ORIGINAL ARTICLE

Natural vegetation cover in the landscape and edge effects: differential responses of insect orders in a fragmented forest

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Abstract Human activities have led to global simplification of ecosystems, among which Neotropical dry forests are some of the most threatened. Habitat loss as well as edge effects may affect insect communities. Here, we analyzed insects sampled with pan traps in 9 landscapes (at 5 scales, in 100–500 m diameter circles) comprising cultivated fields and Chaco Serrano forests, at overall community and taxonomic order level. In total 7043 specimens and 456 species of hexapods were captured, with abundance and richness being directly related to forest cover at 500 m and higher at edges in comparison with forest interior. Community composition also varied with forest cover and edge/interior location. Different responses were detected among the 8 dominant orders. Collembola, Hemiptera, and Orthoptera richness and/or abundance were positively related to forest cover at the larger scale, while Thysanoptera abundance increased with forest cover only at the edge. Hymenoptera abundance and richness were negatively related to forest cover at 100 m. Coleoptera, Diptera, and Hymenoptera were more diverse and abundant at the forest edge. The generally negative influence of forest loss on insect communities could have functional consequences for both natural and cultivated systems, and highlights the relevance of forest conservation. Higher diversity at the edges could result from the simultaneous presence of forest and matrix species, although "resource mapping" might be involved for orders that were richer and more abundant at edges. Adjacent crops could benefit from forest proximity since natural enemies and pollinators are well represented in the orders showing positive edge effects.

Key words Chaco Serrano; edge effect; forest cover; habitat loss; insects; orders

Introduction

Natural ecosystems throughout the world have been degraded and simplified by human activities (Sala *et al.*, 2000). In particular, Neotropical dry forests are among the most threatened biomes on the planet (Grau *et al.*, 2008; Aide *et al.*, 2012). In central Argentina, expansion of agricultural frontiers has led to the loss of 94%

coverage of Chaco Serrano forest, leaving isolated patches of fragmented forest and seminatural habitats surrounded by farmland (Zak *et al.*, 2004, 2008).

In human transformed landscapes, reductions in the amount of natural habitats are frequently associated to declines in insect species richness and abundance (With & Christ, 1995; Fahrig, 2003), often attributed to higher extinction of small populations by stochastic and deterministic processes (Tscharntke *et al.*, 2005). In Chaco Serrano forest in particular, a reduction of the area of forest remnants has been linked to loss of species and changes in community structure of ground-dwelling insects (Molina *et al.*, 2006; Moreno *et al.*, 2013), leaf-miners, and their parasitoids (Cagnolo *et al.*, 2009; Salvo *et al.*, 2011; Fenoglio *et al.*, 2012), leaf-cutting ants

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(Barrera *et al.*, 2015), galling insects (Altamirano *et al.*, 2016), and arthropods on plants (González *et al.*, 2015a), affecting also species interactions and ecosystem processes like herbivory and parasitism (Valladares *et al.*, 2006, 2012; Rossetti *et al.*, 2014). In these and many studies, fragment size has been used as an indicator of habitat loss and fragmentation. However, habitat loss can occur independently of fragment size, therefore its effects may also be evaluated at a larger scale, considering variations in the relative representation of natural ecosystems in the landscape (Fahrig, 2003; Didham *et al.*, 2012). Here, we used the proportion of Chaco Serrano forest cover in the landscape as a surrogate of habitat loss.

In addition to habitat loss, an increase in the proportion of edge habitat is frequently found in transformed landscapes. In this type of landscapes, edges are usually represented by abrupt limits between the remaining natural habitat and the surrounding new modified matrix (Wiens, 1993). These edges typically show increased light incidence, wind and thermal amplitude and lower humidity, in comparison with the interior of fragments (Laurance *et al.*, 2007). In turn, such changes in microclimatic conditions affect populations in multiple ways, including effects on physiology, behavior, phenology, abundance, geographic distribution, and dispersion (Saunders *et al.*, 1991; Ries *et al.*, 2004; van der Putten *et al.*, 2010). At the community level, an increase in the number of species at the edges is the most frequently observed pattern (Odum, 1971; Wirth *et al.*, 2008). Since edge environments tend to increase and become dominant as habitat fragmentation progresses (Rand *et al.*, 2006), it is important to understand edge effects on insect communities, which may impact on the functioning of both natural and human modified environments. Recent studies in Chaco Serrano forests have shown edge effects influencing insect communities and ecological processes involving herbivores and their natural enemies (Valladares *et al.*, 2006; Rossetti *et al.*, 2013; Barrera *et al.*, 2015; González *et al.*, 2015a,b).

In this contribution, we simultaneously evaluated the effects of forest cover in the landscape (measured at 5 spatial scales) and edge/interior habitat on richness, abundance and composition of insect communities sampled with pan traps in a fragmented Chaco Serrano forest. In addition to the community analysis, which we expected to show higher richness and abundance at the forest edge and with increasing forest cover, we searched for particularly susceptible taxa by extending our analysis to the taxonomic order level. In general, previous studies on forest fragmentation effects on Chaco Serrano insects have focused on particular groups such as leafminers, parasitoids or leafcutting ants (see references in the previous paragraphs). The present work seeks to make a valuable contribution

to the understanding of habitat loss and edge effect consequences for an endangered region by assessing, at a landscape scale, the changes in communities captured with broad spectrum traps (Southwood & Henderson, 2000).

Materials and methods

The study was conducted in Córdoba province, central Argentina, in an area (31.10°–31.30°S and 64°–64.30°W) belonging to the Chaco Serrano phytogeographical district, between 500 and 600 m.a.s.l. Mean annual rainfall in the region is 750 mm, with average temperatures ranging between 10 and 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). Currently, native vegetation is restricted to isolated patches surrounded by a cultivated matrix of corn and soybean in summer and wheat in winter (Zak *et al.*, 2004). Based on Landsat Thematic Mapper data and field corroboration, 9 sites were selected with varying proportions of forest cover, the remaining surface being occupied by soybean crops. Landscape circles were centered at the edge of the forest, where edge traps were placed (see below). Chaco Serrano forest proportion in the landscape was estimated from satellite images at 5 spatial scales: circles of 100, 200, 300, 400, and 500 m of diameter. Similar scales effectively explained variations in biodiversity and ecosystem processes in previous studies (Steffan-Dewenter *et al.*, 2001; Thies *et al.*, 2003; Schmidt *et al.*, 2008). Landscape circles were nonoverlapping thus insuring independent samples. The woodland remnants had been isolated for at least 40 years and management of the surrounding matrix was the same for all sites.

At each site, 2 yellow pan traps (diameter 34 cm, depth 9 cm) were placed at the following locations: edge (<5 m from the tree line) and forest interior (25 m from the tree line). The traps were placed on the ground, filled with approximately 3 l of water with a few drops of detergent and left in the field for 3 d (20–22 December 2010). The contents of the pans were then filtered, placed in plastic cups with 70% ethanol and taken to the laboratory. All insects were identified to family level using keys (Triplehorn *et al.*, 2005), separated into morphospecies (Obrist & Duelli, 2010; further referred to as species) by the same operator and saved in reference collections. For the analysis at order level, we considered only those orders representing at least 0.5% of total species richness and/or abundance.

For statistical analyses, we used abundance and species richness of insects (total and for each order) from each trap as response variables. First, we performed correlations between each variable and the proportion of forest in the landscape at the 5 spatial scales and selected the scale with the higher coefficient of correlation for further analyses. When correlations were similar and significant at more than one scale, we performed the subsequent analyses with more than one scale and compared the models as explained below. Due to nonnormal distributions of the data, we used the Spearman-rank correlation index. Then, we ran Generalized Mixed Models (GLMM) with Poisson error distribution and log link function, or negative binomial distribution when overdispersion was detected. Forest cover proportion in each site at the selected scale (as a continuous variable) and location (as factor, with 2 levels: edge and interior) were the explanatory variables, and we included the interaction between both terms to search for differences in the slope between edge and interior. Site was included as a random factor to model data dependence within each site. Models (from the null model without independent variables to the full model that included the interaction) were compared using AICc (small-sample-size corrected Akaike information criterion; Hurvich & Tsai, 1989; Burnam & Anderson, 2002) to select the model with the lowest AICc value. Analyses were performed using the software R (R Development Core Team, 2008; version 2.15.1) and the package lme4 (Bates & Sarkar, 2007). Figures of GLMMs predictions were made with the sjPLot package for R (Lüdecke, 2016).

The composition of total insect communities was analyzed by redundancy analysis (RDA). RDA is a constrained multivariate analysis that allows to determine to which extent environmental variables explain community composition (Legendre & Legendre, 2012). The species abundance data were log-transformed (log N+1). RDA was performed in R using the vegan package (Oksanen *et al.*, 2008). A permutation test (function *anova* in vegan; number of permutations = 999) was used to determine the significance of forest cover in the landscape (at the spatial scale showing the highest correlation with richness and abundance), edge/interior location and their interaction, for community composition (Legendre *et al.*, 2011). Nonsignificant variables ($P > 0.05$) were removed from the final analysis.

Results

A total of 7043 specimens belonging to 11 orders, 108 families and 456 species of hexapods, including insects and springtails were captured. Diptera was the most
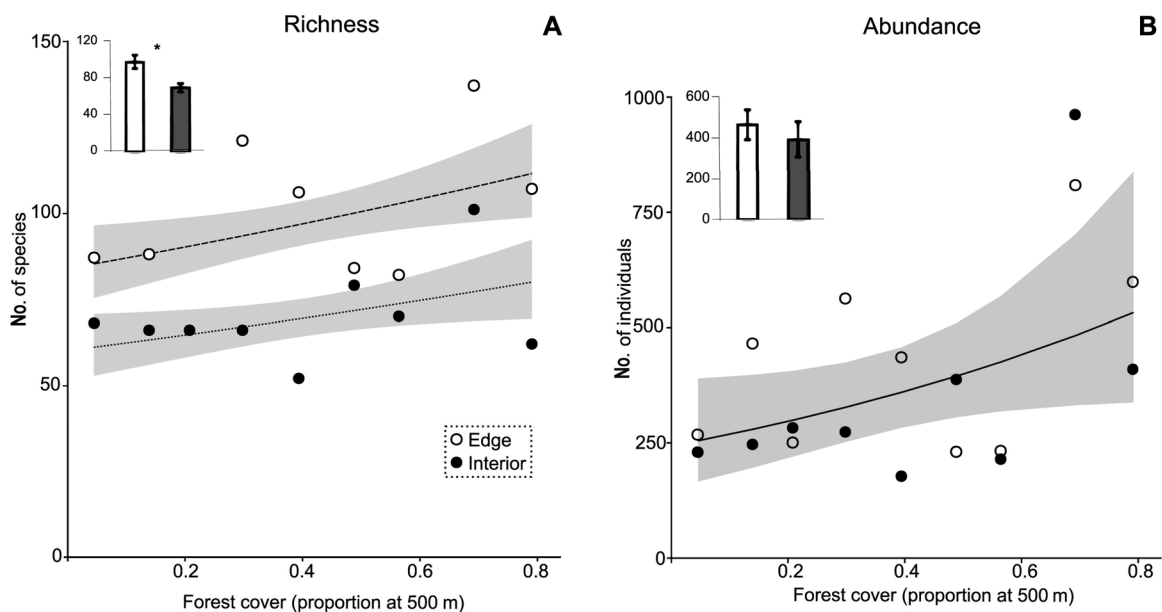

Fig. 1 Total richness (A) and abundance (B) of insect communities in relation to forest cover in the landscape (proportion within 500 m diameter circle) and edge (empty circles) and interior (solid circles) locations. A dashed line represents the regression line for edge, a dotted line for interior and a solid line applies to both locations. Gray areas represent the 95% confidence intervals of GLMMs. Inset bar graphs in the upper-left corner are included, indicating mean ± standard error of edge (white) and interior (gray) locations.

Table 1 Results from generalized linear mixed models evaluating the effects of forest cover and edge/interior location on total insect richness and abundance in Chaco Serrano forests.

	Explanatory variable	*P*	Slope (± SE)	Intercept (± SE)
Richness[p]	Forest cover (500 m)	0.07	0.35 ± 0.19	4.43 ± 0.09 (edge)
	Location	<0.01		4.10 ± 0.05 (interior)
	Interaction	0.48		
Abundance[nb]	Forest cover (500 m)	0.05	0.88 ± 0.45	5.53 ± 0.22
	Location	0.11		
	Interaction	0.38		

Note: The corresponding *P* values, slopes and intercepts (± SE) are provided. For forest cover, the spatial scale at which the analysis was performed is indicated in brackets. The superscript in each response variable indicates the error distribution used in the model (nb = negative binomial; p = Poisson).
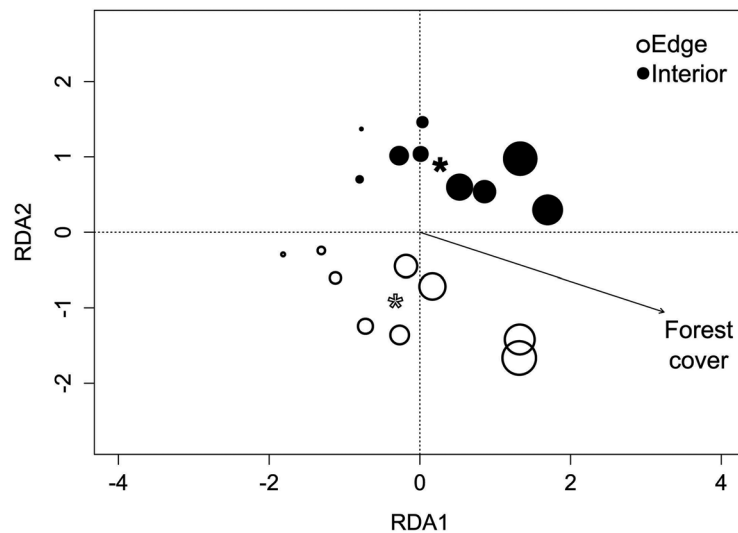
Fig. 2 Two-dimension graph of redundancy analysis based on species abundance (log-transformed) of total insect assemblages from edge (empty circles) and interior (filled circles) locations, in 9 sites with different forest cover (proportion within 500 m diameter circle). The size of the circle is representative of the forest cover. Asterisks indicate the centroid for edge and interior locations.

abundant order with 32% of all individuals, followed by Collembola (25%), Hymenoptera (12%), Thysanoptera (12%), and Hemiptera (11%). With regard to species richness, Hymenoptera was the most diverse order with 189 species (42% of total richness) followed by Coleoptera, Hemiptera, and Diptera (15%–19% of all species).

Correlations between response variables and forest cover at the five analyzed spatial scales showed variations which are summarized in Table S1. Species richness was higher at the edges and marginally increased along with the proportion of forest at 500 m in both locations (Fig. 1A, Table 1). Total abundance did not differ between forest edge and interior, although it was positively related to the proportion of forest in the landscape at the scale of 500 m (Fig. 1B, Table 1). About 20% of the species ($n = 86$) were found exclusively at the interior, while

approximately 40% ($n = 179$) were present only at the edge.

The analysis of the taxonomic composition of insect communities by RDA revealed that edge and interior samples were clearly separated along the second axis (Fig. 2). An array of sites in relation to the proportion of forest cover was also observed, from sites with low forest proportion on the left to sites with high forest cover on the right (represented by increasing size of symbols in Fig. 2). Permutation tests results revealed that community composition was significantly affected by edge/interior location ($F_{1,15} = 1.69$, $P = 0.003$) and forest cover at the 500 m scale ($F_{1,15} = 2.12$, $P = 0.001$). Both variables explained 20% of the total variance ($R^2 = 0.20$). The interaction between forest cover and edge/interior location was not significant ($F_{1,14} = 0.91$; $P = 0.64$).
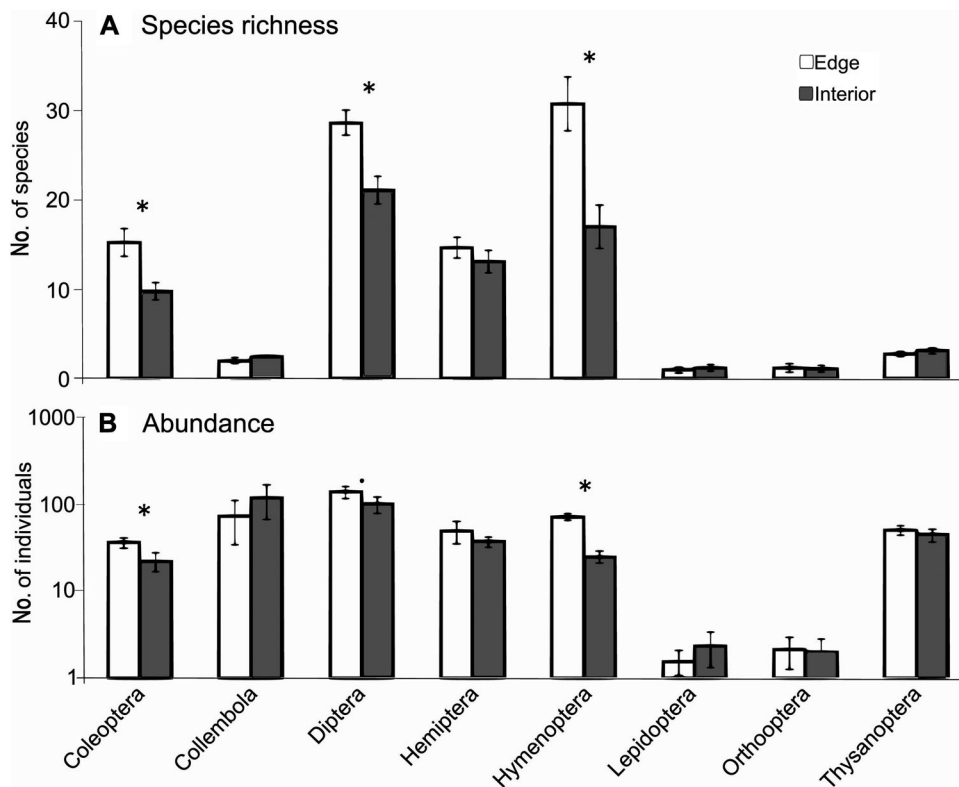
Fig. 3 Total richness (A) and abundance (B) of insect orders at the forest edge (white bars) and interior (gray bars) locations. Abundance is presented in logarithmic scale. Mean ± standard error are represented. Asterisks are used to indicate significant differences, while points indicate marginal differences.

At the Order level, richness of Coleoptera and Diptera was higher at the edge and independent of the amount of forest in the landscape (Fig. 3, Table 2). Hemiptera and Orthoptera did not differ between locations but more species were found in landscapes with higher proportion of woodland (Figs. 4A and B; forest cover at 500 m for Hemiptera and 400 m for Orthoptera). Hymenoptera richness presented an interaction between locations and forest cover at the scale of 100 m. The number of species was always higher at the edge, where it was not related with forest cover; while at the forest interior richness was negatively related with forest cover (Fig. 4C). Abundance showed similar trends to those observed for richness: Coleoptera and Diptera showed more specimens at the edge (although differences were only marginally significant for Diptera; Fig. 3, Table 2), whereas forest cover was positively related to the abundance of Collembola, Hemiptera and Orthoptera (Figs. 5A–C, Table 2). Hymenoptera abundance was higher at the edge and negatively related with forest cover at both locations (Figs. 2 and 5D, Table 2). Thysanoptera showed an interaction between forest cover and location, with a positive relationship

between abundance and forest cover at the forest edge while abundance at the interior was independent of forest proportion (Fig. 5E, Table 2).

Discussion

Habitat transformation through agricultural intensification has resulted in the loss of biodiversity at a global scale (Tilman *et al.*, 2001). Applying a landscape perspective to the interactions between natural and managed habitats (Tscharntke *et al.*, 2005) may contribute to understanding the importance of those changes and achieving conservation goals. Here, we analyzed insect communities sampled with broad spectrum traps in fragmented Chaco Serrano forests considering the proportion of native vegetation in the landscape at different spatial scales, as well as edge effects in order to evaluate the influence of proximity to croplands. We found that abundance and richness of insects were directly related to forest cover and predominantly higher at edges in comparison with forest interior. However, among the 8 studied orders,

Table 2 Results from generalized linear mixed models evaluating the effects of forest cover and edge (E)/interior (I) location on richness and abundance of dominant insect orders in Chaco Serrano forests.

Order	Response variable	Forest cover			Edge/interior location P value	Interaction
		Spatial scale (m)	P value	Slope (± SE)		
Coleoptera	Richness[p]	500	0.702	–	**0.001**	0.487
	Abundance[nb]	500	0.101	–	**0.016**	0.134
Collembola	Richness[p]	500	0.356	–	0.528	0.361
	Abundance[nb]	500	**0.007**	2.68 ± 0.99	0.437	0.605
Diptera	Richness[p]	500	0.305	–	**0.001**	0.961
	Abundance[nb]	100	0.208	–	**0.081**	0.102
Hemiptera	Richness[p]	500	**0.029**	0.57 ± 0.26	0.376	0.690
	Abundance[nb]	300	**<0.001**	2.05 ± 0.37	0.308	0.081
Hymenoptera	Richness[p]	100	0.379	0.13 ± 0.56 (E)	**<0.001**	**0.009**
	Abundance[nb]	100	**0.002**	-1.65 ± 0.69 (I)	**<0.001**	0.085
				-1.37 ± 0.45		
Lepidoptera	Richness[p]	100	0.104		0.655	0.818
	Abundance[nb]	100	0.983		0.525	0.463
Orthoptera	Richness[p]	400	**0.004**	2.49 ± 0.88	0.827	0.334
	Abundance[nb]	300	**0.015**	2.78 ± 1.15	0.791	0.403
Thysanoptera	Richness[p]	100	0.456		0.684	0.950
	Abundance[nb]	500	**0.012**	1.17 ± 0.48 (E)	0.242	**0.050**
				0.18 ± 052 (I)		

Note: The corresponding P value for every explanatory variable is provided. Significant variables are indicated in bold. For forest cover, the spatial scale of analysis and the slope (± SE) of significant relationships are also included. The superscript in each response variable indicates the error distribution used in the model (nb = negative binomial; p = Poisson).
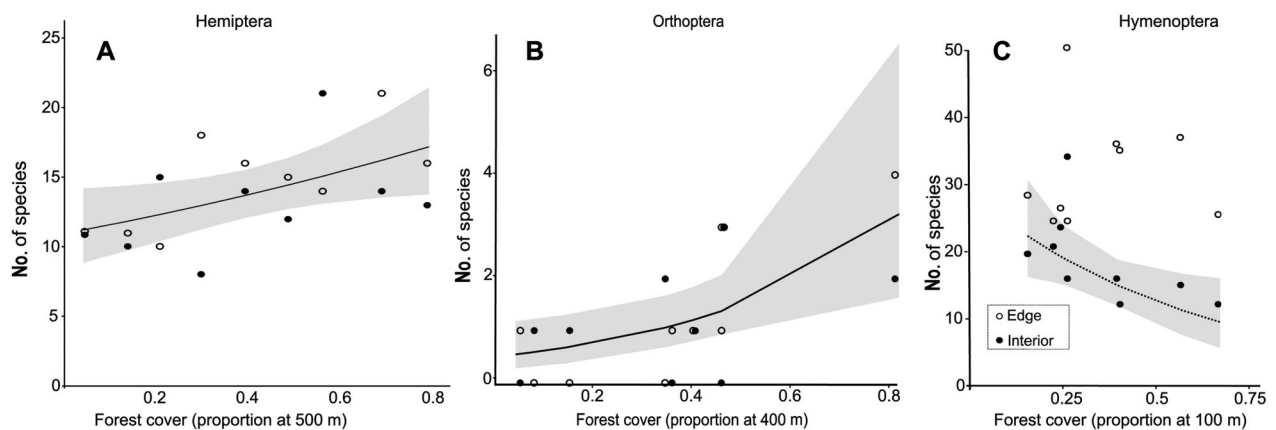

Fig. 4 Richness of Hemiptera (A), Orthoptera (B), and Hymenoptera (C) in relation to forest cover in the landscape (proportion within 500, 400, and 100 m diameter circle, respectively) and edge (empty circles) and interior (solid circles) locations. A solid line is used to represent the regression line of both locations and a dotted line for interior. Gray areas represent the 95% confidence intervals of GLMMs.

different responses to landscape variables and scales were detected, suggesting that sensitivity varies among groups and should therefore be considered.

The analyses of forest cover effects at multiple scales showed that sensitivity varied between orders, with 500 and 100 m appearing as the more effective spatial scales to detect insect responses. This suggests that most orders respond to large or small scale changes in forest cover, respectively. Even in orders where responses were best noticed at intermediate scales, the larger (500 m)
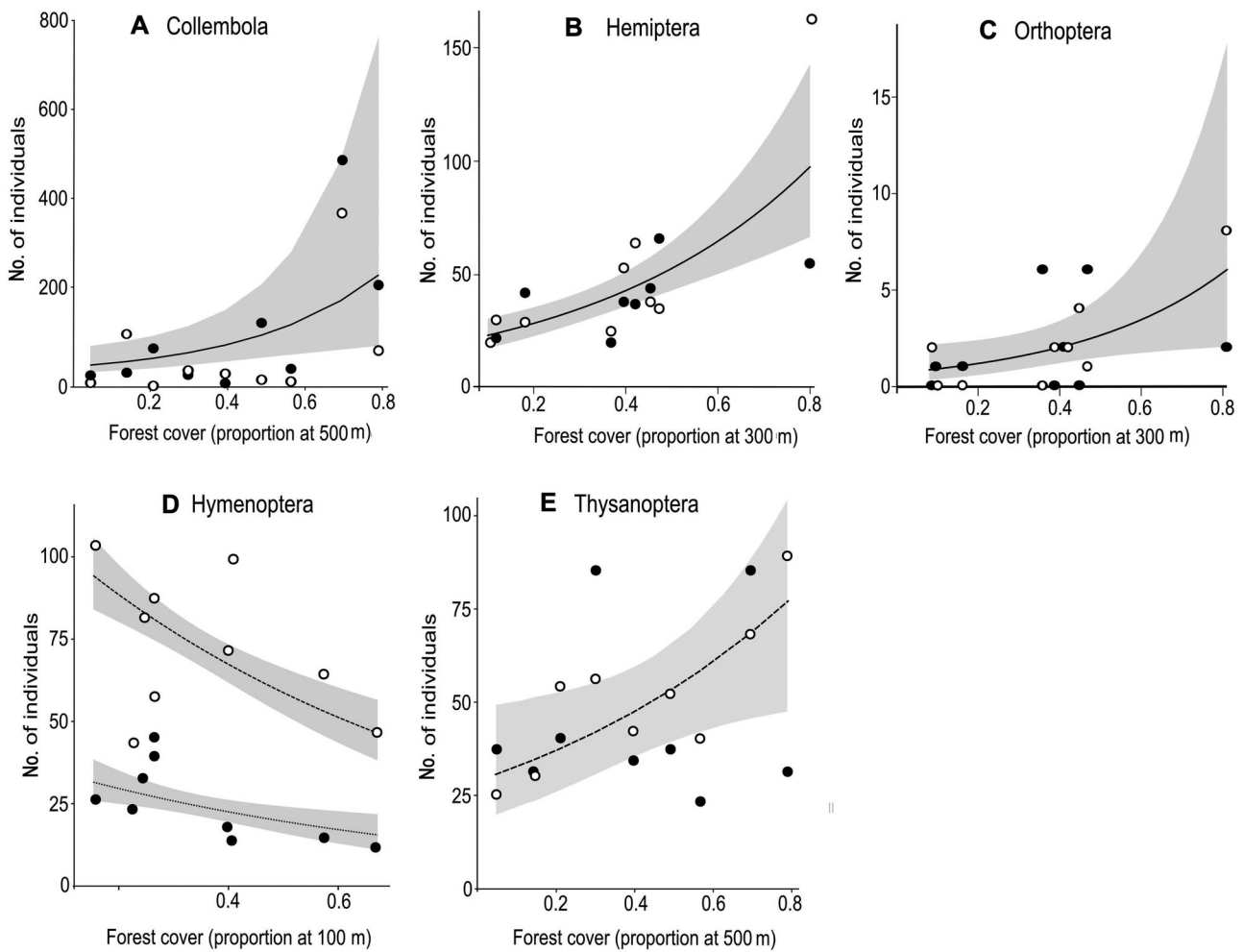
Fig. 5 Abundance of Collembola (A), Hemiptera (B), Orthoptera (C), Hymenoptera (D), and Thysanoptera (E) in relation to forest cover in the landscape (proportion) and edge (empty circles) and interior (solid circles) locations. A dashed line represents the regression line for edge, a dotted line for interior and a solid line applies to both locations. Gray areas represent the 95% confidence intervals of GLMMs.

scale provided very similar results. Different reasons have been proposed for scale-dependent responses, including specific habitat requirements or foraging range (Steffan-Dewenter *et al.*, 2002). Understanding of these differential responses would require a more detailed analyses of functional diversity based on species traits like body size, trophic level, etc. (Gagic *et al.*, 2015). Moreover, some groups might even respond to larger spatial scales than those here explored (e.g., Chaplin-Kramer *et al.*, 2011) and some weak relations might need a bigger sample size to be accurately assessed.

Fewer insect species and specimens were captured by our pan traps in simple landscapes, that is, those dominated by agricultural lands, indicating that habitat simplification in the study region has led to losses of in-

sect biodiversity. These results support landscape scale variables as important determinant of local-scale diversity (Tscharntke *et al.*, 2012). Only a few particular orders (Table 2; Hemiptera, Orthoptera, and Collembola; also Thysanoptera, but see below) displayed a similar trend, with higher abundance and/or richness in forest dominated habitats. Interestingly, these were not the most abundant or species orders, suggesting that the community pattern was not just mirroring the behavior of dominant groups.

The orders that were affected by landscape simplification include mainly herbivores (Hemiptera, represented here mostly by herbivore species, Orthoptera, Thysanoptera) and detritivores (Collembola), which could have consequences for the functioning of the involved

ecosystems. For example, in the same region Moreno *et al.* (2014) found lower litter decomposition in smaller forest patches (which, in our study, were more common in simple landscapes) while herbivory on forest plants decreased with increasing forest fragmentation (Valladares *et al.*, 2006; Videla *et al.*, 2007).

Surprisingly, forest cover showed a negative influence on Hymenoptera abundance and richness, at the scale of 100 m. Negative relationships between Hymenoptera and the proportion of semi-natural habitats were previously reported for honey bees (Steffan-Dewenter *et al.*, 2001, 2002), although at much larger spatial scales. In our study, most species were small parasitoids, probably with limited dispersal ranges (Greenleaf *et al.*, 2007), which would explain responses to small scale changes in landscape structure (Thies *et al.*, 2005). Also, many parasitoids could be specialists, which tend to respond to smaller spatial scales than generalists (Chaplin-Kramer *et al.*, 2011). On the other hand, negative responses to forest area could arise from a preference for hosts in the cultivated matrix (Rand *et al.*, 2006; Schmidt *et al.*, 2008).

In addition to changes linked to the amount of natural habitats, insect communities were affected by their location in either edges or interior of forests. We found more diverse communities at the edge than at the interior of the forest, a pattern consistent with other studies (Didham, 1997; Holland & Fahrig, 2000; Wirth *et al.*, 2008). In contrast, total abundance did not differ between edge and interior, indicating that changes in richness were not just a consequence of the number of individuals captured.

Higher richness in edges could be attributed to the simultaneous presence of both forest and matrix species because, being the transition zone between original native vegetation remnants and the adjacent matrix, edges allow easy access to resources from both habitats (Ries *et al.*, 2004). Increasing similarity in edge and soybean community composition at increasing forest proximity has been reported from the same study area (González *et al.*, 2015b; González *et al.*, 2016), supporting this possibility. An alternative mechanism could be represented by "resource mapping" (Ries *et al.*, 2004), if edges are preferred because they offer better resources in terms of quality or quantity (Wirth *et al.*, 2008). In the case of total insects, since abundance did not differ between locations the first mechanism, that is, co-occurrence of forest and matrix species seems more likely. The observation that more species were found exclusively at the forest edges, with low abundances, suggests that they could actually represent matrix species coming occasionally from the adjacent crops. However, when particular orders showed edge effects, that is, Coleoptera, Diptera, and Hymenoptera, not only richness but also abundance was higher at the edge;

in such cases, "resource mapping" could be the mechanism involved. These 3 orders involve important biological control agent species, therefore their affinity with forest edges could contribute to the provision of ecosystem services in crops (Bianchi *et al.*, 2008). Supporting the possibility of forest edges positively affecting crops in the study region, richer natural enemy assemblages have been recorded on soybean plants closer to the forest (González *et al.*, 2015b) and crop pollination was enhanced by forest proximity (Monasterolo *et al.*, 2015). None of the analyzed orders presented higher richness or abundance at the forest interior, suggesting that forest specialist species, which should be negatively affected by the changes in climatic or biological conditions at edges (i.e., Harris & Burns, 2000; Barbosa & Marquet, 2002), were not prevailing at this taxonomic level. Only Collembola showed a tendency to higher abundance values at the interior, which could be related to the known affinity of this group with high humidity conditions (Pflug & Wolters, 2001).

Thysanoptera exhibited an interaction between forest cover and edge/interior location. Number of collected thrips increased with forest cover only at the edges, which were adjacent to soybean crops. In other words, fewer thrips were captured at the edges when soybean cover was higher. Since pest abundance tends to be related with host crop area (Veres *et al.*, 2013), and given records of soybean crops harboring large Thysanoptera populations in the region (Gamundi & Perotti, 2009), the opposite pattern would have been expected. Benefits from landscape complexity to generalist pests like Thysanoptera species (Chaplin-Kramer *et al.*, 2011) or increased movement between forest and soybean with increasing amount of forest (González *et al.*, 2016), could be mentioned among possible causes for the high thrips abundance at edges in forest-dominated landscapes.

In addition to the observed changes overall and at order level, taxonomic composition of the insect assemblages found at each site was noticeably different between edge and interior locations, and also affected by forest cover, as seen in multivariate analyses. Some authors suggest that agricultural intensification should lead to changes in species composition and homogenization of communities (Ekroos *et al.*, 2010; Gagic *et al.*, 2014; Gámez-Virués *et al.*, 2015). Our results show a clear impact of both habitat loss and edge effects on community composition, but rather than homogenization (which would graphically appear as a tighter clustering of sites with low forest cover in comparison with forest rich sites) we saw a gradient of samples. Sites were arranged across the first RDA axis in relation to forest proportion in the landscape, probably reflecting their low insect species richness and abundance in simple, crop dominated landscapes.

In conclusion, both forest cover and edge effect proved to be influential for insect communities in Chaco Serrano, with differential vulnerability of species grouped at order level. Whereas some orders were responsive solely to forest cover, being impaired by the loss of natural habitats, other orders only benefitted from conditions at the forest edges, irrespective of the amount of forest cover. The generalized impoverishment of insect communities in landscapes with low proportion of natural habitat highlights the relevance of native forest conservation. In addition, the enhanced biodiversity at forest edges needs further consideration to fully understand the role of forest–crop interphase in the maintenance of ecosystem processes and services in cultivated lands.

Acknowledgments

Disclosure

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

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Correlations between spatial scales of analyses and richness and abundance of total communities and particular orders. For each relation, the value of Spearman-rank correlation index is provided, and the values with the strongest correlations are highlighted in bold. For each response variable (abundance and richness) the scale with the higher correlation index was selected as predictor variable for GLMMs (see Methods). Superscripts indicate statistical significance of relations. ($P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$).