,  $d_n$ , and  $p_A$  on visit outputs were not altered by the *Clumpiness* (Fig. 4).

Supplementary tests showed that the number of predators per se and the speed difference did not affect the relation between visit duration and structural metrics (Supplementary material D.1). However, visit duration began to be negatively affected by edge length ( $e_L$ ) and positively affected by distance ( $d_n$ ) when predator speeds on both favourable and unfavourable habitats were ten times lower (supplementary material D.2).

### 3.2. Plot level

#### 3.2.1. Proportion of time spent by predators in each habitat and crop visit duration

Within each plot that offered some alternative favourable habitat ( $p_A \geq 25\%$ ), there was a moderate overlapping in predator visits and, thus, the time spent by predators on banana plants accounted for almost all of the variation in crop visit duration ( $R^2 = 99.10\%$ ).

The predator movement rate was high relative to plot dimensions, and the proportion of time spent in unfavourable habitats was small ( $< 0.077$ ; Fig. 5) or much smaller when alternative favourable habitat was present ( $< 0.007$ ; Fig. 5). The remainder of the predator time was then divided between alternative favourable habitats or banana plants, depending mainly on the relative percentages of these habitats. As a result, time spent by predators on banana plants and crop visit duration were both negatively affected by the percentage of alternative favourable habitats ( $p_A$ ) (Figs. 5 and 6a).

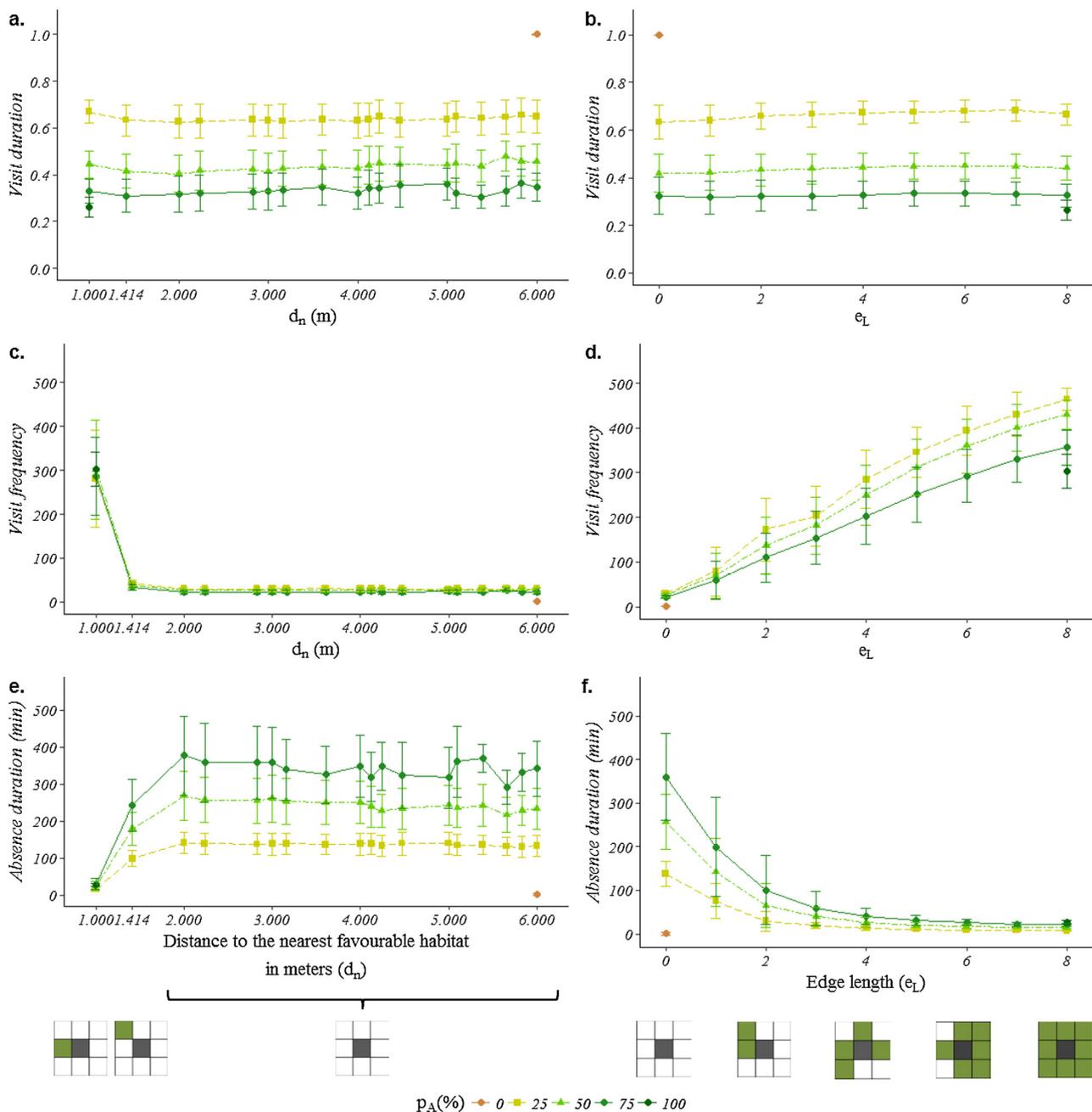
We also found a slight increase in crop visit duration with increasing crop edge length for a given  $p_A$  (Fig. 6a). This slope was the steepest for a  $p_A$  of 25%. This means that time spent on banana plants was also slightly increased by the crop edge length.

#### 3.2.2. Crop visit frequency

As was the case for a single banana plant, a high crop edge length was associated with a high crop visit frequency within a plot. This relation was, to some extent, weaker for plots with a high  $p_A$  (Fig. 6b).

#### 3.2.3. Crop absence duration

*Clumpiness* and crop edge length affected the crop absence duration differently depending on the percentage of alternative favourable habitats ( $p_A$ ) and on the absence or the presence of strips in the plot (Fig. 7). *Clumpiness* had a clear effect in all plots with no strips and intermediate  $p_A$  (25, 50 or 75%), and in those plots with four strips and high  $p_A$  (50–75%) (Fig. 7a). In those cases, given the same  $p_A$ , very disaggregated plots (i.e. plots with low *Clumpiness*) had the shortest crop absence duration. In contrast, crop edge length had a strong effect in plots with 4 (with  $p_A = 25\%$ ) and 8 strips (Fig. 7b). For those plots, and for a given  $p_A$ , the strips surrounding the plants allowed an important change in the crop absence duration: plots with strips close to banana rows had a long crop edge length and thus had a short crop absence duration. Among plots with an intermediate percentage of alternative favourable habitats ( $p_A = 25$ –75%), those with eight strips in the banana plant rows had the shortest crop absence duration, and even a shorter crop absence duration than plots with 100% alternative favourable habitats. Plots with strips that were not in the banana plant rows, in contrast, had the longest crop absence duration.



**Fig. 3.** Effect of the percentage of alternative favourable habitats ( $p_A$ ) and local spatial organisation on visit summary statistics at the banana plant level. Variations in  $p_A$  are represented with shades of brown and green. The effect of  $d_n$  and  $e_L$  on visit duration (a and b), visit frequency (c and d), and absence duration (e and f). Squares at the bottom illustrate the local spatial organisation around the banana plants, with grey cells representing the banana plants, white cells representing the unfavourable habitat, and green cells representing favourable habitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

#### 4. Discussion

Starting from a simple, spatially explicit model for a foraging earwig-like predator in banana fields, we have shown that predator movements and visits to the cultivated plant can be affected by the quantity and the spatial organisation of alternative favourable habitats on a relatively fine scale. By not accounting for broad-scale variations in the local abundance of predators resulting from immigration, reproduction, or mortality, this model allowed us to understand the reductions in per-capita predator effect caused by the dilution effect and indicates strategies to compensate for it.

The model omits some complex behaviours or interactions, such as density-dependent predator movement or the ability of the predator to

assess habitat quality from a distance, which could influence foraging. These omissions may thereby reduce the model's predictive power. Nevertheless, the model is a first step and can be modified in the future by the addition of complexity according to the species and system under consideration.

Our model does not represent the pest or pest damage, and this approach differs from many modelling studies that represent predator and target pest dynamics (Bianchi and Van Der Werf, 2003; Bianchi et al., 2010; Vinatier et al., 2012; Railsback and Johnson, 2014). The inclusion of the pest and pest damage, however, usually requires assumptions regarding pest dynamics and interactions with predators, which can make the results less generalisable or can lead to error propagation if the assumptions are inaccurate. In the current study, the

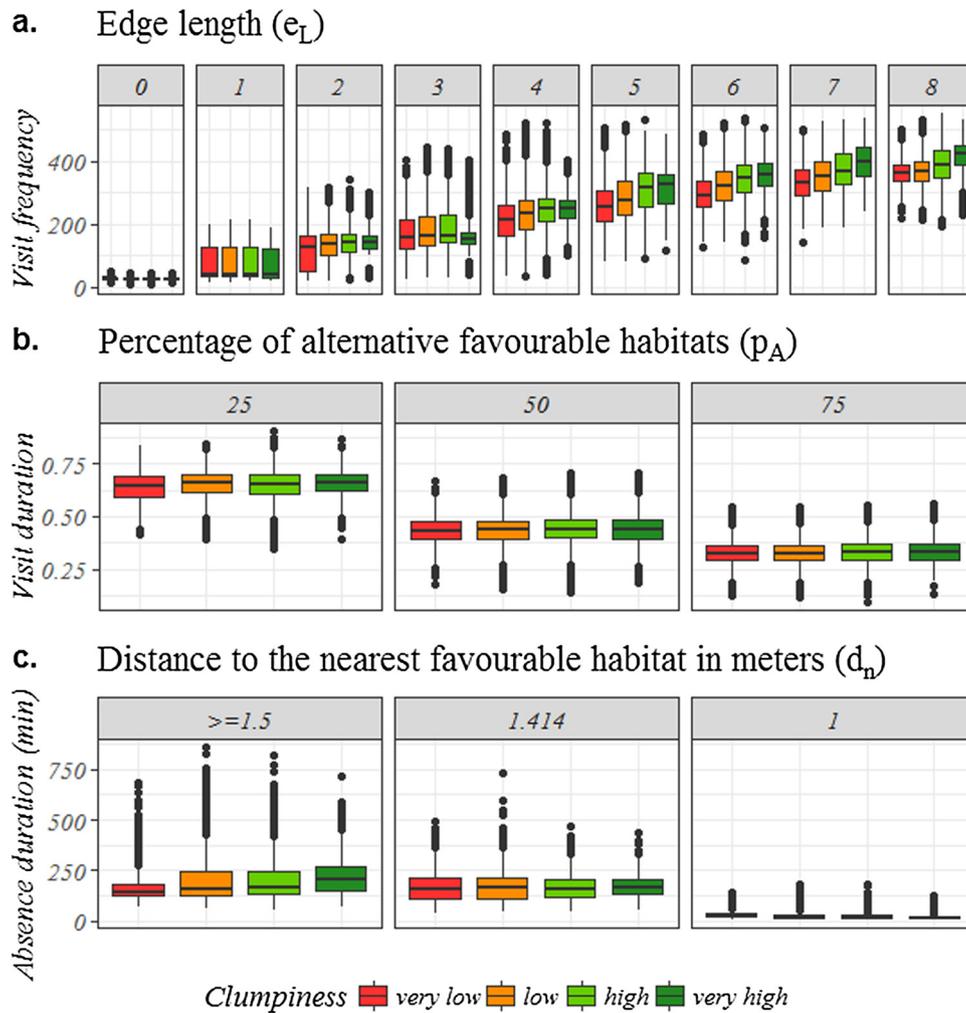


Fig. 4. Effect of the spatial organisation at the plot level on visit summary statistics at the banana plant level for *Clumpiness*.

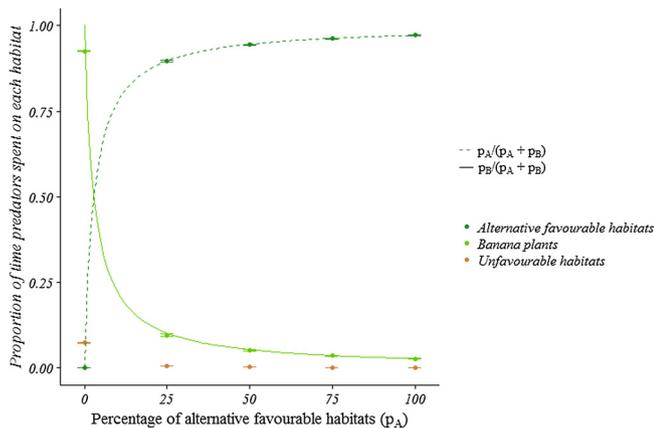


Fig. 5. Proportion of time spent by predators in each habitat type for the duration of the simulation as affected by the percentage of alternative favourable habitats ( $p_A$ ). Times spent by predators in each habitat within a plot were averaged for each  $p_A$ , and standard deviations were all  $< 0.0036$ . Two functions showing the relative percentage of alternative favourable habitat ( $p_A$ ) and banana plants ( $p_B$ ) relative to total favourable habitat ( $p_A + p_B$ ) are indicated by dashed and solid lines, respectively.

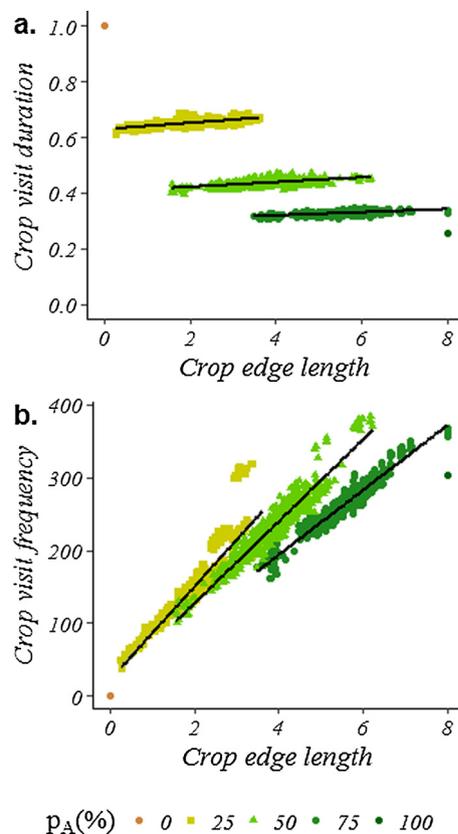
potential effect of the predators on the pests was assessed through their visits to the crop: pest establishment could be prevented by a short absence duration, and the abundance of an established pest could be reduced by a long visit duration or a high visit frequency. These metrics

represent well the per-capita predator effect on CBC if the presence of one predator on the cultivated plant is sufficient to rapidly wipe out pests. For cases in which this assumption is not reasonable, examination of the impact of non-crop habitat addition and the spatial organisation of these non-crops on the number of predators present and the duration of each single visit on the cultivated plant is recommended.

With the model parameterised for an *E. caribbea*-like predator, we found that the duration of banana plant visits ranged from 9.4% to 100% of the simulation period and that absence duration ranged from 4.8 min to 864 min (2.4 days with 6 h of activity per day). However, our model requires validation before the output can be related quantitatively to pest characteristics, such as, for example, the duration of the egg stage of banana weevils (4–7 days; Gold et al., 2001), and before the model can be used to predict predator effects on the pest. The results below were then interpreted qualitatively.

#### 4.1. Dilution effect at the plot level

The dilution effect on predation was observed when the amount of alternative favourable habitat increased at the plot level and not when it increased in the vicinity of the banana plant. The predator diversion from the crop induced a relatively high decrease in the duration of banana plant visits only at the plot level (Fig. 3a & b) and only a small decrease in the frequency of visits. The number of favourable neighbours around banana plants, which could have also diluted the predator effect on a specific banana plant, did not affect the visit duration and even positively affected the visit frequency (Fig. 3d).



**Fig. 6.** Effect of percentage of alternative favourable habitats ( $p_A$ ) and crop edge length at the plot scale on crop visit duration (a) and crop visit frequency (b). Dots with darker green represent plots of banana plants with lower  $p_A$ . black lines represent the linear regression fitted for each  $p_A$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Therefore, as expected, any increase in alternative favourable habitats, if not followed by a local increase in the predator abundance, immediately reduces the CBC by decreasing the duration of the banana plant visits. This indicates that researchers should consider diversified plots for a sufficiently long period to assess an effect on CBC. This indication is consistent with several studies in temperate areas that have shown that predator abundance requires several seasons to increase in response to non-crop habitat addition (Lys et al., 1994; Bostanian et al., 2004). If the pest infestation is widespread, therefore, predator inundation strategies (see definition in Eilenberg et al., 2001) should be more effective in the short term than a strategy based on CBC. Furthermore, any non-crop habitat addition at the plot level should take into account the habitat's ability to increase predator abundance quickly enough relative to the expected increase in pest abundance. More generally, our results on the per-capita predator effect help us to understand how the dilution effect is impacting CBC in the long term. Studies of population dynamics may show that non-crop habitat addition increases predator abundance in the long term; the present study shows that each of those predators account for fewer benefits in terms of CBC.

The dependence of the duration of banana plant visits on the quantity of alternative favourable habitats at the plot level was explained because, unlike the landscape level, where matrix habitats can be very large and risky for species to cross (Fahrig, 2002; Bonte et al., 2012; Haddad et al., 2015), in the plot in our model, the relatively high rate of movement allowed the predator to minimise the time spent in unfavourable habitats if alternative favourable habitats were present (Fig. 5). In our model, each favourable habitat cell equally changed the movements of the predator through space and time, and each banana

plant cell in the plot was visited for an equivalent time driven by the percentage of favourable habitats in the plot (Fig. 3a & b). Consequently, the dilution effect was well explained by the area occupied by the crop in comparison to all favourable habitats. Beyond predator abundance, assessing the relative percentage of the space occupied by the crop and favourable non-crop could thus be useful for understanding and predicting CBC.

The finding that the relative area occupied by the crop and favourable non-crop could greatly affect the duration of banana plant visits by *E. carai-bea* could be extended to many species of ground-dwelling generalist predators that can move rapidly, including ants (Hurlbert et al., 2008), carabids (Wallin and Ekblom, 1988), and spiders (but see Baker, 2007; Casas et al., 2008). However, these findings would be different for habitat specialist species, which are reluctant to cross boundaries (Baker, 2007).

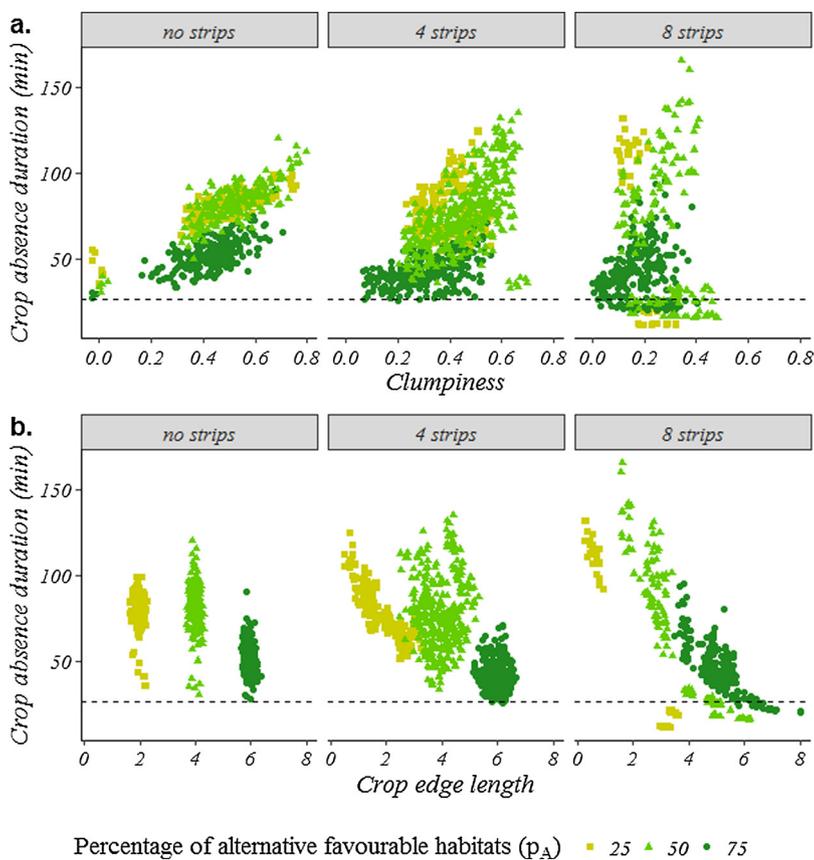
#### 4.2. Edge length at the banana plant level

In contrast to the results suggested by larger-scale studies (Lys et al., 1994; Collins et al., 2002) and larger-scale models (Bianchi et al., 2010; Segoli and Rosenheim, 2012), distance to the nearest favourable habitat was not relevant to CBC according to the output of our model (Fig. 3c & e). We found that the edge length between favourable habitats and crop, but not their distance, could influence banana plant visits via the number of favourable neighbours at the banana plant level. Visits were more frequent (Fig. 3d) and absence durations were shorter (Fig. 3f) when the number of alternative favourable habitats around banana plants increased. The changes induced by edge length were strong, i.e. absence duration could be up to 20 times shorter for a surrounded banana plant than for an isolated banana plant.

These results are consistent with the 'drift-fence hypothesis' concerning connectivity at the landscape level. This hypothesis assumes that corridors intercept dispersing individuals from the surrounding landscape and direct them towards patches connected by corridors (Haddad and Baum, 1999). Although the process of patch colonisation differs from that of banana plant visits, the direct contact between a banana plant and favourable habitats affected the frequency of banana plant visits in the same way that patch connections affect patch colonisation. This effect is not surprising because the link is mathematical for an organism that is walking randomly. The probability that an organism reaches an area is proportional to the angle subtended by this area in its horizon (Haddad and Baum, 1999).

In the model, the edge length for each individual banana plant failed to directly counteract the dilution effect on visit duration. At the plot level, predators spent more time overall on banana plants surrounded by favourable habitats. This increase was greater as the percentage of alternative favourable habitats decreased (Fig. 6a), but the increase was not enough to compensate for the dilution effect. An increasing effect of the spatial organisation of a habitat as its quantity decreases is a common result of broad-scale models of population dynamics (Hill and Caswell, 1999; Hiebeler, 2000; Flather and Bevers, 2002).

Overall, our model predicts that a long edge length benefits CBC. An increase in edge length could reduce the risk of pest establishment on the crop, especially if there are many alternative favourable habitats in the plot. A long edge length could also help to lower the level of a widespread infestation by limiting the dilution effect, especially if there are few alternative favourable habitats in the plot. A model accounting for predator population dynamics also found that an increase in edge length increased the abundance of ground-dwelling arthropod predators when strips of an alternative favourable habitat were established before an annual crop was planted (Corbett and Plant, 1993). On the other hand, the latter authors found that an increase in edge length reduced the predator abundance when the annual crop and strips were established simultaneously. This last result emerged because the model of Corbett and Plant assumed faster movements in the crop than in the



**Fig. 7.** Effects of the percentage and spatial organisation of favourable habitats on crop absence duration at the plot scale. a and b indicate the effect of crop edge length and *Clumpiness*, respectively, as affected by  $p_A$  or the number of strips. Dashed lines indicate the minimum value of crop absence duration for a plot with a  $p_A$  of 100%, which was 26.52 min. In a plot with a  $p_A$  of 0%, crop absence duration was near 0 (max 0.76 min).

alternative favourable habitats. In our perennial crop-based model, such assumptions were less relevant because crop area was low, and the difference of quality between bare soil and other habitats should be much greater than between the alternative favourable habitat and the crop.

#### 4.3. Which organisations of alternative favourable habitats are best for CBC at the plot level?

According to our model, the ‘best’ kind of plot, i.e. the plot with high visit duration and with low absence duration, was one with no alternative favourable habitats. This result is, to some extent, an artefact resulting from the absence of mortality and emigration in the model. In agrosystems, we should expect that a plot without alternative favourable habitats would support increased predator emigration due to a lack of food quantity or diversity and would support increased predator mortality due to increased rates of predation on the predator in unfavourable habitats. A plot without alternative favourable habitats could be good for CBC, however, if the predator can find sufficient food and refuge in crops, as is the case for field overwintering species of carabids during spring and summer in annual crops (cereal or pea) (Holland et al., 2009).

Plots with only favourable habitats, despite a strong dilution effect, had shorter crop absence duration than most plots with intermediate percentages of favourable habitats. This finding means that increasing the fragmentation of favourable habitats tended to reduce the rate of predator movement, as has been observed in fragmented landscapes for butterfly dispersal rate (Baguette et al., 2003) and the activity-density of carabid species (Rusch et al., 2016).

For each given intermediate percentage of favourable habitat, the best spatial organisations of alternative favourable habitats were strips placed in each banana plant row (Fig. 7b). Apart from the effect of crop edge length on the visit duration at the plot level, the effect of

organisation of alternative favourable habitats on crop visits was mainly due to the variation in edge length at the banana plant level. The spatial organisation that should minimise absence duration and thus help prevent pest establishment is therefore the one that maximises the edge length of each banana plant. By increasing edge length equally for each banana plant, plots with strips in each banana plant row had the lowest crop absence durations for a given quantity of favourable habitats. In such plots the crop absence duration was also lower than plots with only favourable habitats, and this finding may result from a higher frequency of visits.

Absence duration was longest, in contrast, when strips were not located in the banana plant row. The use of strips has been experimentally investigated mainly in intercropping systems, and such strips have resulted in a greater increase in predator abundance and pest control in annual crops (Letourneau et al., 2011) than in perennial crops (McIntyre et al., 2001; but see Dassou et al., 2015; Rusch et al., 2016). We did not find studies explicitly comparing the effect of strips located on rows or between rows. The variability in the predator absence and visit duration generated by the overlap or disconnection of strips with banana plant rows is intriguing and supports the idea that the effect of non-crop habitats on CBC depends on the configuration of these habitats.

In the absence of strips, the plot organisation that minimised crop absence duration was a disaggregation of favourable habitats (Fig. 7a). Without strips, the crop edge length barely changed in between plots of similar quantity of alternative favourable habitat (Fig. 7), indicating that a difference in crop absence duration between plots without strips was caused by variations in edge length between banana plants within each plot. As only having a few favourable habitats in direct contact with a banana plant reduces the absence duration dramatically (i.e., short edge length) (Fig. 2f), crop absence duration was reduced by minimising the number of isolated banana plants in a plot.

Together, our results for the effects of strips and aggregations

suggest that non-crop habitat addition may not result in CBC if the non-crop habitat spatial organisation is not managed at the plot level. The results therefore provide insight into the lack of CBC obtained with non-crop habitat addition, such as field margins (Marshall and Moonen, 2002), beetle banks (Frank, 2010), and sown flower or weedy strips (Haaland et al., 2011). According to our model, beetle banks that provide alternative prey to generalist predators should be established before pest arrival or should be located close to the crop (but see Corbett and Plant, 1993).

## 5. Conclusions

The findings of the present study demonstrate that researchers should not only consider population dynamics but also the per-capita predator effect when assessing the effect of non-crop habitat addition on CBC. The balance between these two forces may be the biggest determinant of when additional non-crop habitats are beneficial or detrimental to CBC. We found that the per-capita predator effect is strongly affected by the dilution effect induced by non-crop habitat addition, but that those negative effects could also be partially mitigated by the spatial organisation of the non-crop habitat. At the banana plant level, a long edge length between the crop and non-crop habitat can compensate for this dilution effect by reducing the absence duration of predators on the cultivated plant. At the plot level, the highest edge lengths were in plots with non-crop strips in the banana plant rows, and this spatial organisation resulted in a low crop absence duration. Those spatial organisations of non-crop habitats resulting in low crop absence duration provide a first glimpse of how the judicious addition of non-crop habitats at the plot level could minimise the diversion of predators away from the pests. Overall, our results suggest that the spatial organisation of non-crop habitats is a tool that can be used by farmer to improve CBC. However, side effects should be considered before farmers are advised to implement a given spatial organisation, such as the ability of a specific predator to wipe out pests within a single visit or the potential for competition between crop and non-crop plants, as already investigated in banana fields (Poeydebat et al., 2016).

Given the processes, scales and periods considered in the model, and the use of commonly accepted assumptions about foraging movement, we think the results of the study can be considered fairly robust for a diversity of ground-dwelling predators unless these predators behave very differently in response to habitat quality.

## Acknowledgements

This work was supported by INRA (French National Institute for Agricultural Research, EA division), by CIRAD (French Agricultural Research Centre for International Development), and by the STRADIV project (n° 1504-003) funded by the Agropolis foundation, France.

We thank one anonymous referee for very constructive comments on the manuscript. In particular, he or she suggested the 'per-capita predator effect' notion to better represent one of the key results.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.09.026>.

## References

- Altieri, M.A., Letourneau, D.K., 1982. Vegetation management and biological control in agroecosystems. *Crop Protect* 1, 405–430.
- Arrignon, F., Deconchat, M., Sarthou, J.-P., Balent, G., Monteil, C., 2007. Modelling the overwintering strategy of a beneficial insect in a heterogeneous landscape using a multi-agent system. *Ecol. Model.* 205, 423–436.
- Baguette, M., Mennechez, G., Petit, S., Schtickzelle, N., 2003. Effect of habitat fragmentation on dispersal in the butterfly *Proclissiana eunomia*. *C. R. Biol.* 326.
- Baker, L.B., 2007. Effect of corridors on the movement behavior of the jumping spider *Phidippus princeps* (Araneae, Salticidae). *Can. J. Zool.* 85, 802–808.
- Barraquand, F., Benhamou, S., 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology* 89, 3336–3348.
- Begg, G.S., Cook, S.M., Dye, R., Ferrante, M., Franck, P., Lavigne, C., Lovei, G.L., Mansion-Vaquié, A., Pell, J.K., Petit, S., Quesada, N., Ricci, B., Wratten, S.D., Birch, A.N.E., 2017. A functional overview of conservation biological control. *Crop Protect* 97, 145–158.
- Bell, W.B., 1991. Searching Behaviour - The Behavioural Ecology of Finding Resources, 358.
- Bianchi, F.J.J.A., Van Der Werf, W., 2003. The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. *Environ Entomol* 32, 1290–1304.
- Bianchi, F.J.J.A., Schellhorn, N.A., van der Werf, W., 2009a. Foraging behaviour of predators in heterogeneous landscapes: the role of perceptual ability and diet breadth. *Oikos* 118, 1363–1372.
- Bianchi, F.J.J.A., Schellhorn, N.A., van der Werf, W., 2009b. Predicting the time to colonization of the parasitoid *Diadegma semiclausum*: the importance of the shape of spatial dispersal kernels for biological control. *Biol. Control* 50, 267–274.
- Bianchi, F., Schellhorn, N.A., Buckley, Y.M., Possingham, H.P., 2010. Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. *Ecol. Appl.* 20, 2322–2333.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehoucq, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C., Travis, J.M.J., 2012. Costs of dispersal. *Biol. Rev.* 87, 290–312.
- Bostanian, N.J., Goulet, H., O'Hara, J., Masner, L., Racette, G., 2004. Towards insecticide free apple orchards: flowering plants to attract beneficial arthropods. *Biocontrol Sci. Technol.* 14, 25–37.
- Carval, D., Resmond, R., Achard, R., Tixier, P., 2016. Cover cropping reduces the abundance of the banana weevil *Cosmopolites sordidus* but does not reduce its damage to the banana plants. *Biol. Control* 99, 14–18.
- Casas, J., Steinmann, T., Dangles, O., 2008. The aerodynamic signature of running spiders. *PLoS One* 3.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932.
- Charrier, S., Petit, S., Burel, F., 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agric. Ecosyst. Environ.* 61, 133–144.
- Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., Chaney, K., 2002. Influence of beetle banks on cereal aphid predation in winter wheat. *Agric. Ecosyst. Environ.* 93, 337–350.
- Corbett, A., Plant, R.E., 1993. Role of movement in the response of natural enemies to agroecosystem diversification: a theoretical evaluation. *Environ. Entomol.* 22, 519–531.
- Dassou, A.G., Carval, D., Dépigny, S., Fansi, G., Tixier, P., 2015. Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping. *Biol. Control* 81, 51–57.
- Duyck, P.-F., Lavigne, A., Vinatier, F., Achard, R., Okolle, J.N., Tixier, P., 2011. Addition of a new resource in agroecosystems: do cover crops alter the trophic positions of generalist predators? *Basic Appl. Ecol.* 12, 47–55.
- Eilenberg, J., Hajek, A., Lomer, C., 2001. Suggestions for unifying the terminology in biological control. *BioControl* 46, 387–400.
- Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol. Appl.* 12, 346–353.
- FAO, 2017. Food and Agriculture: Driving Action Across the 2030 Agenda for Sustainable Development.
- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am. Nat.* 159, 40–56.
- Frank, S.D., 2010. Biological control of arthropod pests using banker plant systems: past progress and future directions. *Biol. Control* 52, 8–16.
- Gold, C.S., Pena, J.E., Karamura, E.B., 2001. Biology and integrated pest management for the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). *Integr. Pest Manage. Rev.* 6, 79–155.
- Grimm, V., Railsback, S.F., 2005. Individual-Based Modeling and Ecology. Princeton university press, pp. 448.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rügen, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198, 115–126.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221, 2760–2768.
- Haaland, C., Naisbit, R.E., Bersier, L.-F., 2011. Sown wildflower strips for insect conservation: a review. *Insect Conserv. Divers.* 4, 60–80.
- Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. *Ecol. Appl.* 9, 623–633.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy,

- T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1.
- Henri, D.C., Jones, O., Tsiattalos, A., Thébaud, E., Seymour, C.L., van Veen, F.J.F., 2015. Natural vegetation benefits synergistic control of the three main insect and pathogen pests of a fruit crop in southern Africa. *J. Appl. Ecol.* 52, 1092–1101.
- Hiebler, D., 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. *Ecology* 81, 1629–1641.
- Hill, M.F., Caswell, H., 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecol. Lett.* 2, 121–127.
- Holland, J.M., Birkett, T., Southway, S., 2009. Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl* 54, 19–33.
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12, 197–129.
- Hurlbert, A.H., Ballantyne, F., Powell, S., 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. *Ecol. Entomol.* 33, 144–154.
- Jackson, H.B., Fahrig, L., 2012. What size is a biologically relevant landscape? *Landscape Ecol.* 27, 929–941.
- Joachim, C., Weisser, W.W., 2015. Does the aphid alarm pheromone (E)-beta-farnesene act as a kairomone under field conditions? *J. Chem. Ecol.* 41, 267–275.
- Jonsson, M., Wratten, S.D., Landis, D.A., Gurr, G.M., 2008. Recent advances in conservation biological control of arthropods by arthropods. *Biol. Control* 45, 172–175.
- Kruess, A., Tscharntke, T., 1994. Habitat fragmentation, species loss, and biological control. *Science* 264, 1581–1584.
- Lamb, R.J., 1975. Effects of dispersion, travel, and environmental heterogeneity on populations of the earwig *Forficula auricularia* L. *Can. J. Zool.* 53, 1855–1867.
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175–201.
- Lavigne, C., Achard, R., Tixier, P., Jannoyer, M.L., 2012. How to integrate cover crops to enhance sustainability in banana and citrus cropping systems. In: In: Wuensche, J.N., Albrigo, L.G., Gubbuk, H., Reinhardt, D.H., Staver, C., VanDenBergh, I. (Eds.), *Xxviii International Horticultural Congress on Science and Horticulture for People*, vol. 928. Int Soc Horticultural Science, Leuven, pp. 351–357 1.
- Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutiérrez, C., López, S.D., Mejía, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21, 9–21.
- Lys, J.A., Zimmermann, M., Nentwig, W., 1994. Increase in activity density and species number of carabid beetles in cereals as a result of strip-management. *Entomol. Exp. Appl.* 73, 1–9.
- Mailleret, L., Grogard, F., 2006. Optimal release policy for prophylactic biological control. In: In: Commaul, C., Marchand, N. (Eds.), *Positive Systems, Proceedings*, vol. 341. Springer-Verlag, Berlin, Berlin, pp. 89–96.
- Marshall, E.J.R., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agric. Ecosyst. Environ.* 89, 5–21.
- Martin, A.E., Fahrig, L., 2015. Matrix quality and disturbance frequency drive evolution of species behavior at habitat boundaries. *Ecol. Evol.* 5, 5792–5800.
- Martin, E.A., Seo, B., Park, C.-R., Reineking, B., Steffan-Dewenter, I., 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecol. Appl.* 26, 448–462.
- McIntyre, B.D., Gold, C.S., Kashajia, I., Ssali, H., Night, G., Bwamiki, D., 2001. Effects of legume intercrops on soil-borne pests, biomass, nutrients and soil water in banana. *Biol. Fertility Soils* 34, 342–348.
- Mollot, G., Tixier, P., Lescouret, F., Quilici, S., Duyck, P.-F., 2012. New primary resource increases predation on a pest in a banana agroecosystem. *Agric. For. Entomol.* 14, 317–323.
- Mollot, G., Duyck, P.F., Lefeuvre, P., Lescouret, F., Martin, J.F., Piry, S., Canard, E., Tixier, P., 2014. Cover cropping alters the diet of arthropods in a banana plantation: a metabarcoding approach. *PLoS One* 9, e93740.
- Morris, D.W., 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* 1, 379–388.
- Pei, Y.Z., Chen, M.M., Liang, X.Y., Li, C.G., Zhu, M.X., 2018. Optimizing pulse timings and amounts of biological interventions for a pest regulation model. *Nonlinear Anal. Hybrid Syst.* 27, 353–365.
- Penn, H.J., 2018. Wooded field margins increase potential for cultural and biological control of soybean pests. *Agric. Ecosyst. Environ.* 255, 45–51.
- Poeydebat, C., Carval, D., de Bellaire, L.D., Tixier, P., 2016. Balancing competition for resources with multiple pest regulation in diversified agroecosystems: a process-based approach to reconcile diversification and productivity. *Ecol. Evol.* 6, 8607–8616.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*. v 3.5.0, R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Railsback, S.F., Johnson, M.D., 2014. Effects of land use on bird populations and pest control services on coffee farms. *Proc. Natl. Acad. Sci.* 111, 6109–6114.
- Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603–614.
- Rusch, A., Binet, D., Delbac, L., Thiery, D., 2016. Local and landscape effects of agricultural intensification on Carabid community structure and weed seed predation in a perennial cropping system. *Landscape Ecol.* 31, 2163–2174.
- Schellhorn, N.A., Bianchi, F.J.J.A., Hsu, C.L., 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annu. Rev. Entomol.* 59, 559–581.
- Segoli, M., Rosenheim, J.A., 2012. Should increasing the field size of monocultural crops be expected to exacerbate pest damage? *Agric. Ecosyst. Environ.* 150, 38–44.
- Snyder, W.E., Ives, A.R., 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84, 91–107.
- Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* 47, 561–594.
- Thomson, L.J., Hoffmann, A.A., 2013. Spatial scale of benefits from adjacent woody vegetation on natural enemies within vineyards. *Biol. Control* 64, 57–65.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nohuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309.
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59.
- Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batary, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martinez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control - Five hypotheses. *Biol. Conserv.* 204, 449–458.
- Turner, M.G., 1989. Landscape ecology - the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20, 171–197.
- Vet, L.E.M., Dicke, M., 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37, 141–172.
- Vinatier, F., Lescouret, F., Duyck, P.-F., Martin, O., Senoussi, R., Tixier, P., 2011. Should I stay or should I go? A habitat-dependent dispersal kernel improves prediction of movement. *PLoS One* 6, e21115.
- Vinatier, F., Gosme, M., Valantin-Morison, M., 2012. A tool for testing integrated pest management strategies on a tritrophic system involving pollen beetle, its parasitoid and oilseed rape at the landscape scale. *Landscape Ecol.* 27, 1421–1433.
- Wajnberg, E., Roitberg, B.D., Boivin, G., 2016. Using optimality models to improve the efficacy of parasitoids in biological control programmes. *Entomol. Exp. Appl.* 158, 2–16.
- Wallin, H., Ekbohm, B.S., 1988. Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. *Oecologia* 77, 39–43.
- Wang, X., Blanchet, F.G., Koper, N., 2014. Measuring habitat fragmentation: an evaluation of landscape pattern metrics. *Methods Ecol. Evol.* 5, 634–646.
- Westerberg, L., Ostman, O., Wennergren, U., 2005. Movement effects on equilibrium distributions of habitat generalists in heterogeneous landscapes. *Ecol. Model.* 188, 432–447.
- Wilensky, U., 1999. *Netlogo*. Center for Connected Learning and Computer-Based Modeling, v 6.0.1, Northwestern University, Evanston, IL. <http://ccl.northwestern.edu/netlogo/>.
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030.