Arthropod communities and biological control in soybean fields: Forest cover at landscape scale is more influential than forest proximity

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ABSTRACT

Natural habitats surrounding annual crops influence biodiversity and the provision of ecosystem services within the cultivated habitats. Soybean, an important crop worldwide and the main crop in Argentina, is affected by several pest species, including stink-bugs that damage soybean pods. Here, we studied the effects of Chaco Serrano forests on arthropod herbivores and natural enemies and on biological control of stink bugs on soybean, at landscape (forest cover) and local (forest proximity) scales. We sampled arthropods on soybean plants by using the beating-sheet method, on nine landscapes (with low and high forest cover) and at 5, 25, 50 and 100 m from the forest, during soybean flowering and pod-filling stages. Biological control of stink bug eggs was assessed via sentinel-egg experiments in soybean and forest habitats. We found that landscapes with high forest cover presented higher richness and abundance of natural enemies and higher levels of biological control on stink bug eggs (both in the cropland and in the forest), while a similar trend for herbivores was restricted to soybean flowering stage. Community composition of both functional groups was also affected by forest cover and crop phenological stage. Forest proximity had more limited effects: natural enemies showed more species and individuals at 5 m from the forest than at larger distances and, conversely, stink bug abundance was lower at the closest distance to the forest. We conclude than forest amount at landscape scale is more influential for arthropod biodiversity and biological control in soybean than forest proximity. Moreover, our results suggest that maintaining remnants of forest in agricultural landscapes can be effective for conservation of arthropod biodiversity while contributing to biological control of stink bugs in soybean fields.

1. Introduction

Agricultural intensification is a dominant trend in the global land use change (Sala et al., 2000; Tilman et al., 2001a). As a result, complex and diverse ecosystems with high proportion of natural habitats are transformed into simpler, predominantly man-managed landscapes (Tscharntke et al., 2005). In this scenario, biodiversity losses occur both in the natural (Fahrig, 2003; Steffan-Dewenter et al., 2002) as well as in the cultivated (Benton et al., 2003; Chaplin-Kramer et al., 2011) components of the landscape.

Within cultivated fields, insect communities are influenced by the surrounding landscape structure, most frequently showing increased diversity in complex landscapes where non-crop habitats enhance environmental heterogeneity (Benton et al.,

2003). However, not all species respond in the same way to landscape scale changes (Attwood et al., 2008; Rossetti et al., 2014). Thus, the number of pest species tends to increase with landscape complexity (Chaplin-Kramer et al., 2011), but their specific abundance may be negatively affected by such complexity, benefitting instead from simpler, mostly cultivated areas (Veres et al., 2013). The latter trend can be explained by the resource concentration hypothesis (Kareiva, 1983; Root, 1973), which postulates that large, monospecific and dense plant patches promote establishment and population growth of specialist herbivores, although generalist species can perform better in habitats with higher plant diversity. On the other hand, natural enemies tend to increase both their richness as well as their abundance in complex landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011) where natural or semi-natural habitats provide necessary alternative resources (Bianchi et al., 2006; Duelli and Obrist, 2003; Landis et al., 2000). An increase in natural enemies can also explain reductions of herbivore abundance in complex landscapes, as proposed in the enemies' hypothesis (Kareiva, 1983; Root, 1973).

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In addition to the influence of landscape-scale changes, distance to natural habitats is a relevant aspect at the local scale for arthropods associated with crops. Since non-crop habitats generally act as sources of biodiversity for croplands (Duelli and Obrist, 2003), higher richness and/or abundance of arthropods are expected and frequently found near these habitats (Clough et al., 2005; González et al., 2015; Miliczky and Horton, 2005; Tscharntke et al., 1998).

As a result of changes in biodiversity (Balvanera et al., 2006; Cardinale et al., 2012), ecosystem processes such as herbivory (Valladares et al., 2006) and biological control (Fenoglio et al., 2012; Thies et al., 2011; Tylianakis et al., 2006) have been affected at both landscape and local scales. In particular, the positive responses of natural enemies to landscape complexity tend to result in higher levels of the ecosystem service of biological pest control in diverse landscapes with high amounts of non-crop habitats (Bianchi et al., 2006; Gardiner et al., 2009; Veres et al., 2013) and near fragments of natural vegetation (Bianchi et al., 2008; Kruess and Tscharntke, 2000; Thies and Tscharntke, 1999; Tscharntke et al., 1998).

In Argentina, a main force driving land use change is soybean cultivation. Soybean is an important crop worldwide (Leff et al., 2004), sown in more than 111 million hectares and yielding 276 million metric tons in 2013 (FAO, 2016). Soybean cultivation dramatically expanded in Argentina in the last 30 years, to the point of occupying more than half of the cultivated surface of the country (Aizen et al., 2009). This expansion has led to the displacement of other crops and the advance of the agricultural frontier at the expense of natural ecosystems like Chaco forest (Grau et al., 2008).

Soybean crops are attacked by several pests, among which stink bugs (Hemiptera: Pentatomidae) are particularly harmful in South America fields (Frana et al., 2008; Panizzi et al., 2000). The influence of natural vegetation cover and proximity on soybean pests has been addressed mostly for the soybean aphid in USA and Canada (Mitchell et al., 2014a; Ragsdale et al., 2011), its biological control (Gardiner et al., 2009; Mitchell et al., 2014b) and natural enemies in the crop (Gardiner et al., 2010; Mitchell et al., 2014a). The influence of natural habitats, at local or landscape scales, on biological control of stink bugs on soybean remains unknown, although increased stink bug density at the edges of soybean crops has been observed (Venugopal et al., 2014). Furthermore, there is only scant information on non-crop influence for insect communities in general, on soybean fields outside North America (González et al., 2015).

Here, we studied richness, abundance and community composition of total herbivores, stink bugs and natural enemies, in soybean fields from central Argentina with varying forest cover in the landscape and at varying distances from the forest. In addition, we evaluated the ecosystem service of pest control by means of stink bug egg exposure experiments in the same fields and within the forest fragments, the latter in order to assess the forest potential as reservoir of natural enemies for soybean pests. We expected both herbivores and natural enemies to show higher richness in landscapes with higher forest cover and at smaller distances from it. Abundance of natural enemies should follow the same pattern as richness, but herbivores could be more abundant at crop-dominated landscapes and at larger distance from the forest, following the resource concentration and the enemies' hypotheses. Finally, if natural habitats represent sources of natural enemies, higher levels of biological control would be expected in sites with more forest, and in its proximity.

2. Methods

2.1. Study sites

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, with 750 mm of annual rainfall and average temperatures of 10–26 °C. Vegetation is characterized by a tree layer (height 8–15 m) dominated by *Aspidosperma quebracho-blanco* Schltdl., *Prosopis* spp., *Fagara coco* Engl. and *Lithrea molleoides* (Vell.) Engl.; a shrub layer (1.5–3 m) dominated by *Celtis ehrenbergiana* Torr. and *Acacia* spp.; pastures (0–1 m), vines, and epiphytic bromeliads (Cabido et al., 1991). This system is one of the most affected by agricultural expansion, having lost more than 95% of its original area in Córdoba province (Zak et al., 2004). Based on Landsat Thematic Mapper and field corroboration, nine landscape circles of 500 m diameter were selected (from now on, sites; Fig. 1; Table S1). At all sites, the centre was located on a forest-soybean boundary. Five sites had more than 30% of forest with the remaining area occupied by soybean fields (from now on, sites with high forest cover). In the other four sites, the proportion of forest was below 15% (low forest cover), the rest being occupied by
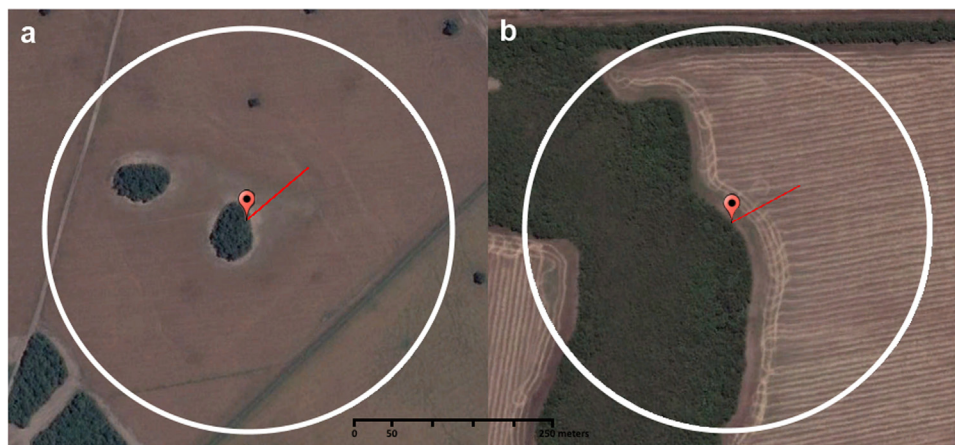

Fig. 1. Examples of circular landscapes with low (a) and high (b) forest cover. Dark green areas are fragments of Chaco Serrano forest, while the crop matrix (uncultivated to enhance the contrast between habitats) is observed in light color. Satellite images were obtained with Google Earth. The landscape with low forest cover is covered by 2.65% of forest and the landscape with high forest cover by 40.39%. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

soybean. This classification (high/low forest cover sites) was based on the 20–30% threshold hypothesis (Fahrig, 2003; Tscharntke et al., 2012), which states these values as the minimum non-crop habitat proportion required to ensure biodiversity maintenance and ecosystem functioning. The representation of other landscape elements (maize fields, roads, field margins, urban/rural constructions) was almost negligible (less than 3%).

2.2. Insect sampling

At each site, arthropods were sampled within soybean fields at 5, 25, 50 and 100 m from the forest edge. These sampling points were always located within a single, large soybean field, with other forest fragments or field margins at least 150 m away, thus ensuring that the forest at the center of the landscape circle was the nearest to the sampling point at each distance (Fig. 1). Sampling was carried out from late December 2011 to February 2012, at two crop stages: soybean flowering (phases V6, V7 and R1 according to Fehr et al., 1971) and pod filling (phases R5 and R6). The sampling method consisted in beating soybean foliage against a 1 m long white vertical beating-sheet (Drees and Rice, 1985) attached to a plastic trough (11 cm diameter). Ten samples were taken at each distance in each site. All arthropods observed on the sheet were counted in the field and 1–5 specimens of each potential morphospecies were placed in plastic vials with 70% ethanol and carried to the laboratory. Specimens were identified to family level, assigned to feeding guilds on the basis of dominant family habits (or subfamily, for families with multiple feeding habits; Triplehorn et al., 2005) and, finally, morphospecies (further referred to as species; Obrist and Duelli, 2010) of herbivores and natural enemies (including predators and parasitoids) were considered for further analyses.

2.3. Biological control experiments

In the same sites and at the same distances from the forest detailed above, an exposure experiment with sentinel eggs was conducted twice, during the reproductive soybean stage (February and March 2014); in the second set of experiments, one site with low forest cover was added (site 10 in table S1). Additionally, in March 2014, sentinel eggs were placed in the forest at each site, within the first 25 m from the forest edge. In each experiment, for every site and position, three egg masses were placed (total n = 258).

In order to obtain eggs for the experiment, adults of the stink bug *Dichelops furcatus* (Fabricius) were collected from soybean crops at the study region and maintained in plastic 5 l jars, in controlled conditions (25 ± 2 °C, 75 ± 5% RH, photoperiod 12:12). Insects were fed with fresh pods of soybean and common bean (*Phaseolus vulgaris* L.). Every 24–48 hs, egg masses were removed from the recipes and kept in plastic dishes in refrigerator (5 ± 2 °C). Twenty four hours before field exposure, eggs were attached to paper pieces (2×3 cm) using a plastic adhesive, and total number of eggs per mass were counted. The paper pieces with egg masses were stapled to the abaxial surfaces of soybean leaves in the crop, or leaves of the common plant *Ipomea purpurea* (L.) Roth in the forest, and were exposed to natural enemies for five days. After this period, egg masses were transported to the laboratory and maintained in controlled conditions (see above) until adult emergence (bugs or parasitoids). The proportion of eggs attacked (total number of eggs preyed or parasitized over total eggs in the mass; Morandin et al., 2014) was used as an indicator of the magnitude of biological control.

2.4. Statistical analyses

We used species richness and abundance of herbivores and natural enemies as response variables in separate Generalized Mixed Models (GLMM), with a Poisson error distribution for richness and negative binomial error distribution for abundance, and with a log link function for both variables. Landscape type (high vs low forest cover), distance (as factor, with four levels) and phenological stages (flowering and pod-filling) were the explanatory variables, and we included the paired interactions between the three terms. Site and repetition (nested within each distance and site) were included as random factors to model data

Table 1

Best models for GLMMs analyzing the effects of forest cover, soybean phenology and distance to forest on richness and abundance of herbivores and natural enemies on soybean plants. For each model AICc value, P-values for each explanatory variable and fixed effect estimates (±standard error) are shown. Intercepts represent high forest cover, flowering stage and, for natural enemies, 5 m from the forest.

Functional group	Response variable	AICc	Explanatory variables	P-value	Estimate (± SE)	
Herbivores	Richness	2607.4	Forest cover	**0,01**	Intercept	1.53 ± 0.05
			Phenology	0.52	Low cover	−0.22 ± 0.09
			Forest x Phenology	**0.04**	Pod-filling	0.04 ± 0.07
					Interaction	0.20 ± 0.10
	Abundance	6973.4	Forest cover	**0.06**	Intercept	5.58 ± 0.20
			Phenology	**<0.001**	Low cover	−0.52 ± 0.28
			Forest x Phenology	**0.09**	Pod-filling	−2.10 ± 0.24
					Interaction	0.57 ± 0.34
Stink bugs	Abundance	297.2	Distance to forest	**<0.001**	Intercept	2.82 ± 0.10
					25 m	3.24 ± 0.09
					50 m	3.10 ± 0.09
					100 m	3.02 ± 0.18
Natural enemies	Richness	81.1	Forest cover	**<0.001**	Intercept	1.50 ± 0.09
			Phenology	**0.06**	Low cover	−0.57 ± 0.09
			Distance to Forest	**0.07**	Pod-filling	−0.14 ± 0.07
					25m	−0.26 ± 0.10
					50m	−0.23 ± 0.10
					100m	−0.18 ± 0.10
	Abundance	2864.9	Forest cover	**<0.001**	Intercept	1.86 ± 0.12
			Phenology	**0.03**	Low cover	−0.67 ± 0.10
			Distance to Forest	**0.003**	Pod-filling	−0.21 ± 0.09
					25m	−0.46 ± 0.13
					50m	−0.35 ± 0.13
					100m	−0.29 ± 0.13

Significant (p < 0.05) and marginal (0.05 < p < 0.10) explanatory variables are highlighted in bold.

dependence. We also used GLMMs to analyze abundance of stink bugs, using data from the pod-filling phase when these insects are most abundant (Frana et al., 2008); the model included stink bug abundance per distance (sum of 10 repetitions) as response variable, with landscape type, distance to the forest and their interaction as explanatory variables.

Data from pest control experiments were analyzed similarly, but a binomial error distribution was used instead for the response variable (proportion of pest control by natural enemies in the egg masses), with a logit link function. Separate GLMMs were performed for crop and forest data; in the first case, the same factors described above were used (landscape type, distance, phenological stage and their paired interactions) while landscape type was the only factor for the analysis of forest data.

Analyses were performed using the software R (R Development Core Team, 2008; version 2.15.1) and the package lme4 (Bates and Sarkar, 2007). All possible models were compared using AICc values and the model with the lowest value of AICc was selected as the best model. Autocorrelation was checked with variograms of the residuals (Zuur et al., 2009).

Changes in community composition of herbivore and natural enemies in relation to landscape types, distance to forest and soybean stages were analyzed using NMDS (non-metric Multi-Dimensional Scaling; Shepard, 1962; Kruskal, 1964) and ANOSIM (Clarke, 1993). NMDS provides a graphical analysis of the variation of insect community composition among samples, using log-transformed (log N + 1) species abundance data to calculate the Bray-Curtis index of dissimilarity. ANOSIM uses permutations of the data to provide significance tests. Both analyses were performed in R with the vegan package (Oksanen et al., 2008).

3. Results

A total of 107,258 arthropods belonging to 12 orders, 65 families and 246 species were recorded in beat sheet samples taken on soybean plants. Hemiptera presented the highest richness, with 78 species (35%), followed by Coleoptera (18%), Araneae (17%) and Hymenoptera (16%). Acari and Thysanoptera were the dominant groups, representing 47% and 44% of total abundance, respectively. Herbivores (94.4% of all specimens collected) were strongly dominated by well-known occasional pests of soybean and other

crops: the red spider mite (*Tetranychus urticae* Koch) with 50% of herbivore abundance followed by the thrips *Caliothrips phaseoli* (Hood) and *Frankliniella schultzei* (Trybom) (Thysanoptera), with 37 and 10% respectively (Fig. S1). Within stink bug species (total abundance = 901) the most abundant were *Nezara viridula* (42.5%), *Piezodorus guildinii* (36.5%) and *Dichelops furcatus* (20.9%). Among natural enemies (2.3% of total arthropods collected), *Geocoris* sp. (Hemiptera: Geocoridae) was the most abundant (12.9% of natural enemy specimens) followed by two spider species, Linyphiidae sp. 1 (10.1%) and *Misumenops* sp. (Thomisidae; 8.1%).

3.1. Arthropods on soybean: herbivores

Richness and abundance of herbivore arthropods increased in landscapes with high forest cover during soybean flowering, while no effect of forest cover was observed at the pod-filling stage (Table 1; Fig. 2a and b; see also Fig. S1 for particular trends of dominant herbivores). No significant influence of distance to the forest on herbivore richness or abundance was observed (Table 1). Community composition of herbivores showed clear temporal variations (R = 0.682; p = 0.001) and differed between landscapes with high and low forest cover (R = 0.063; p = 0.019), as shown by NMDS results (Fig. 3). No effects of distance to forest were detected (R values between −0.044 and 0.007; p > 0.05 for all pairwise comparisons). Stink bug abundance was not affected by landscape type, but was influenced by distance to the forest (Table 1), with the lowest number of specimens being found closest to the forest (Fig. 4).

3.2. Arthropods on soybean: natural enemies

More natural enemy species and specimens were found in sites with high forest cover, at the shortest distance (5 m) from the forest and during soybean flowering, albeit phenology and distance effects were only marginally significant for richness (Table 1; Fig. 5a and b). Community composition was not affected by distance to forest (R values between −0.047 and −0.012; p > 0.05 for all pairwise comparisons), but differed between soybean stages (R = 0.483; p = 0.001) and between landscapes with high vs low forest cover (R = 0.143; p = 0.001). Fig. 6 shows NMDS results for natural enemies, with samples taken during soybean
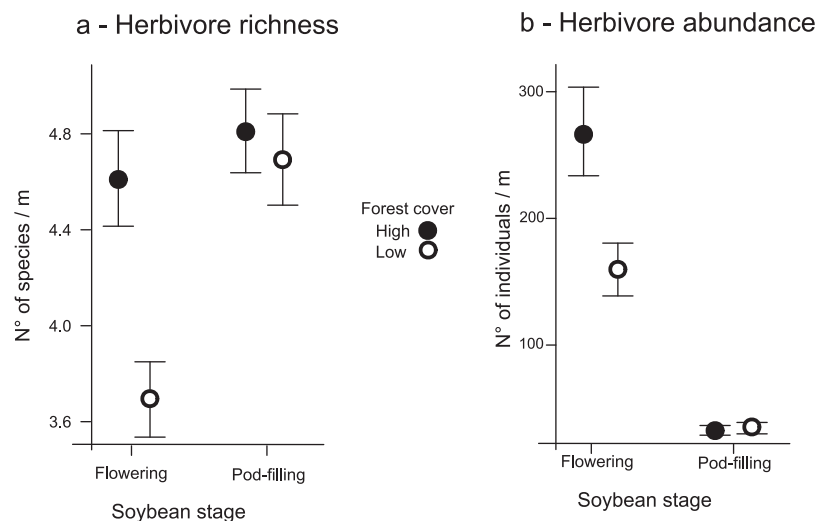

Fig. 2. Richness (a) and abundance (b) of herbivore arthropods captured on soybean plants. Values (mean number of species and specimens per 1 m beating-sheet samples, ± standard error) predicted by GLMMs (see Table 1) for landscapes with high (filled circles) and low (empty circles) forest cover and at flowering vs pod-filling stages are shown.
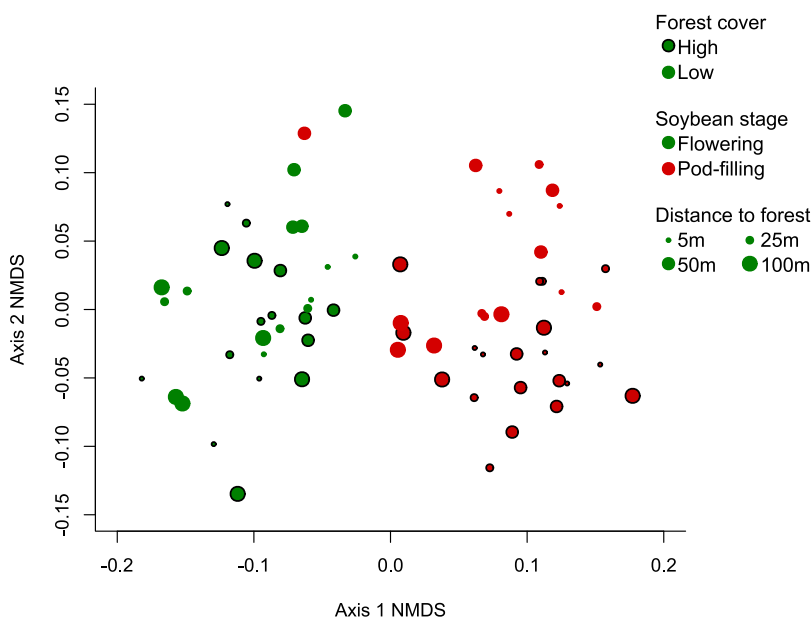
Fig. 3. Two-dimension graph from Non Metric Multidimensional Analysis based on species abundance (log-transformed) of herbivore assemblages on soybean plants. Data for landscapes with high (circles with black margin) and low (circles without black margin) forest cover and at flowering (green) and pod-filling (red) crop stages are shown. The size of the circle is representative of the distance to the forest, with bigger circles indicating greater distances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
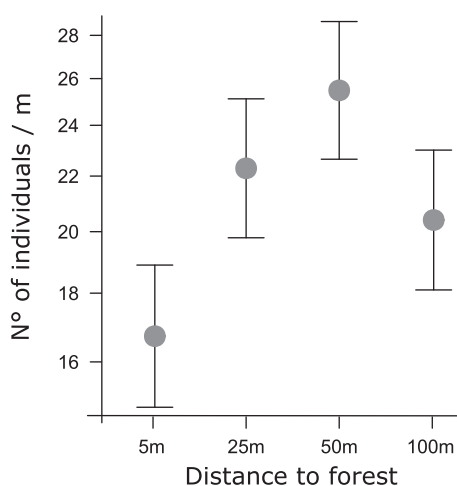

Fig. 4. Abundance of stink bugs captured on soybean plants, at four distances to the forest (5, 25, 50 and 100 m). Points represent mean (±standard error) number of specimens per distance (sum of ten beat sheet samples) from nine sites, predicted by GLMMs (see Table 1).

flowering and pod-filling stages clearly separated along the first axis, while samples from sites with high vs low forest cover are segregated on the second axis, particularly at pod-filling.

3.3. Biological control experiments

Eighty-five percent of egg masses exposed to natural enemies on the crop were recovered, and in 63% of such masses some eggs were preyed or parasitized, with an average of 46.2% ($\pm$3,15) eggs attacked per mass ($24 \pm 3\%$ parasitized and $22 \pm 3\%$ predated). Biological control of stink bug eggs in soybean crops was higher in landscapes with high forest cover, whereas no effects of distance to the forest edge or of crop phenology were detected (Table 2; Fig. 7a). When egg masses were exposed within the forest, attack rates were notably similar to those observed in the cropland (69%

of egg masses and $49 \pm 8\%$ of eggs per mass), with significantly higher levels of biological control in landscapes with high cover of natural vegetation (Table 2; Fig. 7b).

4. Discussion

Annual crops like soybean support a diverse assemblage of arthropods, including pests, occasional herbivores (Kogan, 1986), natural enemies (O'Neal and Johnson, 2010) and other functional groups. Most of these organisms need to move through the landscape across cultivated and natural habitats (Hunter, 2002; Rand et al., 2006), either following changes in resource allocation due to short crop cycles (Wissinger, 1997) or searching for necessary additional resources such as nectar, pollen or breeding/overwintering sites that are only found outside crops (Landis et al., 2000; Veres et al., 2013). Therefore the amount and proximity of non-crop habitats are expected to influence the arthropod communities in croplands. Here, we found that richness and abundance of both herbivores and natural enemies on soybean crops were higher in landscapes with larger forest cover, while only natural enemies benefited from forest proximity. Additionally, our experiment with stink bug eggs showed that biological control was enhanced in forest-rich landscapes, indicating that forest maintenance in productive landscapes can have positive consequences for both biodiversity conservation and ecosystem service provision.

The positive influence of forest cover on soybean arthropods was temporally consistent only for natural enemies. This consistency in beneficial arthropod communities could lead to higher stability in the provision of ecosystem services, as proposed by the landscape insurance hypothesis (Tscharntke et al., 2005; Yachi and Loreau, 1999), although testing this possibility would require long term studies. For herbivores, forest cover influence was instead limited to the crop flowering stage, when their abundance was generally higher than at soybean pod-filling. Considering that the most abundant herbivore, the red spider mite *T. urticae*, had similar abundances in landscapes with low and high forest cover, this trend may reflect the dynamics of the dominant
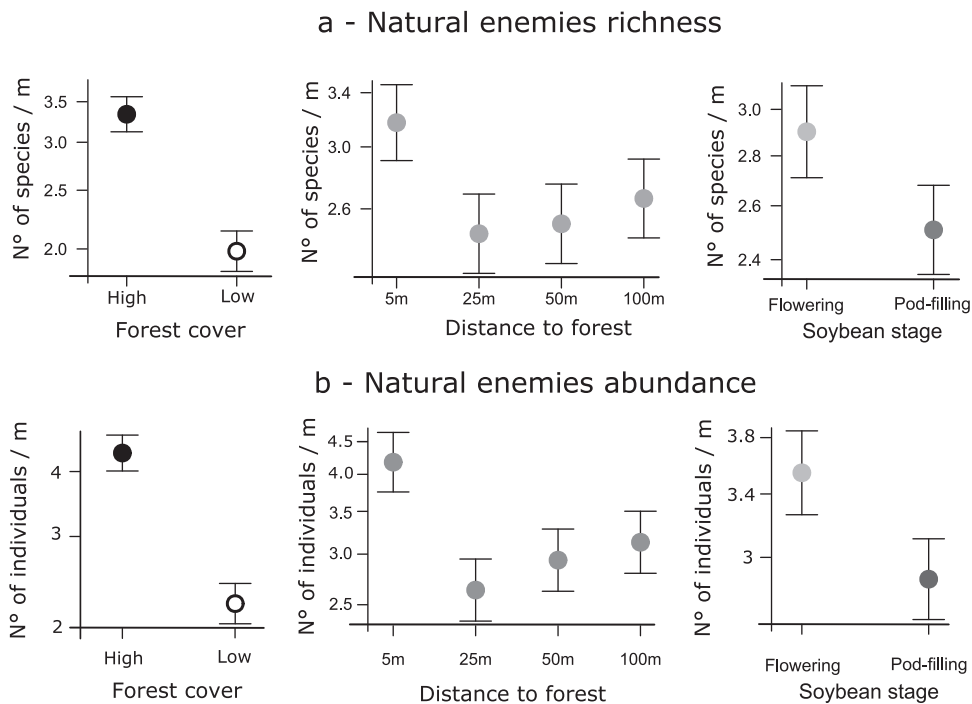
a - Natural enemies richness

b - Natural enemies abundance

Fig. 5. Richness (a) and abundance (b) of natural enemy arthropods captured on soybean plants. Values (mean number of species and individuals per 1 m beating-sheet samples, ± standard error) predicted by GLMMs for landscapes with high (filled points) and low (empty points) forest cover, at the four distances to forest (5, 25, 50 and 100 m) and at flowering and pod-filling stages (only for b) are shown.
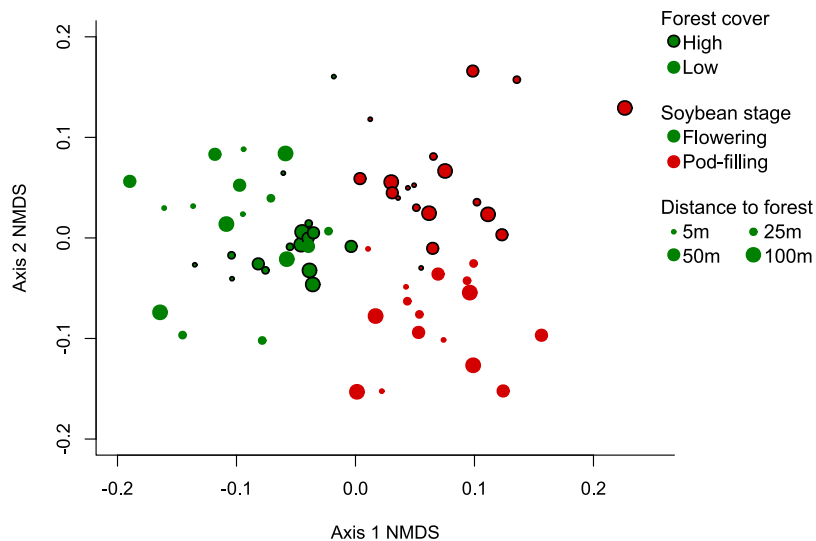

Fig. 6. Two-dimension graph of Non Metric Multidimensional Analysis based on species abundance (log-transformed) of natural enemy assemblages on soybean plants. Data for landscapes with high (circles with black margin) and low (circles without margin) forest cover and at flowering (green) and pod-filling (red) stages are shown. The size of the circle is representative of the distance to the forest, with bigger circles indicating greater distances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

thrips species *C. phaseoli* and *F. schultzei*. These species were, respectively, two and three times more abundant in landscapes with high forest cover than in crop dominated landscapes (see Fig. S1). Generalist pests like thrips (Milne and Walter, 2000; Monteiro, 2002) are expected to benefit more than specialists from landscape complexity (Chaplin-Kramer et al., 2011). Neither spider mites nor thrips are considered main pests of soybean in Argentina, their incidence being rather occasional or sporadic and associated with drought conditions (Molinari et al., 2008; Gamundi and Perotti, 2009). Moreover, given their abundant populations, they

could attract large numbers of predators that might control other, more important pests (Irwin and Yeargan, 1980).

Independently of forest influence at landscape scale, its proximity had no effect on herbivores in general and a negative influence on stink bugs in particular, while natural enemy assemblages on soybean were richer and more abundant in samples taken closest to the forest (5m). Proximity of natural habitats to soybean crops has previously shown positive effects on natural enemies in Argentina (González et al., 2015), while positive (spiders) as well as negative (predators and herbivores) responses

Table 2
Results of GLMMs analyzing the effects of forest cover, distance to forest and soybean phenology on the proportion of biological control, measured through exposure experiments with sentinel stink bug eggs. P-values for all explanatory variables are included, and for the best model AICc values and fixed effect estimates (±standard error) are shown.

Habitat	AICc	Explanatory variables	P-value	Estimate (± SE)	
Crop	263.5	Forest cover	**0.03**	High forest cover Low forest cover	0.21 ± 0.29
		Distance	0.75		−0.92 ± 0.42
		Phenology	0.13		
Forest	81.1	Forest cover	**0.04**	High forest cover Low forest cover	0.59 ± 0.56
					−1.60 ± 0.81

Significant (p < 0.05) and marginal (0.05 < p < 0.10) explanatory variables are highlighted in bold.
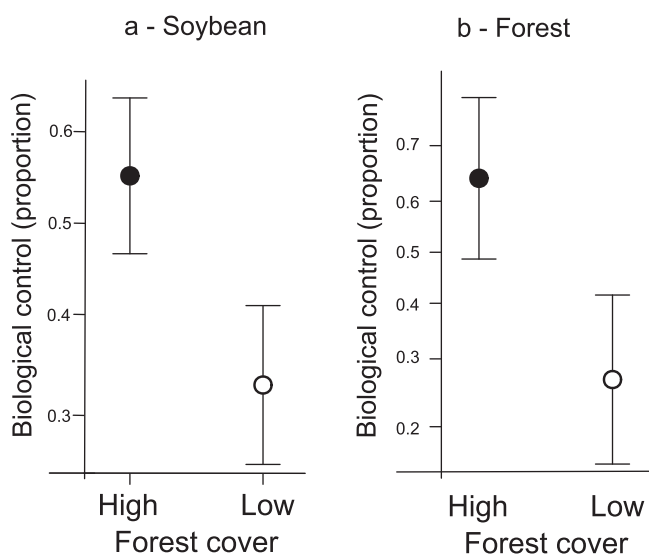

Fig. 7. Biological control in exposure experiments in soybean (a) and forest remnants (b). Values (proportion of eggs attacked ± standard error) predicted by GLMMs for landscapes with high (filled circles) or low (empty circles) forest cover.

were observed in Canada (Mitchell et al., 2014a), with higher abundance of stink bugs at field edges (Venugopal et al., 2014). The opposite patterns for stink bugs and natural enemies found in our study suggests that top-down control could be reducing stink bug density close to the forest, where an intense movement of natural enemies from the forest occurs (González et al., 2016). The present results suggest that the forest is not acting as a source of pests for the crop at the local scale and that soybean crops could benefit from the arrival of beneficial arthropods from nearby natural habitats, even in landscapes with small amounts of forest. This has implications for landscape management and restoration in structurally simple landscapes, where local measures are expected to show stronger results according to the intermediate landscape-complexity hypothesis (Tscharntke et al., 2005, 2012). The lack of interaction between landscape and local variables, means our study did not directly support this hypothesis, but the positive effects of forest proximity (fewer stink bugs and more natural enemies) are still promising. Whether simple habitat management measures such as sowing rows of flowering plants are enough to elicit this local response, or whether complex systems like forest patches are needed, requires further assessment.

Taxonomic composition of arthropod communities on soybean changed with crop phenology, indicating a turnover of herbivores exploiting the changing resources along plant development, and of their associated natural enemies (Aragón, 2002). This turnover might be linked to changes in the intensity of arthropod movement between soybean crops and forest, previously reported by González et al. (2016). Moreover, the amount of forest in the

landscape seems to determine not only the number of species, but also which species of herbivores or natural enemies are using the crop habitat, across the cultivated area. Changes in composition may be as important as biodiversity losses for ecosystem functioning (Tilman et al., 2001b).

Despite the importance of stink bugs as pests of soybean, the influence of non-crop habitats on the biological control of these insects had not been addressed so far. Here, we found a positive link between the amount of forest cover in the landscape and the biological control of stink bug eggs, within soybean crops as well as in forest patches: on average, biological control by predators and parasitoids was 20% higher in forest-rich landscapes. Enhanced control in these complex landscapes is consistent with our observations on natural enemy diversity and with studies on biological control of other pests (Gardiner et al., 2009; Veres et al., 2013). Nonetheless, biological control levels in our crop-dominated landscapes were by no means negligible, suggesting that even small amounts of forests can be important for the provision of ecosystem services. At the local scale, biological control was not significantly influenced by distance to the forest, suggesting that the improved crop protection promoted by forest presence is not limited to its immediate vicinity. On the other hand, the distance range we used may have constrained the detection of these effects. For example, Morandin et al. (2014) found lower egg parasitism in tomato at 200 m from the field edge.

The relatively high biological control levels found within the forest indicates an important role of this habitat as reservoir of natural enemies for the crop. Since stink bugs regarded as pests on soybean were rarely found within the forest (González, 2015), alternative hosts or preys are probably sustaining natural enemy populations there, without posing a risk to the crop. Furthermore, an intense movement of scelionid wasp species (typical parasites of stink bug eggs) between forest and soybean crops in the region (González et al., 2016), supports the idea that forests provide beneficial arthropods to the crop and help maintaining their populations.

In a recent article, Tscharntke et al. (2016) suggested that natural habitats may fail to provide effective biological control if they act as a greater source of pests than natural enemies. However, natural enemies in our study consistently benefited from forest amount and proximity, through different crop phenological stages, with forest cover even enhancing biological control of stink bug eggs. Instead, forest influence on herbivores was restricted to the landscape scale, soybean flowering stage and occasional pests. According to these results, Chaco forests positively affect biodiversity in soybean fields and have a strong potential to enhance the ecosystem service of pest control. Altogether, our study suggests that a land sharing strategy, with co-occurrence of conservation and production uses in the same area (Grau et al., 2013; Green et al., 2005), could be a feasible approach in this region, at least for biodiversity conservation and management of a main pest like stink bugs.

5. Conclusions

In conclusion, we found that forest presence was more important at landscape than at local scale for arthropod communities and biological control in soybean crops. Landscapes with higher forest cover harbored more arthropod species and individuals, influenced community composition and led to higher levels of biological control of stink bug eggs. Our results also advocate for the maintenance of forest fragments in agricultural landscapes. Future studies are needed to assess possible cover thresholds and the role of non-crop habitat structure in these communities and processes.

Disclosure

The authors declare that there are no financial or other types of conflicts of interest that bias this work.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.02.002.

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