

Not all in the same boat: trends and mechanisms in herbivory responses to forest fragmentation differ among insect guilds

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Abstract Habitat fragmentation can alter fundamental ecological interactions such as insect herbivory. Few studies of habitat fragmentation effects on herbivory have examined the mechanisms involved, and differences among insect guilds have been largely ignored. Here, we studied area and edge effects on herbivory by three guilds of phytophagous insects in a fragmented Chaco Serrano forest. We estimated herbivory levels on native *Croton lachnostachyus* plants and assessed plant availability (distance to nearest conspecific) and quality indicators (leaf water, carbon and nitrogen content), as well as richness and abundance of the associated insect community, in order to explore mechanisms underlying herbivory changes. Herbivory by chewing and sap-sucking insects decreased, and herbivory by leaf miners increased in plants growing at the forest edge, compared with those at the interior. Forest area effects were detected only in interaction with edge effects on chewing, leaf mining and total herbivory. Lower herbivory at the edge appeared to be mediated by changes in leaf water and nitrogen content for sap-sucking herbivory, and linked to strong direct effects for chewing damage and total herbivory. Instead, higher damage levels by leaf miners at the forest edge seemed to be driven by increased plant availability and lower water content. Further studies

are needed to unravel the factors involved in the strong direct effects detected here for all herbivory types. These results emphasize the necessity to consider differential responses from diverse phytophagous insect guilds, and factors operating at multiple levels, in order to disentangle, and ultimately understand, forest fragmentation effects on herbivory.

Keywords Insect herbivory · Phytophagous guilds · Chaco Serrano · *Croton lachnostachyus* · Fragment area · Edge effects

Introduction

Habitat fragmentation is a major threat to natural ecosystems at world-wide scale (Sechrest and Brooks 2002). This process involves profound landscape alterations by which large, continuous habitats are divided into a greater number of smaller patches, isolated from each other by anthropogenic matrix and with increasing ratio of edge to interior habitats (Fahrig 2003; Didham 2010; Didham et al. 2012). A growing body of evidence shows disruption of trophic interactions as a consequence of habitat fragmentation (e.g. Aguilar et al. 2009; Hagen et al. 2012; Valladares et al. 2012). Among such interactions, insect herbivory has been widely studied because of its significant impact on plant growth and reproduction (Crawley 1989; Aide and Zimmerman 1990), affecting plant community structure and diversity (Olf and Ritchie 1998; Allan and Crawley 2011).

Studies of habitat fragmentation effects on insect herbivory have most frequently shown a decrease in herbivory with the loss of habitat area (e.g. Arnold and Asquith 2002; Valladares et al. 2006; Vásquez et al. 2007; Simonetti et al. 2007; Savilaakso et al. 2009; Ruiz-Guerra et al. 2010).

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There is also evidence of herbivory being affected by edge conditions (Valladares et al. 2006; Wirth et al. 2008), fragment isolation (Lienert et al. 2002; Elzinga et al. 2005) and matrix effects (Haynes and Crist 2009). Such changes in insect herbivory rates could be related to altered resource availability or quality, since habitat fragmentation has been shown to affect plant density (Lienert and Fischer 2003; Valdivia 2011) and leaf traits (Silva and Simonetti 2009; Ishino et al. 2012). Furthermore, changes in herbivore populations (Savilaakso et al. 2009; Haynes and Crist 2009) or changes in the control of herbivore populations exerted by their natural enemies (Kruess and Tschamtkke 1994; De La Vega et al. 2012) may lead to altered insect herbivory in fragmented habitats.

Regarding plant availability, several studies have reported plant diversity loss (i.e. Cagnolo et al. 2006, 2009; Krauss et al. 2010; Marini et al. 2012) and reduced plant population size (Piotti 2009; Leimu et al. 2010; Vranckx et al. 2012) as fragment area decreases. Also, altered abiotic conditions at the edges, including higher temperature, greater light incidence and lower relative humidity (Chen et al. 1993; Davies-Colley et al. 2000; Christianini and Oliveira 2013), could affect plant seed germination (Ashworth and Martí 2011) and tree mortality (Murcia 1995; Laurance et al. 2000). Plant species with reduced populations may sustain lower herbivory levels according to the resource concentration hypothesis (Root 1973; Connor and McCoy 2001).

Plant quality, playing an essential role for host selection and consumption in herbivores (Schoonhoven et al. 2005), could also explain herbivory alterations in fragmented habitats (Fáveri et al. 2008; Silva and Simonetti 2009). For example, plants in small fragments may have smaller, thicker leaves with lower nitrogen content than plants in continuous forests (Repetto-Giavelli and Cavieres 2007; Silva and Simonetti 2009), whereas plants growing at the forest edge may have lower water content and higher concentration of carbon-based secondary compounds than plants in the interior (Ishino et al. 2012). These changes could impact on leaf palatability, reducing levels of insect herbivory. However, few studies have investigated plant-mediated effects of habitat fragmentation on herbivory (Fáveri et al. 2008; Silva and Simonetti 2009).

Changes in insect populations may also drive herbivory changes in fragmented habitats. An important consequence of habitat reduction is species loss (Koh et al. 2010; Rybicki and Hanski 2013), a pattern that has often been demonstrated for herbivore communities (Barbosa et al. 2005; De la Vega and Grez 2008; Cagnolo et al. 2009; Haynes and Crist 2009; González et al. 2014), with likely consequences on herbivory levels (Savilaakso et al. 2009; De La Vega et al. 2012). On the other hand, because of their higher trophic-level position, natural enemies may be more vulnerable to fragmentation than herbivores (Tschamtkke and Brandl 2004; Cagnolo et al.

2009), leading to reduced natural control and higher herbivory levels in small fragments (e.g. Thies et al. 2003). Likewise, it has been suggested that herbivory may decrease at the edges as a result of increased pressure from natural enemies (Valladares et al. 2006; Wirth et al. 2008).

Herbivory patterns in fragmented forests should thus be the result of different mechanisms acting in concert. Although several works have studied the effects of habitat fragmentation on herbivory, few studies have examined the mechanisms involved (Ledergerber et al. 2002; Fáveri et al. 2008; Silva and Simonetti 2009; Wirth et al. 2008). Besides, herbivores from different feeding guilds may show different levels of vulnerability to fragmentation (Golden and Crist 1999), studies have usually pooled different guilds (Simonetti et al. 2007; Ruiz-Guerra et al. 2010; De La Vega et al. 2012) or considered only one type of damage, e.g. chewers (Arnold and Asquith 2002; Skoczylas et al. 2007; Savilaakso et al. 2009) or leaf miners (Valladares et al. 2006; Woodcock and Vanbergen 2008; Klapwijk and Lewis 2012).

Here, we studied insect herbivory on a native plant (*Croton lachnostachyus* Baill.) within Chaco Serrano forest, part of the most extensive dry forest in South America (Moglia and Giménez 1998) with a high level of fragmentation and conversion to agricultural lands (Aide et al. 2012). Specifically, we asked: (1) do fragment area and edge/interior location impact on insect herbivory and are different guilds equally affected? (2) Can differences in the extent of herbivory be explained by changes in plant traits and/or insect communities, associated to forest fragmentation? We expected herbivory to decrease with fragment area (mainly due to a loss of herbivore richness and abundance) and at the forest edge (as a consequence of microclimatic induced changes in plant quality). Also, we expected herbivory trends and mechanisms to vary among guilds, reflecting differences in their association with the plant hosts, due to differential specialization degree, dispersal capability, nutrient requirements, handling of leaf toughness and other physical or chemical defenses, and even natural enemy exposure (Huberty and Denno 2004; Andrew and Hughes 2005; Peeters et al. 2007; Novotny et al. 2012).

As far as we know, this is the first study simultaneously examining herbivory by three insect guilds in relation to area and edge effects, while also considering possible mechanisms involving plant and insect factors.

Methods

Study area and species

The work was carried out in a Chaco Serrano area (31°09'S–31°13'S and 64°13'W–64°17'W) in Córdoba, central

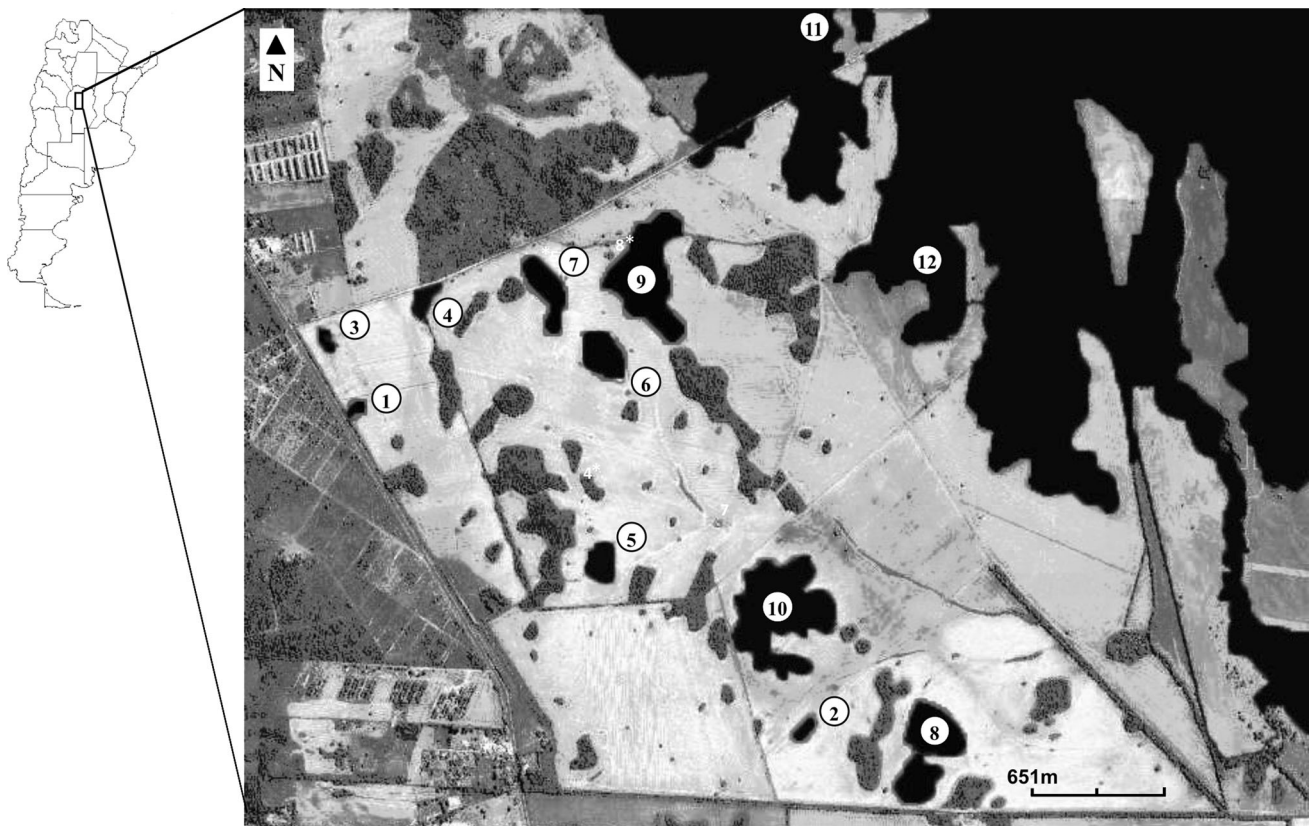


Fig. 1 Location of study area and remnants of Chaco forest where samplings were performed

Argentina. Climate in the region is warm–temperate, with 10 °C minimum to 26 °C maximum mean temperatures and 750 mm annual rainfall concentrated in the summer months (Moglia and Giménez 1998). The forest is currently restricted to a highly fragmented mosaic of forest patches within a predominantly agricultural matrix (Zak et al. 2004). Twelve sites were selected through digital satellite images and field observations, in order to cover a range of forest fragment sizes (0.43 to >1,000 ha) (Fig. 1). All forest remnants had been isolated for at least 40 years, with an average distance of 285 (± 84) m from the nearest larger fragment, and at 634 m asl (± 4 m). Fragment area was not correlated with distance to the nearest larger fragment (Pearson's correlation, $r = -0.44$, $t_{10} = -1.57$, $p > 0.1$) or elevation (Pearson correlation, $r = 0.26$, $t_{10} = 0.85$, $p > 0.1$). At each site, sampling was carried out in two locations: interior (20–25 m from the outer tree line), and edge (within 2 m from the tree line) of the forest. In the same study area, edge and interior habitats similarly defined have previously showed significant differences in herbivory by leaf mining insects (Valladares et al. 2006).

Croton lachnostachyus (Euphorbiaceae) is a native perennial shrub, commonly found in Chaco Serrano forest (Sérsic et al. 2006). This species was selected for the herbivory study because preliminary observations showed

that it occurs in sufficient densities in all the study sites, and their leaves are consumed by leaf mining, chewing and sap-sucking insects.

Herbivory

Insect herbivory was measured as standing levels of leaf damage towards the end of the growing season (May 2010), in order to assess cumulative herbivore damage. Few leaves may remain on the plants from previous seasons, but they are easily recognized by their reddish coloration (Sérsic et al. 2006) and were not included in the measurements. In seasonally dry forests like Chaco Serrano, insect abundance increases along the rainy season and rates of herbivory mirror this pattern (Coley and Barone 1996). Eight individuals of *C. lachnostachyus* at each site and location (edge/interior) and at least 5 m apart from each other, were randomly selected among healthy-looking sexually mature plants (Boege and Marquis 2005). We collected 25 fully expanded and randomly chosen leaves per plant (4,800 leaves in total) and took them to the laboratory to assess herbivory.

Leaf damage was attributed to chewing insects when parts of the lamina were missing, e.g. holes or incomplete leaf margins. Leaf mining damage was recognized as pale

linear or blotch marks (mines) on the leaf surface, where parenchymal tissue had been consumed leaving an internal tunnel covered by the intact epidermic layers. Sap-sucking damage was noticed as pale punctures or scrapes on the leaf surfaces.

Herbivory levels by chewing, leaf mining, sap-sucking and total phytophagous insects were estimated as percentage damaged leaves by each herbivore guild. In order to ensure consistency, measurements were always done by the same person (M.R.R.).

Host availability and quality

To assess whether plant availability varies with fragment area or interior/edge location, isolation was estimated as distance (m) to the nearest conspecific neighbour for all *C. lachnostachyus* plants used in herbivory estimations in the interior and edge of 11 of the studied fragments. From the same plants, 10–12 mature and healthy leaves/plant were collected in February 2010 to measure water, carbon and nitrogen content. Samples were stored in sealed plastic bags and kept in dark containers at 4–5 °C during transport to the laboratory. Leaves were pooled to provide a composite sample from the interior and another from the edge of each fragment. Samples were blotted dry using tissue paper to remove any surface water and immediately weighed. Samples were then oven-dried in paper bags at 60 °C until a constant weight was achieved, then reweighed to obtain a dry weight value. Leaf water content was estimated as (fresh weight – dry weight)/fresh weight and expressed as percentage (Cunningham et al. 1999). Carbon content was estimated as 50 % ash-free biomass (Gallardo and Merino 1993). Nitrogen content was measured by an Auto-analyser RFA 300-Alphen.

Insect community

We sampled insects on five *C. lachnostachyus* plants in the interior and five at the edge of each of the twelve studied forest fragments (120 individual plants). Sampling was conducted in January–February 2010, during the peak of insect activity. On each plant, insects were recorded through visual observation during a maximum of 15 min. Afterwards, plants were shaken on a white cloth to collect additional arthropods (Kogan and Herzog 1979). To avoid possible biases in the sampling due to interactions between collection time and size of forest fragments or location, large and small remnants, and edge/interior location within each remnant, were visited alternately. Furthermore, plants in the edge and interior of each fragment were also alternately sampled to avoid effects of daily variations. In the laboratory, all insects were identified to family level

(Triplehorn et al. 2005). Advantages and limitations of using this taxonomic level are addressed in the Discussion section. Each individual was assigned to one of two functional groups: phytophagous or natural enemies and the specimens not belonging to these groups were not considered in the analyses.

Data analysis

Data from herbivory were analysed using generalized linear mixed models (GLMMs) (Bolker et al. 2009) with location (edge/interior), fragment area (natural log transformed) and the interaction between them as fixed effects. Site (fragment) was included as a random factor to contemplate the spatial correlation between edge and interior of the same fragment (Faraway 2006). Herbivory was the response variable (as % leaves damaged by chewing, leaf mining, sap-sucking or total herbivores) and was modelled assuming binomial probability distribution and log link function.

Mixed linear models (LMM) (Zuur et al. 2009) with Gaussian distribution were performed to evaluate plant availability and leaf traits in relation to fragment area (log transformed) and location (as explanatory variables). Response variables were plant isolation and water, carbon and nitrogen content; no data transformation was required. The interaction between area and location was evaluated in all mixed models.

The insect community was analysed through GLMMs with family richness and abundance of herbivores or natural enemies as response variables, with a Poisson error distribution and a log link function. Fragment area (log transformed) and location were included as explanatory variables and site as random effect, considering also the interaction between area and location. All response variables were calculated as the mean values per plant in each fragment and location. Analyses were performed using the software R (R Development Core Team 2014; version 3.1.1) and the packages lme4 to fit GLMMs models and (Bates et al. 2011) nlmeto fit LMM (Pinheiro et al. 2013).

We conducted structural equation models (SEM) (Shipley 2000) to evaluate the direct and indirect effects of fragment area and location interior/edge on herbivory on *C. lachnostachyus*. We tested four models in total, one for each type of herbivory; variables included in each model were selected based on GLMM results. This one-model approach allowed us to evaluate the extent to which habitat fragmentation influenced herbivore damage through effects on plant availability and leaf traits and/or abundance of herbivores and natural enemies. For total herbivory, we performed a principal component analysis (PCA) on the three leaf traits (water, carbon and nitrogen content) to combine them in a single variable (the first PCA axis,

Table 1 Results of generalized mixed models evaluating fragment area and interior/edge location effects on insect herbivory on *C. lachnostachyus* in Chaco Serrano forest

Herbivory		Explanatory variables	F	df	p
Chewing	Damaged leaves (%)	Area	0.03	1	>0.1
		Location	180.62	1	<0.001
		Location \times area	63.60	1	<0.001
Sap-sucking	Damaged leaves (%)	Area	0.84	1	>0.1
		Location	335.71	1	<0.001
		Location \times area	0.01	1	>0.1
Leaf miner	Damaged leaves (%)	Area	1.31	1	>0.1
		Location	2	1	0.013
		Location \times area	4.19	1	0.039
Total herbivory	Damaged leaves (%)	Area	1.08	1	>0.05
		Location	67.25	1	<0.001
		Location \times area	36.86	1	<0.001

Significant relationships ($p < 0.05$) are shown in bold

explaining 46 % of the variability), in order to reduce the number of parameters and paths of the model. Location was involved in all SEM as dummy variable, with zero value assigned to interior and one to edge; thus, the observed effects refer to changes in the edge with regard to the interior, i.e. edge effects. Site was not included in the model since results of GLMMs and LMMs indicated lack

of effects of the random factor. Multi normality was checked with Mardia's multivariate normality test (Ullman 2006). SEM analyses were carried out using AMOS 5.0 software.

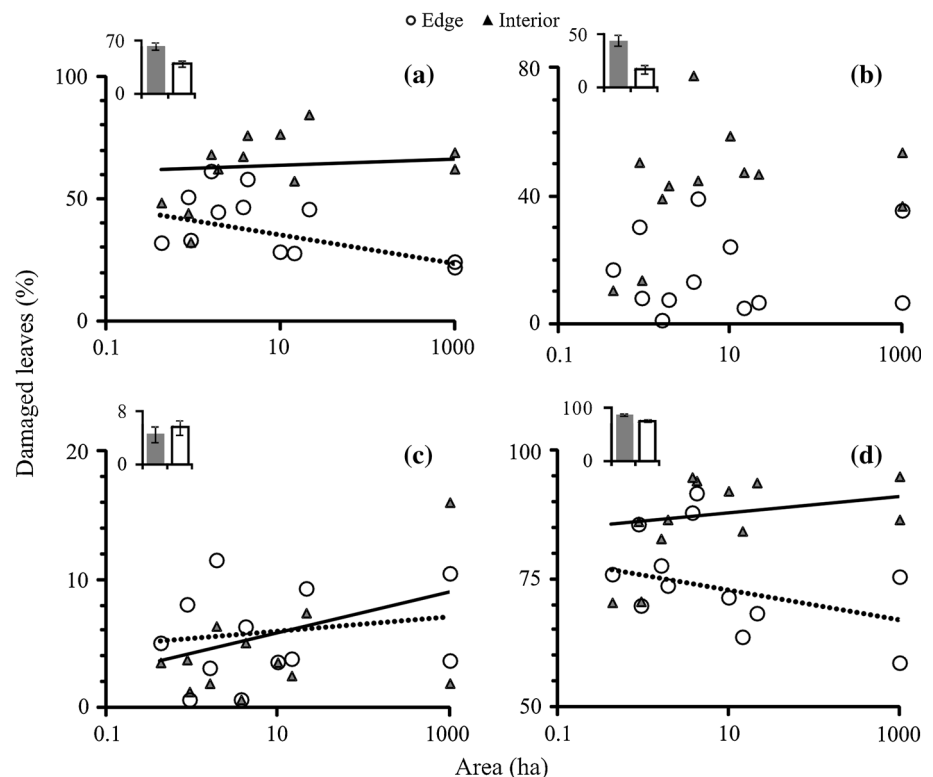
Results

Forest area and edge effects on herbivory

Most leaves of *C. lachnostachyus* plants were damaged, with 80.8 % (± 2.2 , $n = 3,748$) of collected leaves showing some degree of insect herbivory. The most frequently observed damage was attributed to chewing insects, which affected more than half of sampled leaves (51.1 ± 5.2 %), followed by sap-sucking (30.0 ± 4.2 %) and finally leaf mining damage (5.0 ± 0.8 %).

Herbivory responses to habitat fragmentation varied among guilds (Table 1). A significant location effect was observed, with higher damage levels by chewers (Fig. 2a), sap-sucking insects (Fig. 2b) and total herbivory (Fig. 2d) in the forest interior compared with the edge, and with the opposite pattern for leaf miners (Fig. 2c). Moreover, fragment area affected the proportion of leaves damaged by chewers, leaf miners and total herbivory depending on edge/interior location (significant area \times location interaction; Table 1). Herbivory levels in the forest interior tended

Fig. 2 Herbivory by chewers (a), sap-sucking (b), leaf miners (c) and total phytophagous insects (d) on *C. lachnostachyus* plants in relation to fragment area and interior (triangles, solid lines)/edge (circles, dotted lines) location. Each point is the mean of eight plants. Bars indicate mean (\pm SE) herbivory at interior (grey) and edge (white) locations. Lines were only drawn for GLMM models with significant area \times location interaction



to decrease with reduction of fragment area, while the opposite tendency was observed at the edge, albeit not all slopes were statistically significant (Fig. 2).

Forest area and edge effects on plant availability and quality

Mean plant isolation varied between 0.5 and 1.7 m (1.02 ± 0.08 m) for *C. lachnostachyus* plants growing in the studied forest fragments and locations. This plant isolation was significantly smaller at the edge than in the interior and was not related to fragment area (Table 2; Fig. 3a).

Leaf quality of *C. lachnostachyus* plants, as estimated by water (75.9 ± 0.4 %), carbon (43.4 ± 0.1 %) and nitrogen content (3.7 ± 0.1 %), differed according to interior/edge location, without any noticeable relationship to forest area (Table 2). Leaves had significantly higher water content in plants from the forest interior, compared to plants growing at the edge of the forest (Fig. 3b). However, carbon and nitrogen showed the opposite pattern, with lower contents in plants occurring in the forest interior compared to those growing at the edge (Table 2; Fig. 3c, d).

Forest area and edge effects on insect community

The insect community associated with *C. lachnostachyus* was composed by 33 families of herbivores ($N = 744$) and 29 of natural enemies ($N = 330$, including eight families of spiders and mites) (Table S1). Average abundance per fragment and location was 31 (± 3) herbivore specimens and 14 (± 1) natural enemies.

Table 2 Results of mixed linear models evaluating fragment area and interior/edge location effects on plant availability and leaf quality traits of *C. lachnostachyus* in Chaco Serrano forest

Response variables	Explanatory variables	F	df	p
Plant	Plant isolation (m)	Area	1.36	9 >0.1
		Location	37	9 <0.001
		Location \times area	4.28	9 >0.05
Leaf quality	Water content (%)	Area	1.1	9 >0.1
		Location	19.9	9 0.002
		Location \times area	1.67	9 >0.1
	Carbon content (%)	Area	0.23	9 >0.1
		Location	51.02	9 0.001
		Location \times area	2.87	9 >0.1
	Nitrogen content (%)	Area	2.3	9 >0.1
		Location	9.3	9 0.014
		Location \times area	0.00	9 >0.1

Significant relationships ($p < 0.05$) are shown in bold

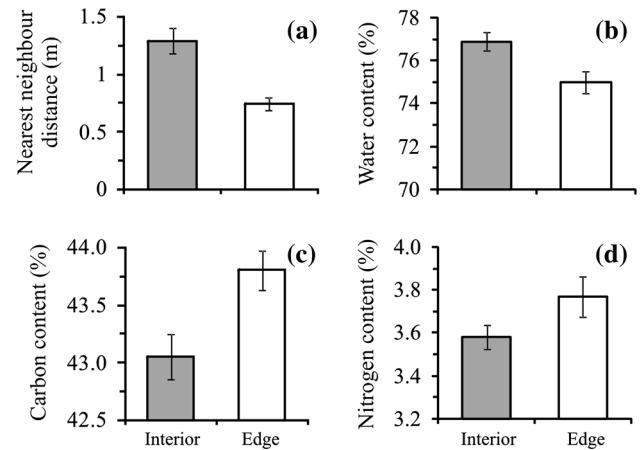


Fig. 3 Plant isolation (a), water (b), carbon (c) and nitrogen content (d) in *C. lachnostachyus* plants from interior/edge locations. Mean of 11 fragments (\pm SE)

There was no significant effect of area, location (edge/interior) or their interaction on the richness of natural enemies, and a weakly significant effect of area on the richness of herbivores (Table 3). Abundance of both insect groups was affected by fragmentation variables. There was a significant effect of area \times location interaction on the abundance of phytophagous insects; in small fragments, the insects were more abundant in the interior forest than at the edge, but this pattern was reversed in bigger fragments (Table 3; Fig. 4). The abundance of natural enemies was only affected by area, with fewer specimens being observed in smaller fragments (Table 3; Fig. 4).

Table 3 Results of generalized mixed models evaluating fragment area and interior/edge location effects on insect community of *C. lachnostachyus* in Chaco Serrano forest

Response variables	Explanatory variables	Z	p
Phytophagous	Abundance	Area	2.00 0.045
		Location	4.74 <0.001
		Location \times area	-4.16 <0.001
	Family richness	Area	1.81 0.069
		Location	-0.41 >0.1
		Location \times area	-0.01 >0.1
Natural	Abundance	Area	1.97 0.049
		Location	1.65 >0.05
		Location \times area	-1.47 >0.1
	Family richness	Area	0.95 >0.1
		Location	0.15 >0.1
		Location \times area	-0.44 >0.1

Significant relationships ($p < 0.05$) are shown in bold

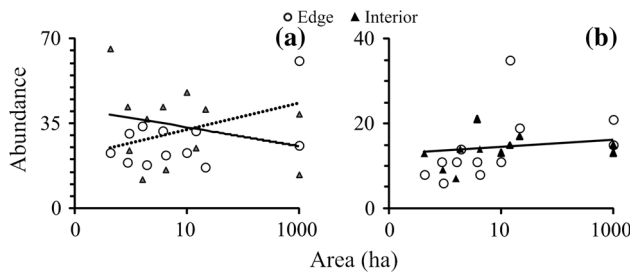


Fig. 4 Abundance of phytophagous (a) and natural enemy (b) insects on *C. lachnostachyus* plants in relation to fragment area and interior (triangles and solid line)/edge (circles and dotted line) location in Chaco forest. Each point is the sum of five plants sampled in each fragment and location

Herbivory versus plant measurements and insect community

The Chi-square test, Bentler CFI, Bentler–Bonnett NFI and goodness-of-fit index (GFI) of our four models indicated an adequate data fit of SEMs (Fig. 5). The analyses showed a direct and negative effect of edge location on herbivory in all models, as well as indirect effects through plant availability and leaf traits which varied among types of damage. Chewing herbivory was positively affected by edge location via reduced plant isolation and increased carbon content. However, such effects did not compensate for strong direct negative edge effects, overall resulting in lower herbivory at

the edge. Regarding sap-sucking herbivory, there was a negative indirect influence of edge location mediated by decreased water content and increased nitrogen (Fig. 5b). On the other hand, leaf mining damage was positively affected by edge location via lower plant isolation and water content, with these indirect effects overriding direct negative edge effects and resulting in higher number of damaged leaves at the edge (Fig. 5c). Finally, total herbivory was only directly affected by plant location, with lower damage levels at the edge of the forest (Fig. 5d).

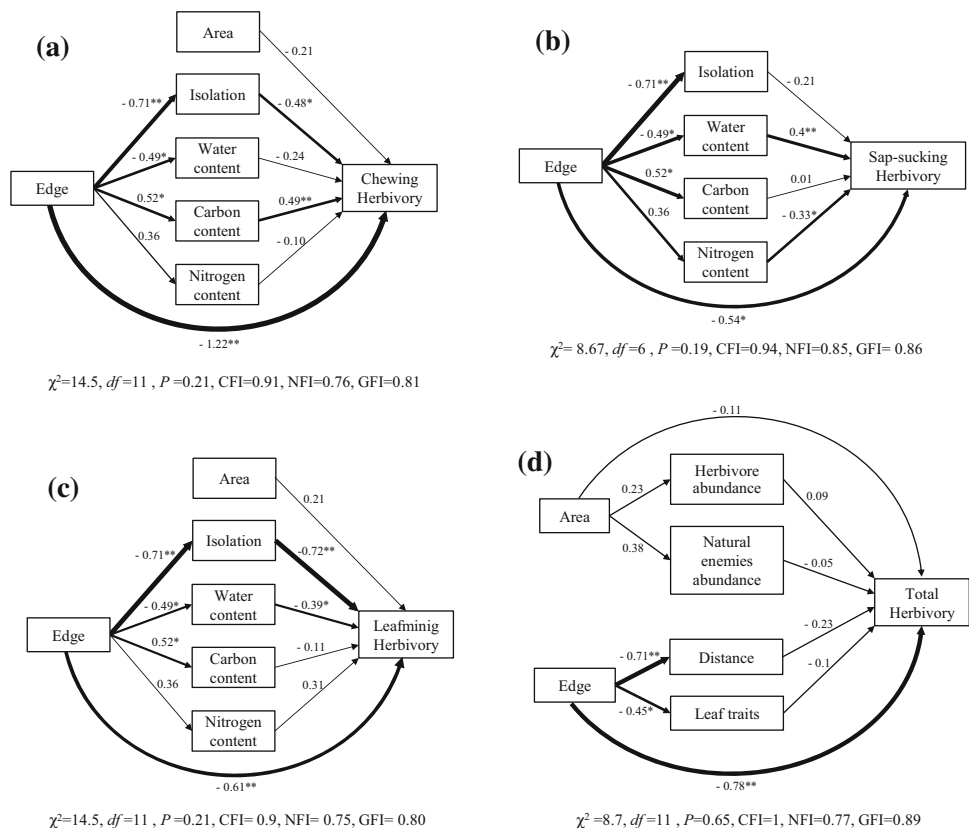
Discussion

Insect herbivory is a key ecosystem process that could be altered by forest fragmentation through direct (herbivores) and indirect (plants and natural enemies) effects. In this study from a fragmented Chaco Serrano forest, we found leaf damage by three insect guilds on the native plant *C. lachnostachyus* to be strongly affected by forest fragmentation. The changes were mainly driven by edge effects on plant availability and chemical traits with important differences among guilds.

Herbivory appears to be pervasive in the Chaco Serrano forest, with 80 % of *C. lachnostachyus* leaves showing damage signs from one or more phytophagous guilds in the present study, and with previous records of 90 % damaged

Fig. 5 Structural equation models examining the direct and indirect effects of fragment area (log transformed) and interior/edge location on chewing (a), sap-sucking (b), leaf mining (c) and total herbivory (d) on *C. lachnostachyus* plants. Arrow thickness indicates the standardized magnitude of each effect, asterisks denote significant factors: ** $p < 0.005$; * $p < 0.05$. Isolation represents the nearest neighbour distance; the location variable is presented as “Edge” effect. Leaf traits represents the first axis extracted from a PCA on chemical variables. **a** $\chi^2 = 14.5$, $df = 11$, $p = 0.21$, CFI = 0.91, NFI = 0.76, GFI = 0.81.

b $\chi^2 = 8.67$, $df = 6$, $p = 0.19$, CFI = 0.94, NFI = 0.85, GFI = 0.86. **c** $\chi^2 = 14.5$, $df = 11$, $p = 0.21$, CFI = 0.9, NFI = 0.75, GFI = 0.80. **d** $\chi^2 = 8.7$, $df = 11$, $p = 0.65$, CFI = 1, NFI = 0.77, GFI = 0.89



leaves on samples of the overall plant community (Cabrera 2011). Indeed, herbivory seems to represent a widespread ecological interaction in fragmented forests, with records of 38–70 % leaves damaged by insects (Souza et al. 2013; Ruiz-Guerra et al. 2010 respectively).

Chewing herbivores were responsible for damage on more than half of the leaves collected in this study. Although few studies have examined herbivory by different insect guilds simultaneously (Smith and Nufio 2004; Andrew and Hughes 2005; Arnold and Fonseca 2011), there is strong evidence that chewing herbivores have a key role in plant biomass removal of ecosystems (Crawley 1989; Schowalter 2000). Moreover, one-third of all collected leaves showed damage by sap-sucking insects and only 5 % of the leaves had signs of leaf miner consumption. Leaf damage by these two herbivore groups could also have a noticeable impact on plant growth and reproduction, via photosynthesis reduction (Wagner et al. 2008; Zvereva et al. 2010) or transmission of plant pathogens (e.g. Kluth et al. 2002; Junior et al. 2006).

The trends: herbivory in a fragmented forest

A strong negative edge effect on herbivory was the dominant emerging trend from our study in fragmented Chaco Serrano. Plants located in the forest interior suffered higher herbivory levels than plants at the edge, from either total, chewing or sap-sucking herbivores. Negative edge effects on herbivory have also been recorded in other fragmented forests (e.g. Skoczylas et al. 2007; Valdivia 2011) although positive responses to edge conditions have more frequently been recorded [see review by Wirth et al. (2008)] and were observed here for leaf mining damage.

Forest area loss, frequently linked to a reduction in herbivory levels (e.g. Woodcock and Vanbergen 2008; Ruiz-Guerra et al. 2010; Schnitzler et al. 2011), influenced herbivory depending on edge/interior location within Chaco Serrano forest: markedly more leaves were damaged by chewers and total herbivores at the interior than at the edge in larger remnants, but such difference was blurred in smaller forests. In the latter fragments, prevalence of edge microclimatic conditions (Davies-Colley et al. 2000) due to a higher perimeter-area ratio (Fletcher et al. 2007) could provide a more homogeneous environment for herbivores, thus smoothing edge/interior differences.

The mechanisms: plant availability/quality and insect community

Among the many possible mechanisms that could be involved in herbivory responses to forest fragmentation, we considered on the one hand, factors inherent to the host plant (availability and quality) and, on the other hand, the

insect community with direct (herbivores) and indirect (natural enemies) effects.

No area effects were observed on either availability or quality of *C. lachnostachyus* plants in the studied forest remnants, but plants at the edge of the forest were less isolated in comparison with those at the interior. Thus, edge microclimatic conditions, e.g. higher light incidence, appear to favour *C. lachnostachyus* populations (Ledergerber et al. 2002), as occurs with fast-growing, early-successional species (Wirth et al. 2008). A positive response to edge conditions might also contribute to compensate (in smaller, edge dominated fragments) for negative effects of habitat loss on the plant population. As predicted, higher water and lower carbon content were found on leaves from interior habitats in comparison with those from edges, which might be attributed to increased sunlight, wind speed and evapotranspiration at the edge (Ishino et al. 2012). Moreover, nitrogen content in *C. lachnostachyus* leaves was higher in edge habitats, probably due to high photosynthetic levels accompanying increased light incidence (Roberts and Paul 2006).

Many studies have reported a positive relation between fragment area and richness of herbivore insects (e.g. Kruess and Tscharncke 2000; Van Nouhuys 2005; Savilaakso et al. 2009) or natural enemies (Srivastava et al. 2008; Cagnolo et al. 2009); however, this trend appeared only weakly in our results. This could be related to the taxonomic level (family) we used, although the same taxonomic resolution proved sufficient to detect area effects in other studies (e.g. Krauss et al. 2010; González et al. 2014). Besides the slight change in richness, phytophagous insects showed a complex abundance pattern, increasing in the interior of smaller forests, but showing the opposite tendency at the forest edges. This pattern could be related to generalist herbivores preferring edge conditions (Wirth et al. 2008) particularly in large forests, where edges are less prevalent. Changes in abundance without changes in richness may suggest differential susceptibility to fragmentation (Tscharncke et al. 2002; Vasconcelos and Bruna 2012), for example if dominant herbivores are strongly affected by edge effects. Natural enemies were less abundant in smaller fragments, which could lead to herbivore population increase in the latter, through release of top-down pressure (Kondoh 2003).

When all factors were simultaneously considered, plant availability and quality played important roles as indirect mechanisms for herbivory changes in response to Chaco Serrano fragmentation, with generalized direct edge effects also contributing to explain those changes.

The lower levels of herbivory most commonly observed on *C. lachnostachyus* plants growing at the forest edges, appeared to be mediated by changes in leaf water and nitrogen content for sap-sucking herbivory and linked to

strong direct effects for chewing damage and total herbivory. The positive turgor pressure required by sap feeders (Huberty and Denno 2004) could explain the link between lower water content and sap-sucking damage at the edges. For chewing herbivory, direct negative effects were so strong as to override significant influences of plant traits, including carbon content and plant isolation.

On the other hand, higher damage levels by leaf miners at the forest edge seemed to be driven by increased plant availability as *C. lachnostachyus* plants grow less isolated, a crucial factor for leaf mining herbivory (Schnitzler et al. 2011; Whitfield et al. 2012). In a lesser degree, lower water content also contributed to the increase of leaf mining damage at the forest edge, in agreement of frequent observations of drought stress facilitating herbivory (Meyer et al. 2006). Only for this trophic guild, such indirect effects overruled the negative direct edge effect observed in all our models.

Further studies are needed to unravel the factors involved in the strong direct effects of edge/interior location here detected for all herbivory types. Microclimatic differences between interior and edge of the fragmented forest, e.g. light, wind, temperature, humidity (Chen et al. 1995; Laurance et al. 2007), may affect morphology, physiology, behaviour and interactions of plants and animals, which may in turn influence herbivory (Roberts and Paul 2006; Lomelí-Flores et al. 2010). Thus, edge-induced changes in chemical or physical plant traits other than the ones here considered or at different phenological stages, may play a role within the negative direct edge effects on *C. lachnostachyus* herbivory. Moreover, the snapshot herbivore communities depicted through our samples may not have captured relevant aspects for the accumulated herbivory levels we measured. Herbivore communities are dynamic, with temporal changes in richness, composition, dominance, abundance and behaviour (Schoonhoven et al. 2005) all of which may impact on the final levels of damage on plants.

When total levels of herbivory were considered, none of the mechanisms studied appeared to be relevant. We were not able to detect insect influence on herbivory, either because dominant species were not affected by forest fragmentation (Tscharntke et al. 2002; Vasconcelos and Bruna 2012); vulnerable species were functionally replaced (Wilby and Thomas 2002) thus providing insurance against habitat loss (Tscharntke et al. 2012), or our sampling failed to capture the appropriate changes in the insect community. On the other hand, the lack of influence of plant traits in the total herbivory model is likely a consequence of conflicting trends operating on the different feeding guilds.

In summary, our study of fragmentation effects on herbivory using a representative plant from Chaco Serrano forest has shown that responses as well as underlying

mechanisms are complex and that, in this context, not all herbivore guilds go in the same boat. This work highlights the importance of considering the variety of herbivore feeding strategies, and the multiple factors acting at plant, herbivore and natural enemy levels, in order to understand the complexity of forest fragmentation effects on insect herbivory, and to unravel the underlying mechanisms for this key ecological interaction.

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