Sharing enemies: evidence of forest contribution to natural enemy communities in crops, at different spatial scales

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Abstract. 1. The increase in cultivated lands has led to ecosystem and biodiversity loss. Arthropod natural enemies, involved in the ecosystem service of biological control, benefit from non-crop habitat and may be affected by its proximity and amount in the landscape.

2. We have evaluated natural enemy richness and composition in relation to forest cover in the landscape and distance from the forest, for a Chaco Serrano forest-soybean crop system. Forest contribution to natural enemies on soybean was also investigated, by assessing similarities between forest and crop assemblages, and examining body size of shared enemies in relation to distance from the forest. In nine landscape circles, yellow pan traps were placed in forest and soybean crops (5, 25, 50 and 100 m from forest edge), which collected 8041 specimens representing 290 species.

3. Species richness of natural enemies was positively related to forest cover and declined from the forest to the furthermost soybean locations, with both forest cover and its proximity affecting community composition. Also, similarity of forest and crop assemblages increased with forest cover and proximity. Finally, forest-crop shared assemblages showed larger average body size at greater distances from the forest, indicating dispersal limitations on forest contribution to the crop.

4. Our results suggest that forest species are important components of natural enemy communities on soybean, and that both the amount of natural habitat and its proximity may influence agroecosystems. We emphasise the importance of non-crop habitat to help maintain natural enemy communities and ensure the ecosystem service of pest control.

Key words. Agroecosystem, biological control, conservation, forest cover, parasitoids, predators.

Introduction

Human activities have led to the degradation and simplification of ecosystems throughout the world (Sala *et al.*, 2000). The increase in the amount of land used for crop production has been at the expense of natural habitats, resulting in major habitat loss and highly fragmented landscapes (Ellis *et al.*, 2010). In turn, the dramatic reduction in non-crop habitats has resulted in losses in farmland biodiversity (Tscharntke *et al.*, 2005).

Natural habitats are not only important for conservation *per se*, but also as sources of biodiversity for croplands, involving many insect and other arthropod species that play important roles as providers of ecosystem services for crops (Duelli & Obrist, 2003; Schellhorn *et al.*, 2014). In this context, a key service is the biological control of crop pests undertaken by natural enemies of

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herbivores, including predator and parasitoid species, which has an estimated value of $4500 million per year in the US alone (Losey & Vaughan, 2006). These natural enemies depend on non-crop habitats for alternative prey or hosts, nectar, overwintering (Letourneau *et al.*, 2011) and refuges against the mechanical (Thorbek & Bilde, 2004) and chemical perturbations (Lee *et al.*, 2001) to which annual crops are periodically subjected (Tscharntke *et al.*, 2005).

On a landscape scale, the amount of non-crop habitat generally affects insect biodiversity positively, both in the natural habitats (Steffan-Dewenter, 2002; Fahrig, 2003) and in croplands (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011). For natural enemies in particular, parasitoids (review in Cronin & Reeve, 2005) and predators (Elliott *et al.*, 1999; Purtauf *et al.*, 2005; Schmidt *et al.*, 2005) have been shown to benefit from complex and diverse landscapes. For example, the additional resources present in non-crop habitats can increase parasitoid and predator populations, as well as extending their longevity and effectiveness (Bianchi *et al.*, 2006), thereby enhancing pest control in landscapes with a high proportion of non-crop habitat (Thies & Tscharntke, 1999; Thies *et al.*, 2005; Gardiner *et al.*, 2009; Veres *et al.*, 2013).

In addition to the amount of natural habitat, local scale factors such as distance to non-crop habitats are also relevant because most species show some degree of dependence to natural habitats (Duelli & Obrist, 2003; Letourneau *et al.*, 2011). The relatively small scales at which natural enemies act (Bianchi *et al.*, 2006) have been reported to lead to higher richness or abundance near natural habitats (Tscharntke *et al.*, 1998; Clough *et al.*, 2005; Miliczky & Horton, 2005). As a consequence, the ecosystem services such as pest control (Tscharntke *et al.*, 1998; Thies & Tscharntke, 1999; Kruess & Tscharntke, 2000) could be less effective as distance from natural habitats is increased.

Neotropical dry forests like Chaco Serrano are among the world's most endangered ecosystems, due to deforestation and fragmentation (Grau *et al.*, 2008). In particular, the Argentine Chaco has suffered the highest deforestation rates of the country (Gasparri & Grau, 2009), with 94% of the Chaco Serrano having been lost over the last 30 years (Zak *et al.*, 2004) in a process closely related to the expansion of croplands (Zak *et al.*, 2008). Soybean (*Glycine max* L.) has recently become the main crop in Argentina, covering over 15 million ha and leading to the loss of native habitats and displacement of other crops (Aizen *et al.*, 2009). Therefore, understanding the relationship between forest remnants and soybean crops in terms of insect diversity and ecosystem services may provide important theoretical as well as practical insights for conservation and sustainable agriculture.

Here, we evaluated richness and taxonomic composition of natural enemy assemblages in both the native Chaco Serrano forest and adjacent soybean crops, in relation to the amount of forest in the landscape (landscape scale) and crop distance from the forest (local scale). At the landscape scale, we expected natural enemy richness to increase with the proportion of forest cover, both in the forest and in the soybean crop. On the local scale, we expected to find a decline in natural enemy richness from the forest to the crop due to habitat simplification (Lewinsohn *et al.*, 2006) and, within the crop, at increasing distance from the forest due to its reduced influx (Tscharntke *et al.*, 1998; Miliczky & Horton, 2005). Moreover, if forest remnants acted as a source of natural enemies for the crops, we would expect a higher similarity between forest and soybean communities at sites with high forest cover and closer to the forest. These alterations at both local and landscape scales are expected to result in changes of the community composition of natural enemies, because of differential vulnerability to the disturbance associated with the agricultural ecosystem. Finally, if natural enemies were contributed from the forest to the crop, dispersal ability would limit their possibilities of reaching deep inside the latter (Kruess & Tscharntke, 1994). For flying insects, such an ability is usually linked to body size (Greenleaf *et al.*, 2007) and, consequently, we expected assemblages in the crop to become increasingly dominated by larger flying insects at greater distances from the forest.

To our knowledge, this is the first study which simultaneously explores the effects of both the amount of forest in the landscape and the distance from the forest, on natural enemy richness in a cultivated field, as well as being the first to analyse in this context the relative contribution of the natural habitat to the agroecosystem. By revealing that forest species largely contribute to natural enemy communities on soybean crops, and that this contribution is affected by forest cover and proximity, we emphasise the need to conserve native vegetation remnants in agricultural landscapes, to maintain biodiversity and ecosystem services.

Materials and methods

The study was conducted in a fragmented landscape (31.10°–31.30°S and 64°–64.30°W) within Córdoba province, in central Argentina. The area belongs to the Chaco Serrano phytogeographical district, which experiences 750 mm of annual rainfall and mean maximum and minimum monthly temperatures of 26 and 10 °C, respectively (Luti *et al.*, 1979). Using the Landsat Thematic Mapper, nine landscape circles of 500 m diameter were selected (hereafter referred to as sites), that encompassed a gradient of forest cover proportion from 0.05 to 0.79, the remaining surface being occupied by soybean crops. The woodland remnants have been isolated for at least 40 years.

At each site, five yellow pan traps (diameter 34 cm, depth 9 cm) were placed at the following locations: forest (<5 m from the tree line) and soybean crops at 5, 25, 50 and 100 m from the forest edge. The traps were placed 20 cm above the ground level, filled with 3 L of water

with a few drops of detergent and left in the field for 3 days (20th–22nd December 2010) at the end of the vegetative and start of the flowering stage of the crop. The contents of the pans were then filtered, placed in plastic cups with 70% ethanol and taken to the laboratory. All arthropods were then identified to family level and assigned to feeding guilds on the basis of family habits (or subfamily, for families with multiple feeding habits; Triplehorn & Johnson, 2005). Natural enemies, that are specimens with predatory or parasitoid habits, were classified to the level of morphospecies (Obrist & Duelli, 2010; further referred to as species) and considered for further analyses. Ants (Hymenoptera, Formicidae) were not included in the analysis because few species were found (<1% of total species and abundance) and most of these were represented by winged individuals, which made the identification to species level more difficult using the keys available for our country.

For statistical analyses, we used species richness of natural enemies as the response variable in a generalised linear mixed models (GLMM) with a Poisson error distribution and a log link function. Forest cover proportion at each site (as a continuous variable) and location (as factor, with five levels) were the explanatory variables, and we included the interaction between both terms to search for differences in the slope among locations. Site was included as a random factor to model data dependence within each landscape circle. Analyses were performed using the software R (R Development Core Team, 2008; version 2.15.1) and the package lme4 (Bates & Sarkar, 2007). Best models were selected using Likelihood Ratio Tests, and autocorrelation was checked with variograms of the residuals (Zuur et al., 2009).

As we were particularly interested in the contribution of the forest to natural enemy diversity in the crop, we also calculated for each site and at the four soybean crop locations, the number of species that were shared with the forest, that is those present at both at a particular location within the crop and in the forest. With this information, we then calculated the similarity between forest and soybean samples using Jaccard's index (Jaccard, 1908), which measures species overlap and is defined as the ratio of the number of shared species to the number of distinct species in two communities. Jaccard's index is expressed as $\theta J = s0/(s1 + s2 - s0)$, where si is the number of species in community i ($i = 1, 2$) and $s0$ is the number of shared species for the two communities. We calculated this index at every site and distance to the forest and a GLMM was performed as described above for total species richness, except that the variable location had only four levels (the four crop distances to the forest) and that we used a normal error distribution.

To search for changes in community composition, we performed a principal component analysis (PCA) with the software PAST (Hammer et al., 2001), using quantitative data ($\log_{10}$ transformed species abundances) of those species with five or more individuals. The two-first principal components were used as dependent variables in GLMMs

with the same explanatory variables of the richness model (see above). Residuals were normally distributed, and therefore we used the nlme package (Pinheiro et al., 2013). Because residuals for the five locations were not homogeneous, we incorporated this heterogeneity in the model using a VarIdent variance structure, which calculates a dispersion parameter for each location (Zuur et al., 2009).

Out of the forest-crop shared species mentioned before, we selected those belonging to families with well-known flying habits and measured total body size (as mean body length of five individuals per species) using a Zeiss Stemi DV4 stereo microscope (see Table 1, for species included). Next, we calculated mean body size for natural enemy assemblages at each of the four soybean locations, weighing the body size of each species by its abundance. Mean body size among locations was compared by means of ANOVA.

Results

In total, 8041 specimens were captured, belonging to nine orders, 55 families and 290 morphospecies. These included 105 predator species in 30 families (83.7% of specimens) and 185 parasitoid species distributed in 25 families (16.3% of specimens). Table 1 provides a list of all families included in this study, along with information on feeding habits and species numbers.

Richness of natural enemies was positively related to the proportion of forest in the landscape and differed among locations (Fig. 1a; Table 2). As expected, richness was higher in the forest (41.2 ± 3.4 spp.) than in the soybean crop, where it decreased with increasing distance from the forest, conforming two groups: 5–25 m (27.5 ± 1.5 for 5 m and 26.9 ± 1.5 for 25 m) and 50–100 m (22.7 ± 1.1 for 50 m and 19.5 ± 0.8 for 100 m). The interaction between forest cover and location was not significant, indicating that the slopes representing the changes in natural enemy richness with forest cover were similar at all locations.

More than half of the natural enemy species associated with the crop were also found in the forest, with the contribution of these shared species ranging from 62 to 92% of species richness, depending on site and distance to the forest. Jaccard's similarity index was positively related with forest cover and presented the lowest values at the longest distance (i.e. 100 m from the forest; Fig. 1b; Table 2), but there was no interaction between forest cover and location.

Community composition, according to the PCA results, revealed a clear separation of forest samples to the left and soybean samples to the right of the first component, which explained 25.2% of the variance. Moreover, crop assemblages showed a distinct gradient of distance to the forest on the second component, with the highest values for assemblages being found at 5 m and the lowest at 100 m (Fig. 2). The first PCA component was related to

Table 1. List of orders and families of natural enemies captured with yellow pan traps in Chaco Serrano forest and soybean crops in central Argentina.

Feeding habit	Order	Family	Number of species
Predators	Acari (Mesostigmata)	Phytoseiidae	1
	Araneae	Anyphaenidae	2
		Araneidae	5
		Clubionidae	2
		Coriniidae	1
		Linyphiidae	4
		Lycosidae	5
		Oxyopidae	3
		Salticidae	7
		Thomisidae	2
	Coleoptera	Cantharidae	1
		Carabidae	6
		Coccinellidae	8
		Histeridae	1
		Lampyridae	2
		Scydmaenidae	1
		Staphylinidae	19
	Diptera	Asilidae	1
		Dolichopodidae	5 (4)
		Empididae	1 (1)
	Hemiptera	Anthocoridae	2 (1)
		Enicocephalidae	1 (1)
		Geocoridae	1
		Pentatomidae	1
		Reduviidae	4 (1)
	Hymenoptera	Sphecidae	3
		Vespidae	10 (2)
	Mantodea	Mantidae	1
	Neuroptera	Chrysopidae	1 (1)
	Orthoptera	Tettigoniidae	1
Parasitoids	Coleoptera	Passandridae	1
	Diptera	Pipunculidae	4 (2)
		Tachinidae	10 (2)
	Hymenoptera	Bethylidae	11
		Braconidae	12 (2)
		Ceraphronidae	12 (3)
		Chalcididae	4
		Crabronidae	3
		Diapriidae	1
		Encyrtidae	16
		Eulophidae	11 (1)
		Eurytomidae	4
		Evaniidae	2
		Figitidae	4
		Ichneumonidae	11
		Mutillidae	1
		Mymaridae	25 (5)
		Perilampidae	2
		Platygastridae	13 (3)
		Pompilidae	8
		Proctotrupoidea	1
		Pteromalidae	6 (1)
		Scelionidae	21 (9)
		Tiphiidae	2
		Trichogrammatidae	3 (1)

The number of species recorded in each family is provided. In brackets, number of flying species shared between forest and crop, used for body length measurements.

both forest cover and location. For the second component, which explained 12.3% of variance, in addition to the difference among locations there was a significant interaction between this factor and forest cover (Table 2).

The mean body size (weighted by abundance) of soybean-forest shared natural enemies (Fig. 3) differed significantly among assemblages found on the crop at different distances to the forest ($P < 0.0001$; $F = 25.47$; d.f. = 3, 6803), with natural enemies found on the crop being on average smaller at 5 m from the forest (3.29 ± 0.02 mm), whereas assemblages at longer distances tended to be increasingly dominated by larger species (3.53 ± 0.03 mm at 25 m, 3.66 ± 0.04 mm at 50 m and 3.72 ± 0.04 mm at 100 m).

Discussion

The transformation of natural ecosystems to agricultural lands and the ensuing landscape simplification have profound implications on insect diversity, leading to a general impoverishment of biodiversity (Tscharntke *et al.*, 2005). Natural enemies of crop pests, which provide the ecosystem service of biological control, have been reported to be strongly affected because most species depend on non-crop habitats to complete their cycles (Duelli & Obrist, 2003; Bianchi *et al.*, 2006; Letourneau *et al.*, 2011). In this study from Central Argentina, we have shown that natural habitats influence agricultural systems at both landscape and local scales, with richer natural enemy communities being found in agricultural landscapes with higher Chaco Serrano cover and at soybean sampling points closer to the forest. Moreover, forest dominated landscapes may represent better sources of natural enemies for the agricultural matrix, as our results revealed that forest-crop similarity increased with forest cover.

A positive relationship between the proportion of forest in the landscape and natural enemy richness, as found in this study, has become a well-established pattern (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011). As the total amount of non-crop habitats in the landscape is reduced and the size of the remaining patches becomes smaller, more species are lost (Kruess & Tscharntke, 2000; Fahrig, 2003), especially for organisms in higher trophic ranks such as natural enemies (Tscharntke *et al.*, 2002; Cagnolo *et al.*, 2009). Our results show the influence of forest proportion on the landscape to be pervasive, affecting natural enemy assemblages in the crop at distances ranging from 5 to 100 m from the forest, as indicated by the absence of interaction between forest cover and distance from the forest. Nevertheless, we did find a strong effect of distance on natural enemy richness in soybean fields, which decreased by about a quarter -in comparison with the natural habitat- at 5 m from the forest and by half at 100 m. This result highlights the importance of the native forest as a source of natural enemies (Duelli & Obrist, 2003) and indicates that soybean plants closer to the forest

Table 2. Results from generalised linear mixed models evaluating the effects of forest cover and trap location on natural enemy richness, forest-crop similarity and first and second components of PCA in Chaco Serrano forest and soybean crops. The corresponding slopes and intercepts (±SE) are provided.

	Explanatory variable	*P*	Slope	Intercept
Natural enemy richness	Forest cover	**0.01**	0.027 ± 0.01	3.58 ± 0.08 (forest)
	Location	**< 0.0001**		3.19 ± 0.08 (5 m)
	Interaction	0.72		3.18 ± 0.08 (25 m)
				3.00 ± 0.09 (50 m)
				2.86 ± 0.09 (100 m)
Forest-crop similarity (Jaccard)	Forest cover	**0.025**	0.019 ± 0.008	0.087 ± 0.007 (5 m)
	Location	**< 0.0001**		0.095 ± 0.007 (25 m)
	Interaction	0.30		0.086 ± 0.008 (50 m)
				0.064 ± 0.006 (100 m)
First component of PCA	Forest cover	**0.006**	0.048 ± 0.01	-1.37 ± 0.17 (forest)
	Location	**< 0.0001**		1.05 ± 0.2 (5 m)
	Interaction	0.53		0.66 ± 0.16 (25 m)
				0.48 ± 0.17 (50 m)
				0.41 ± 0.21 (100 m)
Second component of PCA	Forest cover	0.11	-0.07 ± 0.04 (Forest)	0.77 ± 0.22 (forest)
	Location	**< 0.0001**	-0.14 ± 0.05 (5 m)	1.50 ± 0.27 (5 m)
	Interaction	**0.006**	-0.01 ± 0.05 (25 m)	-0.07 ± 0.27 (25 m)
			0.01 ± 0.05 (50 m)	-0.55 ± 0.27 (50 m)
			-0.001 ± 0.05 (100 m)	-0.69 ± 0.28 (100 m)

PCA, principal component analysis. Bold values in the table are used to highlight significant *P*-values.
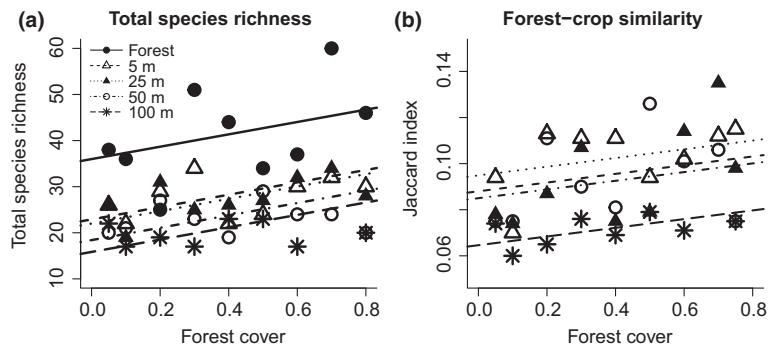
Fig. 1. Variations in natural enemy assemblages in terms of (a) total species richness, (b) forest-crop similarity (Jaccard index), in relation to location (forest or soybean crop at various distances from the forest) and forest cover in the landscape (proportion within 500 m diameter circle). Filled circles: Chaco Serrano forest, filled triangles: soybean crop at 5 m from the forest, empty triangles: at 25 m, empty circles: at 50 m and asterisks: at 100 m. Lines were calculated from generalised linear mixed models (see Table 2 and section 2 for more information). Solid lines: forest, dashed lines: soybean crop at 5 m from the forest, dotted lines: at 25 m, dot-dash lines: at 50 m and long-dash lines: at 100 m.

benefit more (Tscharntke *et al.*, 1998), thereby suggesting that proximity of natural habitats must also be taken into consideration in land management planning for sustainable agriculture.

More than half of the natural enemy species collected on the soybean crop were also found in the forest. The similarity between natural enemy communities of the forest and soybean crops increased with the amount of forest in the landscape and decreased with distance to the forest. Thus, forest-crop shared species –most of which are likely to be natural forest inhabitants – are an important com-

ponent of natural enemy communities on the soybean crop, especially near the forest. Also, the positive relation with forest cover at the landscape scale suggests that the number of forest species moving to the crops may be decreasing in simple landscapes, probably due to species loss and, consequently, to the poor sources available in small forest fragments (Rybicki & Hanski, 2013).

Our study revealed that not only was the number of natural enemy species influenced by forest cover and distance to the forest, but the identity and abundance of the species present in the soybean crop were also affected, as

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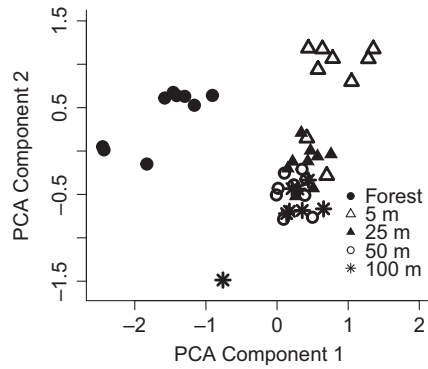
Fig. 2. Two-dimension graph of principal component analysis based on species abundance (log-transformed) in natural enemy assemblages from forest (filled circles) and soybean crop at 5 m (filled triangles), 25 m (empty triangles), 50 m (empty circles) and 100 m (asterisks) from the forest, in nine sites with different forest cover (proportion within 500 m diameter circle).
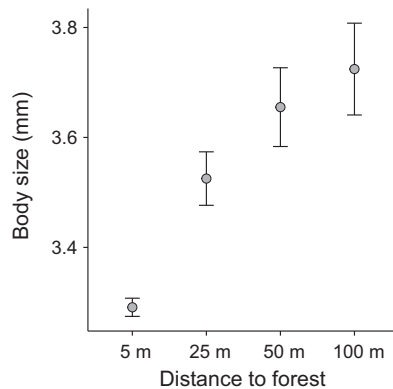
Fig. 3. Mean body size of natural enemies captured on soybean crop at 5, 25, 50 and 100 m from the forest, considering only species that were also found in the forest and tend to disperse by flying. Error bars represent standard error.

indicated by the community composition analysis. Changes in the presence or abundance of particular species with distance from natural habitats were previously described for spiders and parasitoids in orchards (Miliczky & Horton, 2005) and for spiders in wheat (Clough *et al.*, 2005), while a more recent study reported shifts in community composition of aphid natural enemies due to agricultural intensification (Gagic *et al.*, 2014). We, however, have not encountered reports of changes in composition of natural enemy communities occurring simultaneously at both local and landscape scale as described by our results.

As large body size is frequently linked to an increase in dispersal abilities (Greenleaf *et al.*, 2007), small species requiring resources from the forest would therefore find it more difficult to reach soybean plants located far away from the forest, in comparison with larger species. On this

basis, we postulated that if natural enemies were provided by the forest to the crop, assemblages on the latter would tend to become dominated by larger species as distance from the forest increased. Our results supported this expectation, effectively showing that mean body size of natural enemies on soybean increased with distance from the forest. At 100 m from the forest, small species were only rarely found, with mostly larger specimens being captured. Again, our results underscore the need to consider natural habitat proximity in the context of its effects on agroecosystem diversity and functioning.

In addition to the spatial patterns we encountered, the number of natural enemy species was also considered. We identified nearly 300 species of natural enemies, including predators and parasitoids, with 20 species being captured at the sampling locations most distant from the forest, despite soybean crops being under conventional management with frequent insecticide applications. Such diversity supports the proposition that forest remnants and other non-crop habitats may provide an important refuge from chemical inputs for natural enemies (Lee *et al.*, 2001). Moreover, high natural enemy richness may contribute to agroecosystem resilience for the provision of biological control (Tscharntke *et al.*, 2005, 2007) since, according to the insurance hypothesis, more species provide a greater guarantee that some will maintain functioning if others fail (Yachi & Loreau, 1999).

This paper contributes to our understanding of key aspects of the interactions between crop and non-crop habitats, by providing evidence of the positive effects of forest remnants on the diversity of natural enemies on crops at both landscape and local scales. Shared species between forest and soybean most likely represent a 'spillover' (Rand *et al.*, 2006) from the natural to the cultivated habitat. Thus, our study highlights the importance of conserving remnants of non-crop habitats in agricultural landscapes to maintain rich natural enemy communities on crops and ensure the ecosystem service of pest control. This work may contribute to effective land management strategies that harmonise agricultural activities with biodiversity conservation, in the context of the current land sparing versus sharing debate (Fischer *et al.*, 2014). Our findings should encourage policy makers to take into consideration both the amount of natural habitat in the landscape and the distance between crop and non-crop habitats, as they are important aspects of land management that can help sustain forest contribution to the cultivated matrix in terms of biodiversity and ecosystem services.

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