



# Alley cropping agroforestry mediates carabid beetle distribution at a micro-habitat scale

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**Abstract** Temperate agroforestry systems are being strongly promoted for ecological reasons in many regions of the world. Pest management in these highly-structured environments is however barely studied, despite widespread claims of increased biological control enhanced by the presence of trees and grassy strips at their base. The aim of this study is to assess how different carabid species use space in an alley cropping agroforestry system. We carried out spatially and temporally-tight pitfall trap experiments in an old grown agroforestry plot and characterized how the activity density of two abundant carabid species of the field, *Nebria brevicollis* (F.) and *Anchomenus dorsalis* (Pont.), varied with the distance to the strip. The grassy strips were either un-mowed or used to stack branches, and were planted with or without trees. Both

species clearly responded to the differences between strips and culture, but in a different way. *N. brevicollis* had a strong preference for the strip, but only when the strip had trees on it. Conversely, almost no captures of *A. dorsalis* occurred in the strip, whereas plenty were captured in crops. Our results are similar to those obtained on field margins and beetle banks, implying that the rich knowledge drawn from these studies can be applied to alley cropping agroforestry systems. These systems however differ by the regular arrangement of strips, which may support an assemblage of species with varying habitat requirements. These results imply that grassy strips can be managed for increasing their role in conservation biological control.

**Keywords** Agroecology · Conservation biological control · Natural enemies · Pest management

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## Introduction

By enhancing both biodiversity and spatial complexity, agroforestry systems might naturally lend themselves to a greater potential for the control of pests by their natural enemies (Jose 2009; Smith et al. 2013). Many studies have indeed established a positive link between biodiversity and biological control (Le-tourneau et al. 2009; Crowder and Jabbour 2014), as

well as between habitat complexity and biological control (Diekötter and Crist 2013; Veres et al. 2013). There is however relatively little evidence supporting this assertion directly for temperate agroforestry systems (Russel 1989; Stamps and Linit 1997; Smith et al. 2013). Due to the lack of knowledge on pest management in temperate agroforestry systems, the term “agroforestry” does not even appear in the latest books on biological control or pest management, see for example Heimpel and Mills (2017) or Coll and Wajnberg (2017). Moreover, a study by Smits et al. (2012), which quantified the dynamics of aphids and their predators, did not reveal any differences between agroforestry and monocropping fields. A recent study by Martin-Chave et al. (2018a) did however find a significantly higher predation rate of arthropods in agroforestry plots compared to control plots, with no tree on them. Finally, Stamps et al. (2009) found that alley cropping significantly increased alfalfa weevil mortality, but only for two of the four sampling dates. This diversity of results highlights the need to better explain the mechanisms underlying biological control in agroforestry systems. Even in tropical agroforestry, in which biological control has been more intensively studied (see for example Perfecto et al. 2009), most studies focused on how management practices—such as which species are grown, how they are arranged in space, and what are the microclimatic consequences—affect the pest populations, but their consequences for predator species have been much less studied (Rao et al. 2000; Schroth et al. 2000).

A specificity of alley cropping agroforestry systems is the strong patterning in space induced by the alternation between crops and trees. Trees are planted in rows, interspaced with alleys of crops. There is often an unexploited herbaceous strip (understory) at the bottom of the trees (Dupraz and Liagre 2008). For the sake of clarity, we will henceforth reserve the term “strip” only to refer to this uncultivated area in the tree rows. In the context of pest suppression, it remains unclear how this arrangement affects the efficiency of biological control. The spatial heterogeneity induced by the alternation between tree rows and crops might promote a differential use of habitat by predators, for example by using strips as a refuge and reproductive habitat, whereas using crops as a habitat for foraging, or vice versa (Kromp and Steinberger 1992; Fourier and Loreau 2001; Holland et al. 2005). The way predators use space conditions their efficiency at

capturing preys and has thus direct implications for the dynamics at the population level and for pest control. Therefore, the question as to how the spatial arrangement of agroforestry fields affects the utilization of space by individual predators is a key information towards a better understanding of biological control.

We tackle those questions using carabid beetles, one of the most ubiquitous predator group of agroecosystems (Kromp 1999). Their high abundances and their polyphagous habits make them good candidates to control a number of pest species, but much remains to be understood in order to establish their efficiency at suppressing pest populations (Kromp 1999; Holland 2002; Bertrand et al. 2016). Ground beetle communities are very sensitive to perturbation of their habitat, which includes agricultural practices (Eyre et al. 2013). Moreover, many species use both crop and non-crop habitats to complete their lifecycle, but in a different way (Thiele 1977; Marrec et al. 2015). This implies that there is a large scope for improving biological control by adapting practices to predators' biology. Most experimental designs for studying the use of space by carabid beetles are based on large-scale designs, where pitfall traps are disposed 10 m or more apart from each other (e.g. Fournier and Loreau 1999; Olson and Wäckers 2007; Eyre et al. 2009; Smits et al. 2012). Those are valuable designs for characterizing distribution patterns on a landscape, but they do not inform on the mechanisms driving spatial behaviour and habitat choice of individuals. For studying daily movements, the relevant scale is generally much smaller, on the order of a few meters, or less (Thiele 1977; Allema et al. 2014). This inference is based on the observation that, in capture-recapture experiments, individuals often tend to stay near the points they have been released (see the extensive discussion in Thiele 1977, pp. 284–286; see also Thomas et al. 2006). Considering such a small scale is especially important for habitats which are also heterogeneous at a small spatial scale, such as agroforestry fields, intercropping, or permacultures.

Here we report the results of a pilot field study that used a spatially-dense pitfall trap design in order to characterize how two carabid beetle species respond to the structuration imposed by alley-cropping designs at a small spatial scale. In addition, we tested whether manipulating the strip by storing branches on them (Fig. 1), a current—yet, undocumented—practice, had significant effects on patterns of activity density.



**Fig. 1** Left panel: typical agroforestry plot, showing a line of paulownias with a grassy strip, and wheat culture on the right. Bottom-right: a strip used for the storing of branches. Top-right:

diagrammatic representation of how the traps (black dots) were disposed within a plot. Light green: wheat crops; dark green: grassy strip; black squares: trees. (Colour figure online)

This practice may affect beetles' activity density, as the branches may impede individuals' displacements; individuals may also engage in different activities in those strips, for example, by using branches as shelters and hide under it; or again, those strips may host a different community of organisms that interact with the beetles in different ways. All of these factors may render this type of microhabitat more or less attractive, depending on the species considered. To test those questions, we compared activity density patterns resulting from grassy, minimally managed strips, and from strips that had been used for storing branches. Finally, we tested whether any effect of the strip was due to the strip itself, or to the presence of trees on them.

## Materials and methods

### Study site

The experiment was performed in a 10 ha agroforestry field located near Vézénobres, France (44°3'N; 4°8'E). This site has a long history in agroforestry research (e.g. Dupraz 1998; Graves et al. 2010; Martin-Chave et al. 2018a, b). The climate is Mediterranean and the

soil is silty. The field area is located in an alluvial plain and is frequently flooded. The land is entirely managed organically and is mostly used to produce vegetables and wheat (*Triticum turgidum* L.). It is an alley cropping system, in which cultures are interspaced with rows of hybrid walnut trees (*Juglans nigra* × *Juglans regia* L.), paulownias (*Paulownia tomentosa* (Thunb.) Steud.), poplars (*Populus spp.*), and occasionally some other tree species.

### Experimental design

We quantified the activity density of two abundant species of Carabidae (Coleoptera) in the field, *Nebria brevicollis* and *Anchomenus dorsalis*. The study was conducted from April, 22nd to May, 5th, 2016 (14 days), which corresponds to the yearly period of maximum activity of these species (Martin-Chave 2014). We used 16 plots of 25 × 6 m, each containing a strip and wheat culture. Half of them were oriented north–south, and half of them east–west. Tree lines were composed with either 10 m high paulownias or 4 m high poplars, spaced by usually about 5 m. Plots were randomly spread within the whole field, sometimes separated by a few hundreds of meters from each other. Most strips were about 1.5 m wide and

vegetation was about 20–30 cm high at the time of the experimentation (Fig. 1). Crops were 16 m wide. Within each plot, we arranged 4 lines of 4 dry pitfall traps of 8 cm diameter, from the centre of the strip to the centre of the culture, each trap spaced 2 m apart from each other (Fig. 1). They were sampled in a temporally-tight fashion, 5 times a day, at 9 a.m., 11 a.m., 1 p.m., 3 p.m., and 5 p.m. Each plot constituted the statistical unit used to assess the effect of specific management practices.

In addition to testing how the distance to the strip affected activity density, we also tested two additional factors. First, we used blocks with no tree on the strips in order to distinguish whether any observed pattern is due to the presence of the trees on the strips or whether it is due to the strips themselves. Second, we tested whether using the strips for stacking branches affected activity density patterns. These branches were the by-product of the cutting of a large number of poplar trees 4 years before, and were in an intermediate state of decomposition (Fig. 1). Usually, those stacks of branches were partly covered with earth, with some vegetation either on the top or in between the branches.

Overall, the design included 4 replicate plots for each possible combination between factors (presence/absence of trees  $\times$  use of the strip).

### Statistical analyses

We analyzed activity density with generalized linear mixed-effects models, using the lme4 package in R (Bates et al. 2015; R Core Team 2018). Activity density is here meant as the number of captures per trap and per day. The plot identity was included as a random factor affecting the coefficients associated with the effect of the distance to the strip. Setting plot identity as a random factor allowed to account for potential differences due to intrinsic differences between plots, including factors like row orientation and tree type. The distribution retained was of Poisson type, with a square-root link function. Significance was assessed using Wald Chi-square tests. We started the analysis with all possible interaction terms and removed any non-significant term, one at the time, until we reached the minimal adequate model (Crawley 2013). We report both the significance of the terms retained in the final model and those excluded, as

assessed with a Chi-squared test using the anova function in R.

## Results

### Spatial patterns of activity density

Over the course of the experiment, 861 *N. brevicollis* and 915 *A. dorsalis* were captured. *Nebria brevicollis* was clearly more active at night, with captures occurring almost exclusively between 5 p.m. and 9 a.m. (Fig. 2a). *Anchomenus dorsalis* was more active at night and morning, and the capture rate decreased after 11 a.m. (Fig. 2b).

The distance to the strip affected the spatial distribution of both species, although in a rather different way. For *N. brevicollis* (Fig. 3, Table 1), there was a negative association between the distance to the strip and capture rate. There were more beetles in the strip and its neighbourhood (2 m) than further in the culture, but only when the strip had trees. In addition, the overall rate of capture was far greater in plots with trees than in plots without trees (4.6 times), including at 4 m and 6 m from the strip. Thus, most results point to the importance of trees in determining the activity density of this species. The use of strips for storing branches did not have any significant effect on activity density (Table 1).

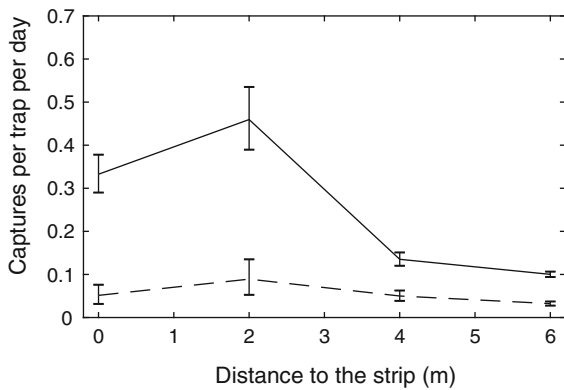
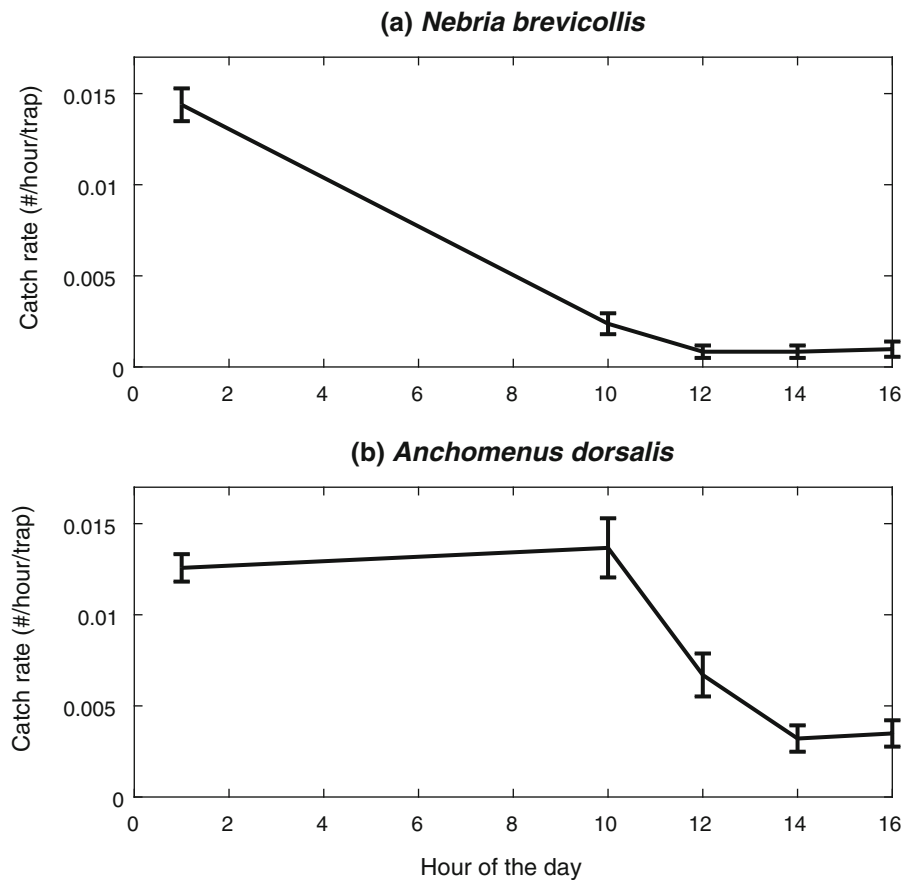
For *A. dorsalis* (Fig. 4, Table 1), neither the presence/absence of trees nor the use of the strips for storing branches had a significant effect on activity density. The rate of capture was significantly greater in the culture than in the strip, with a rate about four times higher in the former than in the latter.

## Discussion

### General patterns of activity density and relation with species biology

Our results show that both species respond to the spatial heterogeneity generated by an agroforestry structure, at a very small spatial scale. Distances of only a few meters are sufficient to generate important differences in the activity density both *N. brevicollis* and *A. dorsalis*. The difference between strips and

**Fig. 2** Captures rate (mean  $\pm$  SE) as a function of the time of the day for **a** *N. brevicollis* and **b** *A. dorsalis*



**Fig. 3** Capture rate (mean  $\pm$  SE) of *N. brevicollis* as a function of the distance to the strip. The solid lines corresponds to blocks with trees on the strip, whereas the dashed line corresponds to blocks with no tree on the strip

culture was especially relevant in mediating the use of space of these two species.

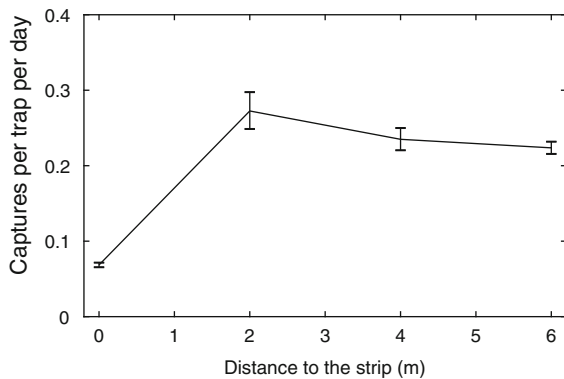
For *N. brevicollis*, the observed patterns are clearly consistent with a preference for the proximity to the

**Table 1** Results of the GLMM analysis on the factors affecting carabid activity density

	<i>N. brevicollis</i>		<i>A. dorsalis</i>	
	DF	<i>p</i>	DF	<i>p</i>
Distance	<b>1</b>	<b>0.519</b>	<b>1</b>	<b>&lt; 0.001</b>
Tree	<b>1</b>	<b>0.022</b>	<b>1</b>	0.133
Strip use	1	0.079	1	0.680
Distance*tree	<b>3</b>	<b>0.020</b>	3	0.124
Distance*strip use	3	0.123	3	0.240
Tree*strip use	1	0.214	1	0.498
Distance*tree* Strip use	3	0.324	3	0.133

The factor ‘Strip use’ refers to whether the strip is used for stacking branches or not. Bolded values correspond to the statistics of the terms retained in the final model

trees. There was a steep decline in capture rates beyond 2 m from the strips (Fig. 3). Capture rates were very low in plots with no tree, and the presence of



**Fig. 4** Capture rate (mean  $\pm$  SE) of *A. dorsalis* as a function of the distance to the strip

old branches in the strips did not compensate in any way for the absence of live trees (Table 1). Despite the absence of trees in these plots, they were still inserted within an overall agroforestry matrix, in which at least some trees were usually present no more than 10 m away or so. It is therefore rather likely that *N. brevicollis* would not be observed at all if trees were even farther away. This preference for proximity of trees may be because of an overall preference of *N. brevicollis* for woodland habitats, as documented in previous studies (Greenslade 1964; Garcia et al. 2000). *Nebria brevicollis* is indeed often absent from arable lands (Thiele 1977). Trees may offer to the individuals resources and shelters they don't find in the crop, and even simple rows of trees may be enough to sustain locally significant populations of *N. brevicollis*. Our finding echoes those from Garcia et al. (2000) who studied how the activity density of this species varied away from a hedge disposed in between two arable fields. Activity density was indeed very high in the hedge but much reduced at distances greater than 5.3 m, and basically null for distance greater than 15 m.

Finally, in *A. dorsalis*, patterns of activity density are also consistent with the idea of habitat preference. Our results indeed demonstrates a clear affinity of the species for the cultures rather than the strip. *Anchomenus dorsalis* is a generalist predator, feeding on aphids, earthworms, Diptera and slugs (Sunderland 1975; Bilde and Toft 1994). Experimentations seem to suggest that this species aggregates where its prey is, especially cereal aphids (Bryan and Wratten 1984). This may be the reason why we found more of them in wheat cultures.

## Managing agroforestry systems for improved conservation biological control

In the discussion above, we mentioned several similarities of our results with studies on field margins, hedgerows and beetle banks. That had not been demonstrated in agroforestry systems before. This implies that the rich knowledge drawn from these lines of research may be transferred, at least partially, to agroforestry systems (e.g. Ries et al. 2004; Olson and Wäckers 2007; Feber et al. 2015; Knapp and Řezáč 2015; Heimpel and Mills 2017). These habitats are largely recognized for improving biodiversity by providing relatively undisturbed habitat (Bianchi et al. 2006; Ernoult et al. 2013; Feber et al. 2015), and for enhancing connectivity between habitats due to their role as ecological corridors (Olson and Wäckers 2007; Marchi et al. 2013). This knowledge may be used, for example, as a baseline for the use of space of other species and serve as a basis to implement management strategies of agroforestry systems. For example, some of these studies demonstrated the importance of microclimate and shelters for conservation biological control (Landis et al. 2000). Here we found that both species were more active during the night and early morning, which may indicate a preference for relatively humid habitats, in comparison to the drier late morning and afternoon. This may be favored by letting the grass grow on the strips rather than mowing it. Similarly, although we did not find a significant effect of storing branches on the use of strips by the beetles, these may still provide a beneficial shelter for overwintering, as many carabid species overwinter under barks or logs (Thiele 1977). It would be interesting to examine this possibility further.

An additional key characteristic of agroforestry systems, and especially alley cropping systems, is the regular arrangement of tree rows within fields, which seems to make the beneficial influence of strips even greater. Indeed, because carabid species respond to the differences between strips and cultures at a very small spatial scale, this regular arrangement may act in synergy with the intrinsic beneficial effects of the strip. The actions might be of different natures. Populations of species favored by boundary or woodland habitats, such as *N. brevicollis*, might be sustained thanks to the presence of trees in the strips. For other species, it may allow for the rapid

colonization of the cultures by beetles in spring time. Indeed, a critical component of successful control of pest populations by ground beetles seems to be linked to the level of predation exerted during the early stages of colonization by pest species, therefore reducing the build-up of abundant pest populations (Sunderland and Vickerman 1980; Griffiths et al. 1985; Holopainen and Helenius 1992). Some species, such as *A. dorsalis*, migrate from hedgy habitats to arable lands in spring, and vice versa in fall (Coombes and Sotherton 1986; Kromp and Steinberger 1992; Holland 2002; Jensen et al. 2012). This colonization process may be quite a slow process, as shown by Coombes and Sotherton (1986), with a delay of about 3 weeks between the peak of capture in boundary habitats and the peak of capture within the field. In agroforestry systems, strips may play the same role than hedgy habitats but their regular arrangement within the field may enable these species to spread more rapidly in the crops early in the season.

Our results take all their importance when considering the large body of literature showing that even subtle differences in the foraging strategies of predators can have substantial consequences on the resulting dynamics at the population levels and its interaction with a prey population (Turchin 1991; Morozov 2013; Wei and Lutscher 2013). Therefore, the high sensitivity of beetles to small scale spatial heterogeneity and to strip management, together with the coexistence of species with varying habitat requirements, comforts the idea that accommodating strip and crop design and management carries a great potential for improving conservation biological control in agroforestry systems, as it does in other agroecosystems (Colazza et al. 2017).

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