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# Forest remnants contribute to parasitoid conservation: experimental evaluation of parasitism on a leafminer host

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**Abstract** Worldwide, intense forest fragmentation has resulted in mosaic landscapes in which biodiversity and a number of important ecological processes are threatened. Insect parasitism is a vital component of herbivore population regulation, hence the study of parasitism and parasitoid richness in fragmented forests embedded in an agricultural matrix is relevant from conservation and management perspectives. Here, we investigated through experimental field exposure of the leafminer *Liriomyza commelinae* (Diptera: Agromyzidae) the effects of forest remnant size and edge/interior location on parasitism, species richness and parasitoid community composition. Two consecutive experiments were performed in which pots with mined plants were placed in remnants of Chaco Serrano forests in Central Argentina. Parasitism levels (on average above 50 %) and number of parasitoids species (in total, 20 species) were independent of forest remnant size. However, higher parasitism and species richness were found at the forest edge compared with the interior although the differences in species richness failed to reach statistical significance. Parasitoid community composition was not related to forest size whereas assemblages from interior habitats showed closer similarity than those from the edges. The results suggest forest remnants could play an important role as reservoirs of parasitoids with potential to control crop pests, a possibility heightened by the positive edge effects which could facilitate the transfer of

this valuable ecosystem service to the adjacent cultivated land.

**Keywords** Parasitoid richness · Remnant size · Edge effect · Field experiment · Habitat fragmentation

## Introduction

Landscape fragmentation by human activities like agriculture (Vitousek 1997) leads to progressive subdivision of natural habitats into smaller and isolated patches with an increased edge surface (Saunders et al. 1991; Laurance 2008). This phenomenon has been pointed out as one of the main causes of biodiversity loss (Sala et al. 2000; Tscharntke et al. 2012) affecting also a number of key ecological processes like herbivory (e.g. Thies et al. 2003), pollination (e.g. Aizen and Feinsinger 1994) and parasitism (e.g. Kruess and Tscharntke 2000).

Parasitoid insects, whose larvae develop by feeding on other insects and ultimately cause their death, are involved in the regulation of herbivorous populations (Hawkins et al. 1997; Hassell 2000; Rauch and Weisser 2007). Reduction of parasitoid populations could in turn trigger herbivory increases by releasing herbivores from top-down control (Kruess and Tscharntke 1994). Because of their higher position in the food chains, parasitoids are expected to be more affected by habitat fragmentation than their hosts (Holt et al. 1999; Thies et al. 2003). Reduced parasitism levels have been recorded in smaller habitats (Kruess and Tscharntke 2000; Valladares et al. 2006), and such reduction can be linked to parasitoid species loss (Kruess and Tscharntke 2000; Fenoglio et al. 2012). However, not all parasitoids species are equally affected: specialist and rare parasitoids appear to be

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most vulnerable to habitat loss (Cagnolo et al. 2009), while generalist parasitoid richness might even increase in small fragments (Monmany and Aide 2009).

Parasitism rates can also differ between the interior of the habitat and the artificial edges created by fragmentation, with positive (Roth et al. 2006; Valladares et al. 2006; Woodcock and Vanbergen 2008), negative (Cronin 2003) or no edge effects (McGeoch and Gaston 2000; Elzinga et al. 2005) being reported in various fragmented systems. Microclimatic changes at the remnant boundaries, including lower humidity, higher temperature and higher light incidence (Murcia 1995; Davies-Colley et al. 2000), can affect abundance, diversity and behaviour of parasitoids (Tschardt et al. 2002; Reeve and Cronin 2010). Edge-driven effects could depend on intrinsic characteristics of parasitoid species (e.g. dispersion, foraging and searching capability) and also, on the level of contrast between the original habitat and the matrix (Murcia 1995; Ries and Sisk 2010). Edge effects could strongly influence the parasitism patterns at the landscape level, particularly in highly fragmented systems with increased proportion of edge habitat (Ries et al. 2004; Fletcher 2005).

Here we study, through field experiments, the effects of remnant size and edge location on percent parasitism, species richness and community composition of parasitoids on a leafminer host, in a fragmented Chaco Serrano forest from Central Argentina. This system is part of the most extensive dry forest in South America (Moglia and Giménez 1998), a biome with a high level of habitat conversion to agricultural lands in the last decades (Aide et al. 2012). In the study area, 94 % of forest has been cleared in only 30 years (Zak et al. 2004). A handful of observational studies have investigated area (Monmany and Aide 2009; Schnitzler et al. 2011) and/or edge effects (McGeoch and Gaston 2000; Woodcock and Vanbergen 2008) on parasitism levels in fragmented forests. However, an experimental approach allowing to relate more directly parasitism and forest fragmentation variables is almost absent, with the exception of a host density manipulation experiment analyzing parasitism by three individual parasitoid species in continuous forest versus fragments (Roth et al. 2006). As far as we know, this is the first experimental study simultaneously addressing parasitism and parasitoid species richness in relation to remnant size and edge effects in a fragmented forest.

Previous observational data have shown higher percent parasitism associated to higher parasitoid diversity on leafminers in larger remnants and at the edges of Chaco Serrano forests (Valladares et al. 2006), with the area-related pattern being driven by specialist parasitoids and host abundance (Fenoglio et al. 2012) whereas edge effects could be linked to improved host location due to higher light incidence, for visually hunting parasitoids (Salvo and Valladares 2004). By experimentally exposing a host

which is rare in the forest (Cagnolo 2006) and associated with generalist parasitoids (Fenoglio et al. 2009), we explore parasitism by generalist parasitoids while avoiding local host abundance effects on parasitism. Specifically, our predictions are (1) the size of forest remnants will have weak or no effects on either parasitoid species richness or percent parasitism, because only generalist parasitoids will be involved; (2) parasitism and species richness will differ between the forest edge and the interior, reflecting the different microenvironmental conditions in both habitats and (3) parasitism will be associated to parasitoid species richness, assuming a positive relationship between species richness and functioning. Additionally, we looked for changes in parasitoid community composition in relation to forest size and edge effects.

## Materials and methods

### Study site

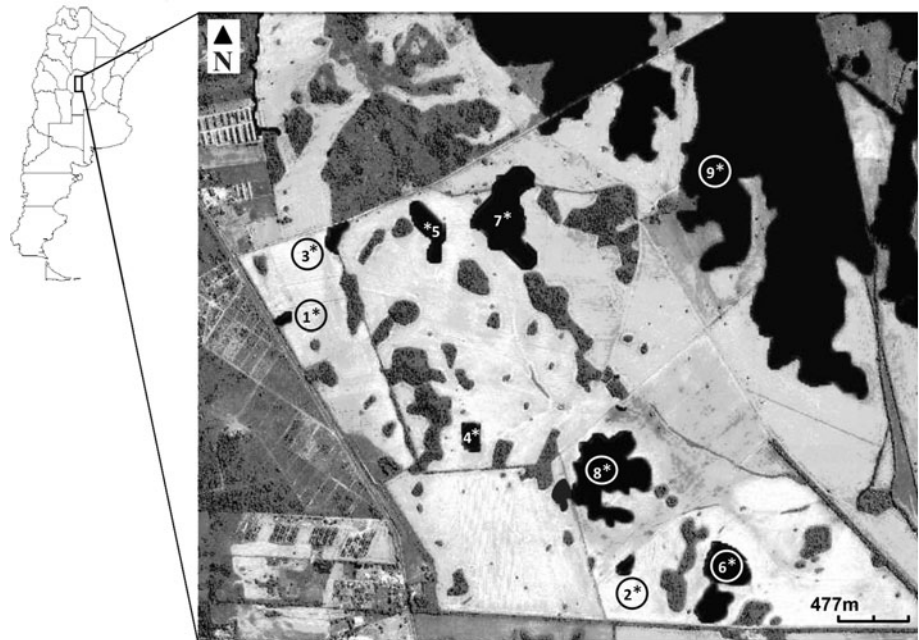
The study was performed in an area of Chaco Serrano forest (31°09'S to 31°13'S and 64°13'W to 64°17'W) in central Argentina. The climate in the study area is warm temperate to subtropical, with 10 °C minimum and 26 °C maximum mean temperatures and 750 mm annual rainfall (Moglia and Giménez 1998). Currently the forest is represented by a highly fragmented mosaic of patches surrounded by a predominantly agricultural matrix (Zak et al. 2004), mostly soya or maize in summer when the experiment was carried out. Nine remnants ranging from 0.4 to 1,000 ha, were selected through digital satellite images and on-site observations, in order to cover a forest size gradient (Fig. 1). All forest remnants had been isolated for at least 40 years, with an average distance of  $316 \pm 105$  m to the nearest larger fragment, and average elevation of  $632 \pm 5$  m.

### Study system

We studied the parasitoid assemblages on the specialist leafminer *Liriomyza commelinae* (Frost, 1931) (Diptera: Agromyzidae) developing on its natural host plant *Commelina erecta* L. (Commelinaceae). The plant and leafminer proved fairly tolerant to manipulation in previous studies (Fenoglio et al. 2010), therefore providing a suitable model system to carry out field experiments. *C. erecta* is a perennial herb widely distributed in natural, urban and cultivated habitats in north and central Argentina (Sérsic et al. 2006), with low abundance—0.07 % of total cover—in the study area (Cagnolo 2006). The leafminer *L. commelinae* feeds on species within Comelinaceae; in Argentina has been exclusively found on *C. erecta* (Valladares 1984) and mainly on disturbed sites (Fenoglio and Salvo 2009). Larvae



**Fig. 1** Location of the forest remnants where experiments were carried out. *Circles* indicate remnants used in the study of area effects (2008, 2009), *asterisks* indicate remnants used in the study of edge effects (2009)



develop inside the leaf lamina, pupae remain in the mine and adults emerge after approximately 13–15 days from egg deposition (Smith 1987).

Twenty-five parasitoid species have been recorded on *L. commelinae* in the study region. These species are mostly primary, solitary larval or larval–pupal Hymenoptera parasitoids, with wide host ranges in the region (Fenoglio and Salvo 2009). Among parasitoids of leafminers, obligate hyperparasitism is rare (Askew 1975) and we know of no records of hyperparasitoids associated with *L. commelinae* (Fenoglio & Salvo 2009). The leafminer populations usually sustain high parasitism levels, fluctuating between 32 and 71 % in urban sites (Fenoglio et al. 2010).

#### Field experiments

Two field experiments were performed in April 2008 and 2009. Plants of *C. erecta* were collected in the campus of Córdoba National University and any mined leaves removed. Plastic pots (30 cm × 12.5 cm, 13 cm deep) containing 3–5 plants were placed in cages (cardboard and voile, 60 cm × 36 cm × 36 cm deep) with 4 females and 2 males of *L. commelinae* (from a laboratory colony) per pot during 70 h to allow mating and oviposition (following methodology from Salvo et al. 2005). Two days later, after checking larval emergence, plants were taken to the field sites.

#### Remnant size

The effects of remnant size on parasitism, species richness and community composition were evaluated in both experiments. Three and two pots with mined plants were

placed on 2008 and 2009 respectively, in the interior (20–25 m from the outer boundary) of six forest remnants. In all cases, the experimental plants were placed under the canopy of *Celtis ehrenbergiana* (Klotzsch) trees to reduce possible effects of environmental heterogeneity on the measured variables. After 10 days exposure the plants were taken to the laboratory and mined leaves were kept in plastic bags until adult flies and parasitoids emerged. Parasitoids were identified and percent parasitism were calculated as  $[(\text{parasitoid adults} \times 100)/(\text{parasitoid adults} + \text{L. commelinae adults})]$ .

#### Interior/edge location

Edge effects on parasitism, species richness and community composition were studied in 2009. Two mined *C. erecta* pots were placed at the edge (within two meters from the outer limit of the forest), and two pots in the interior (as described above) of nine forest remnants, including the six remnants used in the study area. In all cases, the pots were placed in southeast facing edges. The effects of area and its interaction with interior/edge location were also investigated in this experiment.

#### Data analysis

Remnant size effects on parasitism and species richness were analyzed by means of mixed linear models (Zuur et al. 2009) with percentage parasitism or species richness as response variables and remnant size as explanatory variable. Year was added to the models as a random factor to account for annual variability. A linear model using the

number of mined leaves in each experimental pot as the response variable, with year and area as fixed factors, was performed in order to avoid biases due to variation in resource availability for parasitoids.

The effects of interior/edge location were evaluated through mixed linear models with percentage parasitism or species richness as response variables, location as fixed factor and site (remnant) as random factor to account for the non-independence of edge and interior from the same remnant. Also, remnant size and its interaction with location were included in these models and then were simplified removing non significant variables. In all mixed linear models, percent parasitism and remnant size were arcsine and log transformed respectively to satisfy parametric assumptions. Data obtained from the three pots within a fragment (2008) and from the two pots within a position (2009) were pooled to avoid pseudoreplication. In order to avoid biases due to variation in resource availability for parasitoids, we also performed mixed linear models with the number of mined leaves in each experimental pot as the response variable.

Parasitoid species composition was studied through correspondence analysis (Legendre and Legendre 1998), using abundance data of parasitoid species in the 2009 experiment to explore similarities in assemblages according to interior/edge location and remnant size (by correlating eigenvalues of first and second axes from the correspondence analysis with remnant size).

To analyze if changes in percent parasitism were related to variations in species richness, simple linear regressions were performed with species richness as independent variable and parasitism as dependent variable. Three separate regressions were conducted with 2008 data and each location (interior and edge) in 2009.

In order to avoid biases due to factors other than area and edge/interior location, we checked the influence of isolation and elevation on percentage parasitism and parasitoid species richness, by linear regression analyses. All statistical analyses were performed using R 2.12.2 software (R Development Core Team 2011).

## Results

In all, 996 adult insects (flies plus parasitoids) were recovered from both experiments, 60 % of them being parasitoids. Twenty species of parasitoids were identified (Table 1), in Eulophidae, Figitidae, Pteromalidae and Braconidae (Hymenoptera Parasitica).

### Remnant size

In the experiments aimed to evaluate remnant size effects, parasitism levels on *L. commelinae* reached a mean value

of  $52 \pm 9$  %, varying from 0 to 100 % among forest remnants, but such variations were not related to remnant size ( $F_{1,9} = 0.91$ ,  $P > 0.1$ ; Fig. 2a). Between none and five parasitoid species were recorded in each remnant, with parasitoid richness also being independent of forest size ( $F_{1,9} = 0.65$ ,  $P > 0.1$ ; Fig. 2b). Bias of the results due to variations in the amount of resource offered to parasitoids in the experiments was negligible, since the number of mined leaves in each pot ( $26 \pm 2$  mined leaves out of  $144 \pm 7$  total leaves) did not vary significantly with year or remnant size ( $F_{1,9} = 0.20$ ,  $P = 0.67$  for year;  $F_{1,9} = 2.81$ ,  $P = 0.13$  for remnant size).

Eigenvalues of first and second axes from correspondence analysis based on parasitoid species abundances were not significantly correlated to remnant size (Pearson correlation, first axis:  $r = -0.36$ ;  $P = 0.24$ ; second axis:  $r = -0.19$ ,  $P = 0.55$ ).

### Interior/edge location

Leafminer larvae sustained significantly higher percent parasitism on plants located at the edge in comparison with those in the interior of the forests ( $F_{1,8} = 8.4$ ,  $P = 0.02$ ; Fig. 3a) with no significant interactions between location and remnant size effects ( $F_{1,7} = 1.23$ ,  $P > 0.1$ ). Species richness showed a similar trend, ranging from 1 to 11 species at the edge and from 0 to 7 species at the interior, although these differences did not reach statistical significance ( $F_{1,8} = 3.58$ ,  $P = 0.09$ ; Fig. 3b), and were independent from remnant size (interaction:  $F_{1,7} = 0.46$ ,  $P > 0.1$ ). The amount of resource available to parasitoids in each pot [ $31 \pm 4$  mined leaves within  $165 \pm 6$  total leaves (interior) and  $36 \pm 6$  mined leaves within  $186 \pm 7$  total leaves (edge)] was independent of edge/interior location (mixed model:  $F_{1,8} = 0.38$ ,  $P > 0.05$ ), thus ruling out such variations as a source of bias for our results.

Examination of the correspondence analysis of parasitoid assemblage composition explained a 44 % of variance in the first two axes (Fig. 4) and suggested a distinction, albeit incomplete, between assemblages from edge and interior habitats, the latter being more closely grouped. In addition, three parasitoid species were exclusively recorded at the interior and eight species were only found at the forest edge (Fig. 5). The latter species caused relatively high percent parasitism (on average higher than 10 %), more than three times the average parasitism by parasitoid species found only in the interior, which may contribute to the differences in total parasitism between both locations.

Percent parasitism was not related to parasitoid species richness either in 2008 ( $R^2 = -0.01$ ,  $F_{1,4} = 0.93$ ,  $P > 0.1$ ) or in 2009 (interior:  $R^2 = -0.19$ ,  $F_{1,5} = 0.01$ ,  $P > 0.1$ ; edge:  $R^2 = 0.06$ ,  $F_{1,7} = 1.5$ ,  $P > 0.1$ ).

**Table 1** Parasitoid species recorded on *L. commelinae* through experimental exposure in Chaco Serrano forest remnants

Species	Abundance
<b>Eulophidae</b>	
<i>Chrysocharis caribea</i> (Bouček)	15
<i>C. flacilla</i> (Walker)	16
<i>C. vonones</i> (Walker)	159
<i>Chrysocharis</i> Förster sp. 1	136
<i>Chrysocharis</i> Förster sp. 2	54
<i>Chrysonotomyia</i> Ashmead sp. 1	31
<i>Chrysonotomyia</i> Ashmead sp. 2	11
<i>Diglyphus websteri</i> (Crawford)	37
<i>Proacrias thysanoides</i> (De Santis)	6
<i>P. xenodice</i> (Walter)	1
<b>Pteromalidae</b>	
<i>Halticoptera</i> Spinola sp. 1	2
Miscogasterinae sp. 1	1
Miscogasterinae sp. 2	2
<i>Thinodytes</i> Graham sp. 1	1
<b>Braconidae</b>	
<i>Phaerotoma luteoclypealis</i> (Van Achterberg and Salvo)	77
<i>Phaerotoma</i> Förster sp. 1	11
<i>Phaerotoma</i> Förster sp. 2	2
<i>Phaerotoma</i> Förster sp. 3	2
<i>Phaerotoma</i> Förster sp. 4	1
<b>Figitiidae</b>	
<i>Agrostocynips enneatoma</i> (Diaz)	23

The analysis of variables other than the target factors of this study, showed that neither isolation nor elevation showed significant effects on either parasitism (isolation:  $R^2 = -0.06$ ,  $F_{1,7} = 0.57$ ,  $P > 0.1$ ; elevation:  $R^2 = -0.07$ ,  $F_{1,7} = 0.48$ ,  $P > 0.1$ ) or parasitoid species richness data (isolation:  $R^2 = -0.02$ ,  $F_{1,7} = 0.84$ ,  $P > 0.1$ ; elevation:  $R^2 = 0.19$ ,  $F_{1,7} = 2.9$ ,  $P > 0.1$ ).

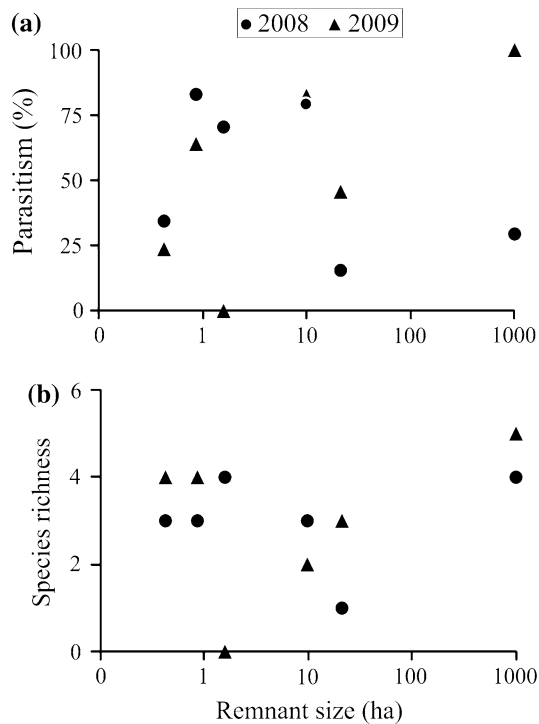
## Discussion

In the present work we have explored, through experimental host exposure, remnant size and edge effects on parasitism levels, species richness and parasitoid community composition. Both percent parasitism and the number of parasitoid species supported by the leafminer host were independent of forest size, but we found higher percent parasitism and a tendency to larger parasitoid assemblages when the hosts were placed at the forest edge in comparison with those at the interior. Such results are particularly interesting from a perspective of landscape conservation.

The experimental exposure of *L. commelinae* larvae to forest parasitoids was notably successful in terms of the high parasitism levels obtained, with over 50 % of exposed larvae being parasitized on average, thus reaching similar levels to those sustained by this host in its more common habitats (Fenoglio and Salvo 2009). Also, the forest remnants provided 20 species able to parasitize this host in the short time of the experiments here reported, which compares extremely favourably with the 20–25 species recorded in studies encompassing larger spatial and temporal scales in urban environments (Fenoglio and Salvo 2009; Fenoglio et al. 2010). It must be noted that the experimental host here employed shares parasitoids with the worldwide leafminer pest *Liriomyza huidobrensis* (Blanchard). Thus, Chaco Serrano forest remnants could act as reservoirs of generalist parasitoids for potential pests.

We observed no relationship between percent parasitism and remnant size, in accordance with studies in other forests (Roth et al. 2006; Schnitzler et al. 2011) and in semi-natural grasslands (Brückmann et al. 2011). Even higher parasitism in smaller fragments has been reported in other systems (Roth et al. 2006; Woodcock and Vanbergen 2008; Monmany and Aide 2009). In our study, this outcome could be expected from the generalist habit of parasitoids exploiting *L. commelinae* (Fenoglio and Salvo 2009). Reduction of parasitism in smaller forests has been linked to the loss of specialist parasitoids (Fenoglio et al. 2012) which have proven extremely vulnerable to fragmentation of Chaco Serrano (Cagnolo et al. 2009). Instead, generalist species have the possibility to switch to different hosts—as did the parasitoids colonizing our experimental larvae—thus their populations may remain unaltered or even benefit from habitat fragmentation (Monmany and Aide 2009; Brückmann et al. 2011). However, it must be noticed that several works have showed negative effects of habitat loss on parasitism (e.g. Kruess and Tschardtke 2000; Thies et al. 2003; Elzinga et al. 2005). Multiple factors, including spatial scale, system complexity, host and habitat specialization, body size, mobility, among others, may underlie the relationship between parasitism and habitat size (Tschardtke et al. 2002). From our results, in the Chaco Serrano forest a group of parasitoids could maintain high levels of parasitism, which would enhance the conservation value of small forest fragments embedded in an agricultural matrix.

The positive edge effects on parasitism along the forest size gradient is in agreement with the pattern previously found by Valladares et al. (2006), for total parasitism on leafminer communities in fragmented Chaco Serrano forests. Higher percent parasitism at the edge could be associated to the greater species richness in this location, since nearly three times more species were reared exclusively at the edge. However, species richness failed to reach

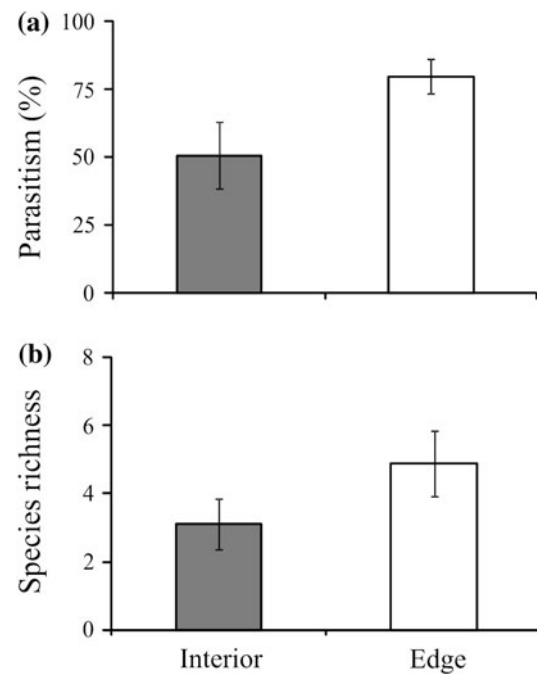


**Fig. 2** Percent parasitism (a) and parasitoid richness (b) on *L. commelinae* in relation to Chaco Serrano forest remnant size in 2008 (circles) and 2009 (triangles). No significant effect of remnant size on parasitism ( $F_{1,9} = 0.91$ ,  $P > 0.1$ ) or species richness ( $F_{1,9} = 0.65$ ,  $P > 0.1$ )

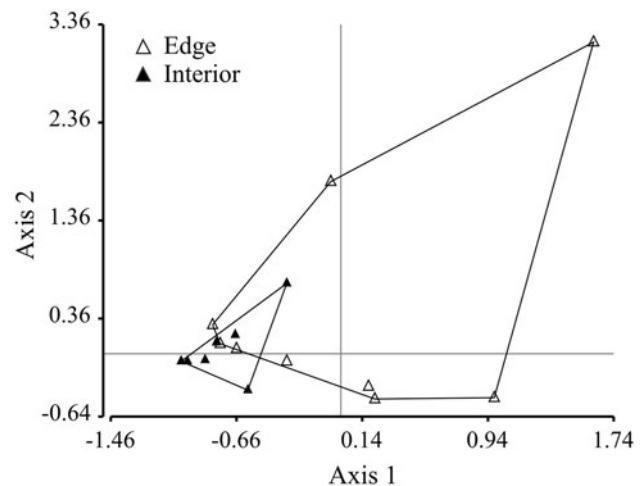
significant differences between the two locations, neither was it related to percent parasitism.

Parasitoid assemblages at the interior showed a closer resemblance than those found at the forest edges suggesting a greater turnover of species in the latter. This composition pattern might explain the lack of significant differences in species richness, and contribute to the differences in parasitism, since each edge-exclusive species caused on average three times higher percent parasitism in comparison with those found exclusively at the interior (see Fig. 5). Higher parasitism at the edges could be linked to enhanced sunlight exposure (Davies-Colley et al. 2000; Weathers et al. 2001) which could facilitate host searching by visually hunting leafminer parasitoids (Casas 1988; Salvo and Valladares 2004). Another possibility involves parasitoids staying longer in forest boundaries as a negative response to cross the inhospitable matrix (Fagan et al. 1999; Roth et al. 2006), although we were not able to discriminate among the different possible mechanisms leading to the observed higher parasitism in forest borders.

Our experiments allowed us to control for host abundance, which was an underlying factor for community parasitism patterns in fragmented Chaco Serrano (Fenoglio et al. 2012). Considering that *L. commelinae* is usually rare in the forest (Cagnolo 2006) and given the small size of our



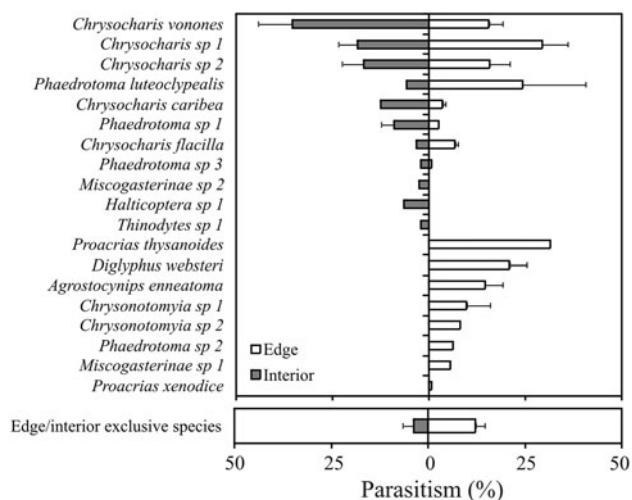
**Fig. 3** Mean ( $\pm$ SE) percent parasitism (a) and parasitoid richness (b) on *L. commelinae* at interior (grey bars) and edge (white bars) locations in Chaco Serrano forest remnants. Significant differences among edge and interior for parasitism ( $F_{1,8} = 8.4$ ,  $P = 0.02$ ), but not for species richness ( $F_{1,8} = 3.58$ ,  $P = 0.09$ )



**Fig. 4** Correspondence analysis ordination of parasitoid assemblages associated to *L. commelinae* mines on *C. erecta* plants located at the interior (black triangles) and edges (white triangles) of forest remnants. First and second axis of the ordination explained 24 and 20 % of variance respectively

experimental patches within remnants offering at least 40 other hosts (Cagnolo et al. 2009), the high parasitism levels by the 20 species here observed suggest that parasitoid communities retain the capability to detect and attack new or commonly absent hosts, even in small forests. Moreover, higher parasitism levels and richer parasitoid assemblages





**Fig. 5** Percent parasitism (mean  $\pm$  SE of all sites where species occurred) caused by each parasitoid species on *L. commelinae* at the interior (grey bars) and edge (white bars) of forest remnants in 2009. The lower section shows average parasitism caused by species found exclusively at either edge or interior location

at the edge of the forests suggest also a plausible extension of this service to the agricultural matrix, given the recognized role of edges as interfaces for the exchange of organisms between natural and cultivated systems (Blitzer et al. 2012).

Considering the current situation of Chaco forests, which are disappearing at an alarming rate with consequences not yet properly evaluated or understood, this work highlights the essential role of forest remnants for the conservation of important ecological processes. Having in consideration that habitat fragmentation represents one of the main threats for biodiversity and several ecological processes, we have shown that Chaco Serrano forest remnants could act as reservoirs of generalist parasitoids for potential pests, providing biological control services to the crop matrix (Landis et al. 2000). Our results suggest that conservation of forest remnants, would contribute not only to preserve natural biodiversity but also to sustainable pest management strategies for agroecosystems. This possibility deserves further investigation to encompass different systems and multiple ecosystem services.

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