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Arthropods on plants in a fragmented Neotropical dry forest: A functional analysis of area loss and edge effects

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Abstract Loss and fragmentation of natural ecosystems are widely recognized as the most important threats to biodiversity conservation, with Neotropical dry forests among the most endangered ecosystems. Area and edge effects are major factors in fragmented landscapes. Here, we examine area and edge effects and their interaction, on ensembles of arthropods associated to native vegetation in a fragmented Chaco Serrano forest. We analyzed family richness and community composition of herbivores, predators, and parasitoids on three native plant species in 12 fragments of varying size and at edge/interior positions. We also looked for indicator families by using Indicator Species Analysis. Loss of family richness with the reduction of forest fragment area was observed for the three functional groups, with similar magnitude. Herbivores were richer at the edges without interaction between edge and area effects, whereas predators were not affected by edge/interior position and parasitoid richness showed an interaction between area and position, with a steeper area slope at the edges. Family composition of herbivore, predator, and parasitoid assemblages was also affected by forest area and/or edge/interior situation. We found three indicator families for large remnants and five for edges. Our results support the key role of forest area for conservation of arthropods taxonomic and functional diversity in a highly threatened region, and emphasize the need to understand the interactions between area and edge effects on such diversity.

Key words area loss, Chaco Serrano, edge effect, forest arthropods, functional groups, habitat fragmentation

Introduction

The world's biodiversity is facing one of the major extinction events in history (Chapin *et al*., 2000), driven mainly by degradation and fragmentation of natural habitats due to anthropogenic activities (Forman, 1995; Ellis *et al*., 2010). Habitat fragmentation is the process by which extensive and continuous landscapes are transformed into small and isolated remnants (Fahrig, 2003) that end up surrounded by a highly contrasting matrix, mostly agricul-

tural or urban (Wiens *et al*., 1993). As fragments become smaller, the proportion of edge habitat increases, leading to changes in microclimatic conditions (e.g., temperature, humidity, wind, solar radiation) and biotic components of the ecosystem (Saunders *et al*., 1991; Laurance *et al*., 2007).

Area and edge effects have been recognized as the most important factors in fragmented landscapes (Didham *et al*., 2012). The loss of species as habitat size decreases (Kruess & Tscharntke, 2000; Fahrig, 2003) is a well-known example of the species–area relationship, which underlies the consideration of habitat size as a major feature for conservation purposes (He & Hubbell, 2011). In small patches there are fewer resources (Root, 1973), higher extinction rates due to emigration–immigration dynamics (MacArthur & Wilson, 1967), and increased susceptibility to stochastic events due to smaller

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populations (Drakare *et al.*, 2006), leading to impoverishment and composition changes in local communities (Fletcher *et al.*, 2007).

The "edge effect" originally described by Odum (1971), explained the increased biodiversity usually found in ecotones, as a consequence of juxtaposition of species from each of the adjacent habitats. However, edges in anthropogenically fragmented landscapes tend to be much more abrupt and contrasting, and consequently show highly variable patterns among species and taxonomic or ecological groups (Ries *et al.*, 2004). The amounts of area and edge tend to covary in a landscape, and the effects of both factors are likely to be interdependent (Fletcher *et al.*, 2007). Moreover, these and other components of fragmentation can affect species directly, or indirectly, via endogenous threats like increased competition or disruption of species interactions (Fischer & Lindenmayer, 2007).

In terrestrial ecosystems, arthropod communities comprise more than one million of described species, are distributed in a large variety of habitats, and exploit a wide range of resources and microhabitats (Schowalter, 2000; Triplehorn *et al.*, 2005). They are also involved in many ecological processes due to their multiple feeding habits, with a variety of functional groups such as herbivores, detritivores, predators, parasitoids, and pollinators. They are key providers of ecosystem services like pollination, nutrient cycling, regulation of primary production, and pest control (Speight *et al.*, 2008). Among the myriad of arthropod communities, those associated with plants are particularly relevant because plants and herbivorous arthropods account for over half of all terrestrial biodiversity, and almost two thirds of it if natural enemies (predators/parasitoids) of those herbivores are added into the equation (Hamilton *et al.*, 2010).

Arthropods are markedly affected by habitat fragmentation (Hunter, 2002), in terms of abundance (Ozzane *et al.*, 1997; Zabel & Tscharntke, 1998; Tscharntke *et al.*, 2002; Jennings & Tallamy, 2006), diversity (Thomas *et al.*, 1992; Daily & Ehrlich, 1995), community structure (Driscoll, 2008), species interactions (van Nouhuys, 2005; Valladares *et al.*, 2012), and ecosystem processes (Aizen & Feisinger, 1994; Kruess & Tscharntke, 2000; Valladares *et al.*, 2006). However, not all species respond in the same way to changes in the landscape, and various traits have been shown to confer differential vulnerability to habitat fragmentation (Zabel & Tscharntke, 1998; Cagnolo *et al.*, 2009). In this context, highly specialized species or groups (Steffan-Dewenter & Tscharntke, 2000) and those occupying higher trophic levels (Holt *et al.*, 1999) seem to be consistently more sensitive to the effects of fragmentation.

Neotropical dry forests are among the world's most endangered ecosystems due to deforestation and fragmentation (Grau *et al.*, 2008; Aide *et al.*, 2012). Among such forests, the Argentine Chaco suffers the highest deforestation rates of the country (Gasparri & Grau, 2009), with 94% of Chaco Serrano having been lost within 30 years (Zak *et al.*, 2004) in a process that is closely related to the expansion of soybean crops (Zak *et al.*, 2008). In this system, habitat fragmentation effects have been shown for insects developing inside plant leaves and for the ecosystem processes in which they are involved (e.g., Valladares *et al.*, 2006; Cagnolo *et al.*, 2009; Fenoglio *et al.*, 2012). However, little is known about how arthropods externally associated to the native vegetation respond to fragmentation in Neotropical dry forests. For extremely diverse groups such as plant-associated arthropods, diversity estimations based on higher taxonomic levels such as family (Báldi, 2003; Grimbacher *et al.*, 2008), have proved effective to evaluate community responses in disturbed habitats (Basset *et al.*, 2008). The family level approach allows the assessment of broader community trends (e.g., Zilihona & Nummelin, 2001; Yu *et al.*, 2006; Bennet & Gratton, 2012) and is particularly useful when taxonomic knowledge is limited. Also, it allows the comparison of different areas at a local scale (Williams & Gaston, 1994; Balmford *et al.*, 1996b) to be done with fewer resources, yet maintaining efficiency in terms of conservation priorities (Balmford *et al.*, 1996a) and enabling detection of critical factors for both richness and community structure (Heino & Soininen, 2007).

Here, we simultaneously examine area and edge effects on ensembles of arthropods found on the surface of native plants in fragmented Chaco Serrano. Specifically, we aimed at: (i) evaluating whether there is a general family richness trend or if it differs between functional groups; (ii) examining changes in community composition related to forest fragmentation; and (iii) determining groups that are particularly sensitive to fragment size or edge/interior position and could therefore be considered as potential indicators of fragmentation in the region. We expected arthropod family richness to be directly related to remnant area, according to the species–area relationship, with a stronger effect on natural enemies than on herbivores, because of their smaller populations and dependence on their prey (Kruess & Tscharntke, 1994; Holt *et al.*, 1999). Moreover, within natural enemies we expected parasitoids to be the most vulnerable, because of their higher specialization (Tscharntke *et al.*, 2002). We also expected richer communities at the edges, where families from both the forest and the matrix could co-occur. Finally, if families show differential responses to habitat fragmentation, either because of family shared traits
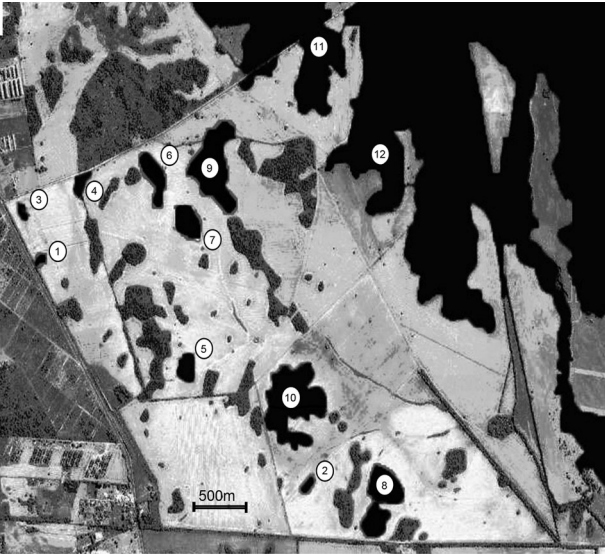
Fig. 1 Location of Chaco Serrano forest remnants utilized as study sites (in black). Numbers goes from the smallest (1) to the largest (12) fragments.

or dominant species-specific traits, we expected changes in community composition beyond those in family numbers.

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, with 750 mm of annual rainfall and average temperatures of 10–26 °C (Luti *et al*., 1979). Through digital satellite images (Landsat Thematic Mapper) 12 woodland fragments were selected, ranging in area from 0.4 ha to more than 1 000 ha (Fig. 1). Isolation (measured as the distance to the nearest fragment) was kept as homogeneous as possible (316 ± 105 m) and was not correlated with fragment area ($P = 0.47$). The woodland remnants had been isolated for at least 40 years and were embedded in an agricultural matrix largely dominated by soybean crops at the time of the study.

In order to obtain a representative sample of arthropod communities on shrub plants, reducing bias from variations in vegetation composition among sites, we sampled insects on three native species of perennial shrubs that reach 2–3 m high: *Cestrum parqui* L'Hér. (Solanaceae), *Croton lachnostachyus* (Müll.) Baill. (Euphorbiaceae), and *Eupatorium hookerianum* Griseb. (Asteraceae). The shrub layer is very well developed in Chaco Serrano, cov-

ering 10%–80% of the ground (Cabido *et al*., 1991). The selected species were present in all remnants and are common components of the forest understory. In each forest remnant, we sampled five individuals of each species in the edge (<5 m from the tree line) and five in the interior (approximately 25 m from the tree line) thus including a total of 120 individual plants per species. In the same area, a similar design was effective for the detection of edge effects in herbivory and parasitism rates (Valladares *et al*., 2006).

Sampling was conducted in the summer months of January and February 2010. On each individual plant, arthropods were collected through visual observation for up to 15 min. After that, plants were shaken three times on a white cloth to collect additional arthropods (Kogan & Herzog, 1979). Although visual examination was carried out as unobtrusively as possible, some disturbance of arthropods that show thanatosis behavior may have occurred, nonetheless any slight bias thus produced would have been equally spread with regard to the studied factors. Large and small remnants were visited alternately, to reduce bias due to interactions between sampling date and size of forest fragments. Also within each fragment, edge and interior plants were sampled alternately to reduce possible effects of daily variations. In the laboratory, all insects were identified to family level and assigned to one of three functional groups: herbivores, predators, and parasitoids (Triplehorn *et al*., 2005). Subfamily level was used for families including multiple functional groups (e.g., Formicidae).

For statistical analyses, we estimated family richness (log-transformed average from 15 plants, that is, five of each species, sampled in each fragment and edge/interior position). A Generalized Mixed Model (GLMM) with richness of each functional group as dependent variable, fragment area as covariable (log-transformed to linearize the relationship), functional group as fixed factor, and interaction term area × functional group in order to test for differences in functional group responses to fragment area was performed. Site (fragment) was included as a random factor to model the dependence between edge and interior. We used additional GLMMs to test for the combined effects of edge/interior position (as fixed factor) and remnant area on the richness of each functional group, considering also the area × position interaction; site was also included as a random factor (as above-mentioned). Analyses were performed using the software R (R Development Core Team, 2008; version 2.15.1) and the package nlme (Pinheiro *et al*., 2013). Best models for each variable were selected via backward elimination of nonsignificant variables using Likelihood Ratio Tests, starting from full models including variable interactions. When necessary,

a VarIdent structure was used to model heterogeneity in the residuals of edge and interior (Zuur *et al.*, 2009).

To search for changes in family community composition we performed a principal component analysis (PCA) with the software Past (Hammer *et al.*, 2001), using quantitative data (log transformed family abundances). The first and second principal components were used as dependent variables in regressions against fragment area and in paired *T*-tests (to compare values at edge/interior). Species Indicator Analysis (see Dufrêne & Legendre, 1997) was applied to identify families most strongly related to edge/interior position or to small/large fragments (the three smallest versus the three largest fragments). We calculated Indicator Values (Ind-Val) for each family, based on specificity (how specific is a family to certain habitat, in relation to all types of habitats) and fidelity (a measure of how widespread is the family in all the sites or samples of that habitat). The Ind-Val goes from 0 to 100 (higher values representing higher affinity with particular sites) and is tested for significance using permutations. We only performed the analysis with those families with more than 30 sampled individuals and considered indicator families those with a *P*-value equal or smaller than 0.05 (Bakker, 2008). The analysis was performed with the software PC-ORD 5.1 using Monte Carlo randomization set at 1 000 permutations.

We checked for plant density effects that might underlie the studied area or edge effects, by carrying out a correlation analysis of plant density and family richness. Density of the selected plant species was estimated as number of plants/m^2 along six 2×10 m transects (three at the edge and three at the interior) on each remnant. Richness of the three functional groups was not related to plant density ($P > 0.05$ in all cases). We also checked for spatial autocorrelation as a potential source of bias, by performing a Mantel test, which compared the community composition matrix (family abundances) with the matrix of geographic distances (latitude and longitude of each fragment center). These calculations were performed using the statistical program Past (Hammer *et al.*, 2001). The Mantel test ruled out spatial autocorrelation effects ($P = 0.3$).

Results

We sampled a total of 4 645 specimens in 13 orders and 84 families (Table S1). Although dominated by insects (altogether, 84.8% individuals and 86.9% families recorded), samples included other arthropods, for example, spiders and mites. In total, herbivores were represented by 41 families and accounted for 79.9% total abundance, whereas 29

predator families (17.9% of total individuals) and 14 parasitoid families (2.2% of total individuals) were recorded. At each forest remnant, between 0 and 13 insect families and 0 and 297 individuals were found on the selected plant species.

All three functional groups were negatively affected by the reduction of forest fragment area. Family richness varied among groups, with herbivores showing the highest average values (3.28 ± 0.28 families per plant) followed by predators (1.99 ± 0.09) and parasitoids (0.12 ± 0.01) being the lowest; however, the magnitude of the area effect did not differ among groups, as indicated by the nonsignificant interaction term (Table 1).

Herbivorous insects were richer at the forest edge than at the interior (edge: 3.82 ± 0.49, interior: 3.13 ± 0.23) and in both positions, richness was positively related to woodland area, displaying similar slopes (interaction term $P > 0.05$; Fig. 2A; Table 1). Predator richness was also related to forest area but did not differ between positions (Fig. 2B; Table 1). Parasitoid richness showed a significant interaction between area and position, increasing with forest area more pronouncedly at the edge (Fig. 2C; Table 1).

Herbivore family composition (Fig. 3A) showed a negative relationship between the first PCA axis (explaining 23.4% variance) and remnant area ($R^2 = 0.23$; $F = 6.67$; $P = 0.017$), as well as a positive relationship between area and the second principal component ($R^2 = 0.18$; $F = 4.82$; $P = 0.039$; this component explained 16.8% of variance). For predators (Fig. 3B), the first principal component (18.4% of variance) showed a differentiation in family composition according to edge/interior position ($t = 2.83$; $P = 0.01$) while the second component was directly related to area ($R^2 = 0.22$; $F = 6.10$; $P = 0.021$) and explained 14.6% variance. Parasitoid composition (Fig. 3C) was mainly affected by fragment area, to which the first PCA axis was related ($R^2 = 0.38$; $F = 14.38$; $P = 0.001$). This component explained 57.5% of variance, while the second explained 20.4% and was not related to the analyzed variables.

According to our indicator species analysis, Chalcididae, Noctuidae, and Thomisidae were linked to big forest remnants (Ind-Val = 66, 67.1, and 82, respectively). Also, five families were selected as edge indicators (Acrididae, Chalcididae, Meloidae, Phytoseiidae, and Thripidae, Ind-Val = 41–71), whereas no families qualified as indicators for the forest interior (Table 2).

Discussion

In this study, from a highly endangered Neotropical dry forest in central Argentina (Aide *et al.*, 2012), we have

Table 1 Summary of GLMMs results for the analysis of area and edge effects on variations in arthropod family richness in Chaco Serrano forest. For each explanatory variable the degrees of freedom (df), the change in the likelihood of the model (*L*) and the *P*-value are given. The slope is represented by only one value when interaction is not significant. The intercept is represented by only one value when there were no differences between functional groups or positions. The standard error of slopes and intercept are provided. All terms in bold are those that were significant (i.e. the *p* value was lower than 0.05).

|	Explanatory variable	df	*L*	*P*	Slope	Intercept
Functional Group	Area	1,11	7.99	**0.005**	0.03 ± 0.01	1.54 ± 0.04 (Herbivores)
	Functional group	1,20	115.23	**<0.0001**		1.05 ± 0.03 (Predators)
	Interaction	1,20	3.91	0.17		0.08 ± 0.01 (Parasitoids)
Herbivores	Area	1,10	13.04	**0.001**	0.16 ± 0.03	1.30 ± 0.13 (Edge)
	Position	1,11	6.47	**0.011**		1.11 ± 0.07 (Interior)
	Interaction	1,10	0.23	0.63		
Predators	Area	1,10	4.03	**0.04**	0.11 ± 0.05	0.54 ± 0.07
	Position	1,11	0.79	0.38		
	Interaction	1,10	2.93	0.09		
Parasitoids	Area	1,10	17.84	**<0.0001**	0.17 ± 0.02 (Edge)	0.02 ± 0.02 (Edge)
	Position	1,11	0.41	0.37		0.13 ± 0.05 (Interior)
	Interaction	1,10	10.73	**0.001**	0.03 ± 0.03 (Interior)	
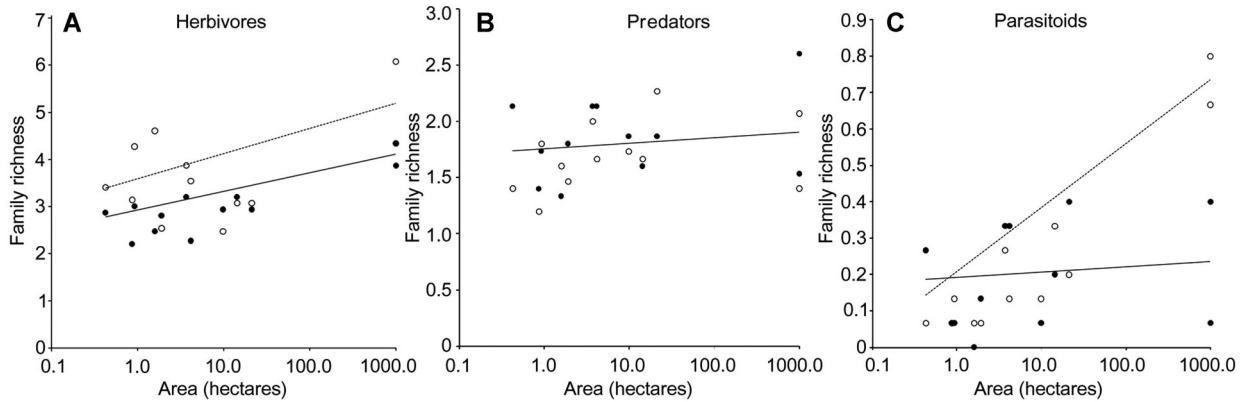
Fig. 2 Relationships between forest area and family richness of herbivores (A), predators (B), and parasitoids (C) for edge (empty circles) and interior (solid circles) positions. Dashed lines represent the regression line for edge and solid lines for interior. In (B) the regression line applies to both positions.

shown consistent effects of fragment area and rather heterogeneous edge effects on three functional groups of arthropods associated to native forest vegetation. Also, the composition of herbivore, predator, and parasitoid family assemblages was linked to these habitat fragmentation components.

In agreement with our expectations, the reduction of forest fragment area resulted in impoverished herbivore, predator, and parasitoid assemblages being found on the native vegetation. These results are consistent with those reported for insects developing within plant leaves (i.e., leaf miners and their parasitoids) in the same region (Cagnolo *et al.*, 2009), and also with most studies on habitat loss effects on species richness (see the review by Watling & Donelly, 2006; Rybicki & Hanski, 2013). However, our results did not support predictions from the trophic level hypothesis (Holt *et al.*, 1999), which could be due to conflicting trends such as the degree of specialization within each functional group (Drakare *et al.*, 2006). For example, the predominantly narrow host ranges of herbivores (Schoonhoven *et al.*, 2005) could increase their vulnerability to habitat loss, thus compensating for trophic
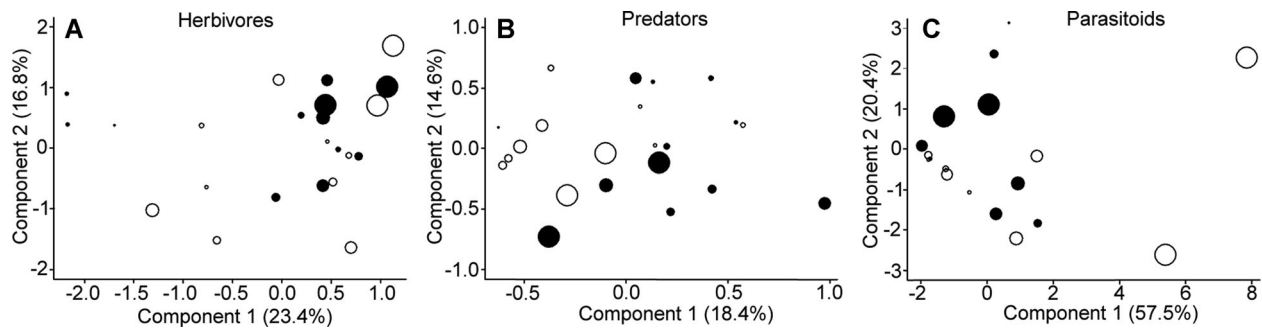
Fig. 3 Biplots of the principal component analysis based on family abundances of (A) herbivores, (B) predators, and (C) parasitoids. For each axis, the amount of variance explained is provided. Empty circles represent edge and solid circles interior positions. The size of the circles is representative of the forest area.

Table 2 Results of indicator species analysis. Habitat refers to category of remnant size or position for which the family was an indicator. Indicator values (Ind-Val) and *P*-values (*P*) are provided.

Family	Habitat	Ind-Val	*P*
Chalcididae	Large remnants	66.0	0.008
Noctuidae	Large remnants	67.1	0.003
Thomisidae	Large remnants	82.0	0.007
Acrididae	Edge	71.6	0.020
Chalcididae	Edge	53.6	0.040
Meloidae	Edge	41.7	0.040
Phytoseiidae	Edge	60.3	0.020
Thripidae	Edge	46.9	0.030

rank-related differences with their consumers. Moreover, the effects of area loss on biodiversity appear to be complex and modulated not only by specific traits but also by ecological interactions among organisms (Valladares *et al*., 2012).

Edge effects, that is, physical and biotic changes resulting from the creation of abrupt, artificial limits between two systems (Bierregaard, 2001), can have a crucial role for biodiversity in fragmented landscapes (Laurance *et al*., 2007). They are likely to interact with the effects of fragment size (Didham *et al*., 2012), although this interaction has seldom been explicitly analyzed. In this context, different trends were shown in the plant-related arthropod communities from Chaco Serrano. Such heterogeneity is not surprising, since inconsistency has been signaled as the norm rather than the exception in studies on edge effects (Ewers *et al*., 2007). Also, some effects may not have been fully captured by our study design, since edge effects may extend up to 100 m into some forests (Yu *et al*., 2006; Baker *et al*., 2013).

On the one hand, herbivores appeared to benefit from edge conditions, supporting the pattern reported by Wirth *et al*. (2008). Increased richness at the forest edge could result from the possibility of access to both forest and matrix resources, or from resource mapping, if plant resources are more abundant or have better quality at the edges (Ries *et al*., 2004; Wirth *et al*., 2008). In smaller remnants, with higher proportion of edge habitat, edge conditions could become dominant and edge–interior differences in biotic and physical conditions could become blurred. However, herbivore family richness showed similar variations for plants situated either at edge or the interior along the range of fragment sizes, suggesting an influence from the matrix (Kupfer *et al*., 2006; Ewers *et al*., 2007) rather than vegetation quality changes, as a possible explanation for the positive edge effect. The lack of relationship between richness and density of the specific sampled plants (see Materials and methods section) also supports this reasoning.

On the other hand, natural enemies showed edge effects only for parasitoids, and interacting with those of area: parasitoids were more diverse at the edge than at the interior in big remnants, with differences fading in small ones. This pattern could be linked to favorable conditions at the edge, such as improved host finding due to increased light incidence (Valladares *et al*., 2006), combined with the area effect *per se*. In larger remnants, richer parasitoid communities and marked differences between edge/interior conditions would provide more parasitoids moving from the shaded interior to the luminous edges, whereas in small remnants a reduced parasitoid community would move indistinctly between edge and interior habitats with rather similar light conditions. Importantly, high diversity of parasitoids at the edges of large forest remnants could be a positive aspect for the ecosystem service of pest control and its transfer to the cultivated matrix (e.g., Bianchi *et al*., 2008).

We have used taxonomic families as a surrogate of species richness, an approach previously used in other studies on insect communities (e.g., Vance *et al*., 2007; Hillstrom & Lindroth, 2008; Bennet & Gratton, 2012) and recognized as a practical, fast way to perform biomonitoring programs in highly diverse systems (Williams & Gaston, 1994). Although patterns observed at this taxonomic level may have blurred or masked some species-specific responses, such limitations are compensated by the possibility of detecting general trends in a large group of organisms, such as arthropods on plants. Moreover, similar arthropod community responses to forest disturbance at species, genus, and family level have been reported (Timms *et al*., 2013). In our study, using family level allowed us to detect both area and edge effects in the arthropod communities found on native plants in Chaco Serrano.

Accompanying the changes observed on family richness, the taxonomic composition of arthropod assemblages varied with forest area, for all three functional groups. Surprisingly, edge effects were found on predator assemblages, possibly reflecting changes in the abundance of particular predator families with varying degrees of resilience to the new conditions resulting from fragmentation.

Although Indicator Species Analysis was intended to use at species level (Dufrêne & Legendre, 1997), we argue that extending its use at family level would allow the detection of groups of species responding to habitat fragmentation in a similar way. This analysis revealed Noctuidae as a sensitive family to forest remnant area, in agreement with a general trend for Lepidoptera species to be markedly affected by fragmentation (e.g., Summerville & Crist, 2001; Veddeler *et al*., 2005; Ribeiro *et al*., 2012) and supporting their use as target group in biodiversity studies (Bonebrake *et al.*, 2010). Also, spiders and parasitoid wasps tend to be particularly sensitive to habitat loss (e.g., Gunnarson, 1988; Ozzane *et al.*, 1997; Kruess & Tscharntke, 2000; Cagnolo *et al.*, 2009; Anderson *et al.*, 2011), a trend supported by our recognition of Thomisidae spiders and Chalcididae wasps as indicators of large forest remnants. Indicator families were also identified for edge habitat, including generalist herbivores (Acrididae, Meloidae, and Thripidae), which tend to be more abundant at edges (Knight & Holt, 2005; Wirth *et al.*, 2008) and may benefit from access to resources in the matrix, for example, soybean crops (Reisig *et al.*, 2012). At higher trophic levels, the generalist predator mites Phytoseiidae and Chalcididae parasitoids were also identified as edge indicators, probably reflecting resource mapping (Ries *et al.*, 2004) to abundant crop pests. Species on both families have been used as successful biological control agents (Kostiainen & Hoy, 1996; Waterhouse, 1998). These results provide a basis for future research on the use of family indicators for rapid assessments in short-term studies, and for further examination at species level in order to understand the underlying mechanisms.

To our knowledge, no other study has simultaneously examined the effects of habitat area and edges on family richness and composition of herbivore, predator, and parasitoid arthropod assemblages in Neotropical dry forests. Our results have shown that forest fragmentation affected richness and composition of arthropod communities found on native vegetation in Chaco Serrano, through area and edge effects. Area effects were consistently important for all three functional groups studied, reinforcing the major role of habitat area for biodiversity conservation (He & Hubbell, 2011) and indicating that the dramatic loss of forest experienced in the region (Zak *et al.*, 2004) has negative consequences that could be leading to local extinctions of entire families of arthropods. The more heterogeneous responses to edge effects need deeper examination including the forest–matrix interactions, since the resources offered by crops could lead to movements of herbivore and natural enemy arthropods across the landscape (Ries *et al.*, 2004). Almost two thirds of the invertebrate species found in an agricultural landscape depend on nearby natural or seminatural habitats (Duelli & Obrist, 2003), thus maintenance of forest fragments is important not only for conservation purposes, but also to ensure arthropod-provided ecosystem services in the crops. Future studies in the Chaco ecosystem need to incorporate the forest–crop matrix interactions on a landscape scale in order to understand the reciprocal positive and negative effects for both systems.

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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. List of sampled orders and families. For each of the families, the total abundance and the functional group are provided.