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ORIGINAL PAPER

Galling insects in a fragmented forest: incidence of habitat loss, edge effects and plant availability

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Abstract Galling insects tend to be highly sensitive to changes in their host plants or their environment. Here we analyze the effects of Chaco Serrano forest fragmentation on gall inducing species associated with four native plants species, simultaneously examining area and edge effects as well as the role of host plant availability on such effects. At edge and interior locations in each of nine forest sites in an area gradient in Central Argentina, we estimated herbivory as (1) the proportion of galled plants and (2) the number of galls per plant. Herbivory variations in relation to forest area and edge/interior locations were analyzed with generalized linear models, whereas the influence of plant availability in mediating area and edge effects was assessed by Structural Equation Models. Different responses to fragmentation were observed, depending on the insect species and also on the chosen herbivory indicator. Significant edge and area effects were detected in four and two out of ten performed models, respectively. When significant, edge effects were mostly positive and consistently direct rather than mediated by plant availability; instead, area effects varied from positive and led by plant abundance, to negative and independent of plant availability. Our study provides new evidence of a tendency for galling insects to benefit from edge conditions, while showing less consistent effects regarding forest size. Our results also suggest a very limited role for plant availability as a mechanism mediating fragmentation effects on herbivory by galling insects.

Keywords Chaco Serrano · Insect–plant interaction · Fragmentation · Edge effect

Introduction

Galling insects, with over 13,000 known species (Espírito-Santo and Fernandes 2007), show the most complex insect–plant interactions in the natural world (Shorthouse et al. 2005). These herbivorous insects induce the development of atypical plant growths, known as galls, via deviation of the standard morphogenetic pattern of the host organs (Isaias et al. 2014). The plant reaction, usually involving hyperplasia and hypertrophy, can be triggered by factors linked to oviposition and larval development (Wells 1921), although the molecular mechanisms leading to gall formation have not yet been elucidated (Oliveira et al. 2014). Galls provide adaptive advantages to galling herbivores, including shelter against unfavorable environmental conditions such as desiccation and extreme temperatures, protection against natural enemies and enhanced nutritional quality (Stone and Schönrogge 2003).

Galler species have frequently been used as indicators of environmental quality because of their high sensitivity to changes in either their host plants or their environment (Toma et al. 2014). Thus, various studies have addressed responses of gall forming species to water stress (Schowalter et al. 1999), soil fertility (Cuevas Reyes et al. 2003), altitude (Pontes Ribeiro and Basset 2007), rainfall (Veldtman and McGeoch 2003), temperature (Blanche

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2000), environmental pollution (Bagatto and Shorthouse 1991), urbanization (Julião et al. 2005). In particular, according to the "hygrothermal stress hypothesis" (Price et al. 1987, 1998; Fernandes and Price 1988) galling insects would thrive in xeric habitats, due to sclerophylly related plant traits (long-lived leaves, reduced probability of leaf abscission, low nutrient status, resource stability and predictability, and high chemical defense) favoring galling development, added to a lower top–down pressure resulting from lower abundance and performance of natural enemies and diseases (Fernandes and Price 1988, 1992).

Forest loss and fragmentation have been linked to global biodiversity loss and alteration of ecological processes such as herbivory (Guimarães et al. 2014). In fragmented forests, decreasing remnant size is typically accompanied by an increase in the amount of edge habitat, where greater sun and wind exposure lead to a more variable temperature, wind and humidity conditions compared to the forest interior, which generally (1) increases the levels of convective cooling at edges, hence decreasing the energy budgets for ectothermic flying insects (Merckx et al. 2008), and (2) negatively impacts forest specialists tuned to more stable micro-climatic conditions (Laurance 2004; Merckx et al. 2012). Area and edge effects may interact with each other and appear to be the most influential components of habitat fragmentation on species composition (Slade et al. 2013; Didham et al. 2012).

Galling insects seem to benefit from forest fragmentation, according to the few studies addressing this issue. Higher gall density has been observed in small than in large forests (Wang et al. 2005; Chust et al. 2007; Malinga et al. 2014; Maldonado-López et al. 2015) although the number of galls was not related to fragment size in other cases (Julião et al. 2004; Dunley et al. 2009). Edge conditions also appear to favor these insects, since greater gall richness and abundance have been reported at the borders compared to the interior of fragmented forests (Araújo et al. 2011; Araújo and Espírito-Santo 2012; Akkuzu et al. 2015; Maldonado-López et al. 2015). However, particular galler species can be more abundant at the forest interior (Araújo et al. 2011; Julião et al. 2004). Area and edge effects on galler species have rarely been simultaneously considered (Julião et al. 2004; Maldonado-López et al. 2015) and their possible interactions (Didham et al. 2012) have not been examined for these insects.

Here, we analyze the effects of Chaco Serrano forest fragmentation on galler species associated with four native plants species, simultaneously examining for the first time for this insect group, area and edge effects, their interaction, and the role of host plant availability on such effects. In Chaco Serrano, belonging to the most extensive and threatened dry forest in South America (Zak et al. 2004), area loss has negatively affected plant and insect diversity and abundance as well as herbivory rates, with variable edge effects (e.g. Cagnolo et al. 2006, 2009; Valladares et al. 2006; Rossetti et al. 2014; González et al. 2015). Changes in plant diversity and abundance in fragmented forests (Vranckx et al. 2012) could underlie changes in herbivore abundance, as proposed by the resource concentration hypothesis (Root 1973; Connor and McCoy 2001).

Specifically, we asked: (1) does insect gall abundance vary with fragment area and edge/interior location? (2) Can such variations be explained by changes in plant abundance? Since galling insects seem to prefer environmentally stressed habitats, as proposed by the hygrothermal stress hypothesis (Fernandes and Price 1992; Medianero et al. 2003; Gonçalves-Alvim and Fernandes 2001), we expected gall abundance to be higher at the forest edge. Also, because smaller remnants tend to be dominated by edge conditions (Laurance et al. 2007) we expected gall abundance to be negatively related to fragment area, particularly at the interior (interacting area and edge effects). Finally, considering the high specialization of galling insects (Shorthouse et al. 2005), we expected resource availability as indicated by plant abundance, to play a role in mediating area and edge effects on gall abundance.

Materials and methods

Chaco Serrano is a seasonally dry forest, with 750 mm annual rainfall concentrated mostly in the warm season (October–April) and mean temperatures between 26 °C (maximum) and 10 °C (minimum) (Luti et al. 1979). The native vegetation comprises an open tree layer (up to 15 m high), 1–3 m high shrubs covering 10–80 % of the ground, a herbaceous layer (up to 95 % cover), and many vines and epiphytes Cabido et al. 1991). The forest is currently restricted to isolated patches within an intensely managed agricultural matrix, largely dominated by wheat in winter and soy in summer.

The study was conducted on nine forest remnants (hereafter referred to as sites), including six fragments (0.5–29 ha) and three sites representing continuous forests (more than 1000 ha), located between 31°10–31°30S and 64°00–64°30W, at approximately 700 masl. Since host phenology represents a crucial issue for gallers (Yukawa 2000; Toma and de Souza Mendonça 2014), sampling was carried out in two periods: January–February and April–July 2007, thus covering the main forest vegetation growth period (Tiedemann 2011). In each site and occasion, three transects covering an area of 100 m^2 (50 m long × 2 m wide) were run at the forest edge (along the tree line) and three transects at the interior (approximately 20 m from the tree line). Different transects were traced at each sampling date. Four native plant species occurring in all the selected remnants and presenting insect galls were selected for the study: *Celtis ehrenbergiana* (Klotzsch) Liebm (Celtidaceae), *Geoffroea decorticans* (Gill ex Hook et Arn.) Burkart (Fabaceae), *Solanum argentinum* Bitter and Lillo and *Lycium cestroides* Schltdl (both Solanaceae). All individuals of these focal species occurring along the above mentioned transects were carefully observed and the number of galls was recorded. Two variables of herbivory by galling insects were thus estimated for each plant species: gall abundance (number of galls per plant) and frequency (as proportion of galled plants), pooling data from both sampling dates prior to statistical analysis.

Data analysis

We analysed the variations in the number of galls per plant using generalised linear mixed models (GLMMs) (Bolker et al. 2009) with Poisson error, considering location (edges versus interior), fragment area (log transformed) and their interaction as fixed factors. Whenever dispersion was observed, data were fitted to the negative binomial distribution (Ludwig and Reynolds 1988). Site was incorporated as a random effect in order to account for non-independence of data from edges and interior of the same forest remnant (Faraway 2006). Similar models were constructed to analyse the proportion of galled plants, using binomial error distribution with a logit link function. Mixed models were conducted using the lme4 (Bates et al. 2011) package in the R 3.2.0 environment (R Development Core Team 2014).

In those cases in which GLMM indicated significant effects of fragment area or location on either estimator of herbivory by galling insects, we conducted structural equation models (SEM) (Shipley 2000) in order to evaluate the role of plant abundance on such effects. In these models, location was included 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. Site was not included in the model, considering that GLMMs indicated relatively low random factor variance (0–0.5). Multi normality was checked with Mardia's multivariate normality test (Ullman 2006); Chi square test, Bentler–Bonnett NFI and Akaike's Information Criterion (AIC) were used as measures of goodness-of-fit. SEM analyses were carried out using AMOS 5.0 software.

Results

Examination of 1460 plants of the four focal species revealed 5,406 insect galls, belonging to five galling species (Table 1). These included four Cecidomyiidae (Diptera): *Allodiplosis crassa* Kieffer and Jörgensen on *Geoffroea decorticans*, Cecidomyiidae sp 1 on *Solanum argentinum*, Cecidomyiidae sp 2 and sp 3, both on *Celtis ehrenbergiana*, and one Braconidae (Hymenoptera): *Allorhogas cordobensis* Martinez et al. (2011), on *Lycium cestroides*.

The *A. crassa*-*G. decorticans* interaction was the most common, with galls in nearly half of the observed plants and an average of 26 galls per plant, whereas the least frequent interaction was represented by Cecidomyiidae sp 1–*S. argentinum*, affecting just a fifth of the plants with <2 galls per plant on average (Table 1).

Habitat fragmentation effects on galling insects according to each species and herbivory measurement (gall abundance and frequency) are shown in Fig. 1. Location was a significant factor in four out of ten performed models, whereas significant area effects were detected only in two models (Table 2). The number of *A. crassus* galls on *G. decorticans* plants was higher for forest edges and decreased with forest area, although only in plants located at the forest interior (significant area: location interaction, Fig. 1a). Positive edge effects were also observed on gall abundance of Cecidomyiidae sp 2 on *C. ehrenbergiana* (Fig. 1g), whereas the opposite trend was observed for *A. cordobensis*, with more galls on *L. cestroides* plants at the interior in comparison with the edge of forests (Fig. 1c). The proportion of galled plants was related to fragmentation variables only in the Cecidomyiidae sp 1–*S. argentinum* interaction, increasing as fragment area became smaller and, albeit marginally, at forest edges (Fig. 1f). Variations in plant abundance with regard to area and edge effects, which have been included in our models to explain herbivory trends, are shown in supplementary information (Fig. S1; Table S1).

A more detailed exploration of the above described fragmentation effects on gall herbivory was provided by structural equation models, except for *A. cordobensis* where SEM models failed to show any significant relationship. According to these analyses, edge effects on galls were consistently positive and direct rather than mediated by plant availability (Fig. 2a–c). Instead, area effects were more variable in sign as well as in mechanism, from positive and mainly indirect (via plant abundance) in *G. decorticans* (Fig. 2a), to negative and direct (despite positive area effects on host plant abundance) in *S. argentinum* (Fig. 2b) and in *C. ehrenbergiana* (where plant abundance was unaffected by forest fragmentation) (Fig. 2c).

Discussion

Habitat fragmentation is generally acknowledged as a major threat for the maintenance of global biodiversity, with far reaching consequences on ecosystem functioning

Table 1 Summary statistics of herbivory estimations by galling insects on selected plant hosts in Chaco Serrano forest

Plant–insect interaction	Herbivory estimate				N
	Galls per plant		Galled plants (%)		
	Range	Mean (SE)	Range	Mean (SE)	
Geoffroea decorticans–Allodiplosis crassa	0–109.50	26.30 (8.48)	0–100.00	0.44 (7.79)	17
Lycium cestroides–Allorhogas cordobensis	0–6.00	1.93 (0.46)	0–100.00	0.40 (9.26)	17
Solanum argentinum–Cecidomyiidae sp 1	0–3.11	1.47 (0.18)	1.78–60.00	0.22 (4.27)	16
Celtis erhembergiana–Cecidomyiidae sp 2	1.22–47.75	9.29 (2.40)	32.11–93.33	0.32 (4.83)	18
Celtis erhembergiana–Cecidomyiidae sp 3	0–5.44	2.65 (0.32)	0–71.74	0.42 (4.23)	18

N number of sites/locations in which the plant species was observed

(Haddad et al. 2015). However, galling insects are still notoriously underrepresented in fragmentation studies (Guimarães et al. 2014). Here, we analyzed area and edge effects on herbivory by galling insects in an endangered seasonally dry forest, aiming to disentangle, for the first time for these highly specialized herbivores, possible interactions between both fragmentation factors, as well as the role of host plant availability in mediating such effects.

Each of the four sampled plant species supported one or at most two galler species. This galler assemblage included all species known to occur on the studied plant hosts (Altamirano 2009; Gagné and Jaschhof 2014; Houard 1933; Martínez et al. 2011, Fernandes et al. 2002). Herbivory by galling insects was particularly important in *G. decorticans*, with each individual plant supporting on average 26 galls. The remaining focal plants showed lower herbivory levels, with three to ten times fewer galls per plant, but in all cases large variations were observed among sites. Most galls were induced by Cecidomyiids, as observed in other studies at global (Maia and Fernandes 2004) or local scales (Fernandes et al. 2002; Quintero et al. 2014; Rodrigues et al. 2014).

Herbivory by galling insects showed different responses to forest fragmentation, depending not only on the insect–plant interaction but also on the chosen indicator of herbivory levels (gall abundance or frequency). The number of galls per plant, showing significant effects in three out of five cases, appeared to be more sensitive than the proportion of galled plants (only one case), in terms of reflecting changes in forest area or edge/interior location. Measurements of gall density provide the variable most frequently used to estimate herbivory by these insects. However, herbivory frequency as estimated by the proportion of plants with galls, contributes another useful evaluation scale for the effects of environmental factors (Cuevas Reyes et al. 2014).

A positive edge effect was the most frequent trend for herbivory by galling insects in Chaco Serrano, consistent with the predominant evidence from galls in other fragmented systems (Araújo et al. 2011; Akkuzu et al. 2015; Maldonado-López et al. 2015) and with a general pattern of increased herbivory in edge habitats, attributed to improved host plant quality and relaxation of natural enemy pressure (Guimarães et al. 2014). However, plants of *L. cestroides* growing at the interior of the forest supported a greater number of *A. cordobensis* galls than plants at the edges. Differential responses to edge conditions have been also mentioned in other studies (e.g. Barrera et al. 2015; Delgado et al. 2013), with particular gall inducing species being more abundant at or even restricted to either edge or interior of patches (Julião et al.2004; Araújo et al. 2011). Preference for interior conditions suggests that this species could act as an indicator of forest health.

Forest area loss is often related to reductions in herbivory levels (e.g. Valladares et al. 2006; Schnitzler et al. 2011), as shown here by fewer *A. crassus* galls on *G. decorticans* plants at the interior of smaller forests. However, herbivory by galling insects in particular, tends to increase in smaller remnants (Wang et al. 2005;Chust et al. 2007; Malinga et al. 2014; Maldonado-López et al. 2015), which was supported here by the proportion of *S. argentinum* plants bearing Cecidomyiidae sp 1 galls. The expansion of favorable edge conditions to interior locations in small fragments (Laurance et al. 2007) could underlie this negative relationship with forest area, whereas a different mechanism must be involved in the *A. crassus* case, as discussed below.

According to our results, host plant abundance would not play a significant role in the most frequently reported trend for galling insects in fragmented forests, i.e. higher herbivory levels at the edge in comparison with the interior of forest remnants. Mechanisms for those positive edge effects, may instead involve direct effects of microclimatic conditions on galling insects (Stoepler and Rehill 2012) or, as predicted by the hygrothermal stress hypothesis, bottom–up factors such as improved host plant quality

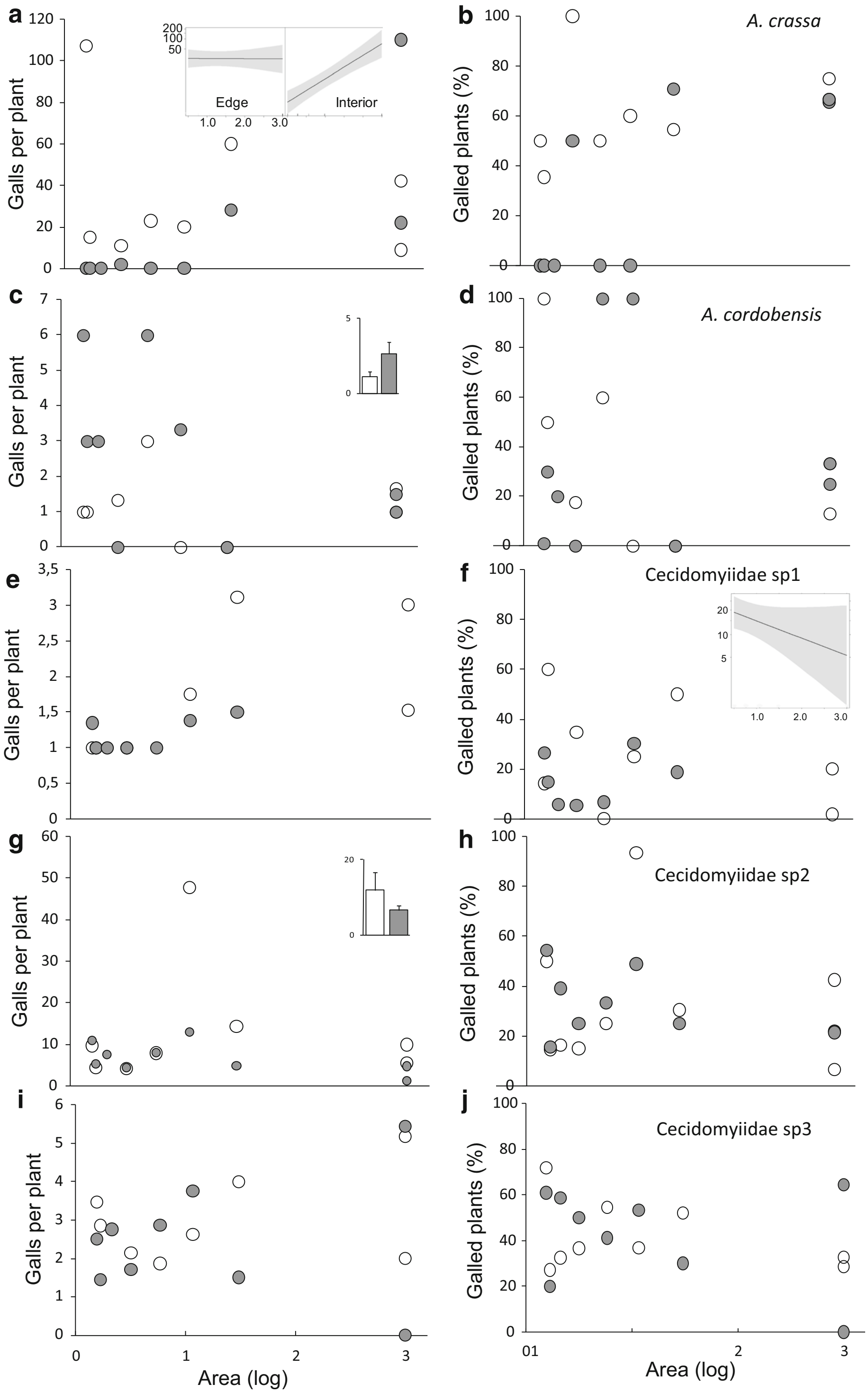

Fig. 1 Herbivory by galling insects in four plant species in Chaco Serrano Forest: number of galls per plant (*left*, **a**, **c**, **e**, **g**) and percentage of plants with galls (*right*, **b**, **d**, **f**, **h**) in relation to remnant area, at interior (*grey circles*) and edge (*white circles*) locations. *Insets* depict significant trends, with *bars* indicating mean (±SE) herbivory at interior (*grey*) and edge (*white*) locations

(Fernandes and Price 1992; Ishino et al. 2012) or top–down factors e.g. release from natural biological control if natural enemies cannot tolerate harsh edge conditions (Price and Clancy 1986; Fernandes and Price 1992; Wirth et al. 2008).

Instead, changes in plant abundance became relevant when area effects were detected in our system (i.e.G. *decorticans* and *S. argentinum*). According to our results, host plant availability was largely responsible for the number of *A. crassa* galls on *G. decorticans* plants along the forest size gradient. This result is supported by the strong direct link shown by most gall species to the density of their host plant (Cuevas Reyes et al. 2014), as could be

Table 2 Results of generalized linear mixed models evaluating fragment area and interior/edge location effects on herbivory by galling insects on four plant species in Chaco Serrano forest

Plant–insect interaction	Response variable	Explanatory variable	χ^2	*p*	Random effects (variance)
Geoffroea decorticans/Allodiplosis crassa	**Galls per plant**	**Location**	**36.34**	**<0.0001**	0.527
		Area	**3.55**	**0.059**	
		Location × area	**230.05**	**<0.0001**	
	Proportion of plants with galls	Location	0.3478	0.555	0
		Area	2.1462	0.143	
		Location × area	0.0032	0.955	
Lycium cestroides/Allorhogas cordobensis	**Galls per plant**	**Location**	**4.950**	**0.026**	0.290
		Area	1.290	0.256	
		Location × area	0.760	0.383	
	Proportion of plants with galls	Location	0.531	0.466	0
		Area	0.314	0.574	
		Location × area	0.509	0.476	
*Solanum argentinum/*Cecidomyiidae sp 1	Galls per plant	Location	0.442	0.506	0
		Area	2.004	0.157	
		Location × area	0.252	0.616	
	Proportion of plants with galls	**Location**	**3.105**	**0.078**	0.277
		Area	**4.194**	**0.040**	
		Location × area	1.079	0.299	
Celtis erhembergiana/ Cecidomyiidae sp 2	**Galls per plant**	**Location**	**23.059**	**<0.0001**	0.374
		Area	1.052	0.305	
		Location × area	1.268	0.260	
	Proportion of plants with galls	Location	0.869	0.351	0.195
		Area	0.191	0.661	
		Location × area	0.523	0.470	
Celtis erhembergiana/ Cecidomyiidae sp 3	Galls per plant	Location	0.220	0.639	0
		Area	0.588	0.443	
		Location × area	1.456	0.228	
	Proportion of plants with galls	Location	0.300	0.584	0.029
		Area	0.062	0.803	
		Location × area	1.460	0.227	

Significant ($p < 0.05$) and marginally significant ($p < 0.1$) relationships are shown in bold

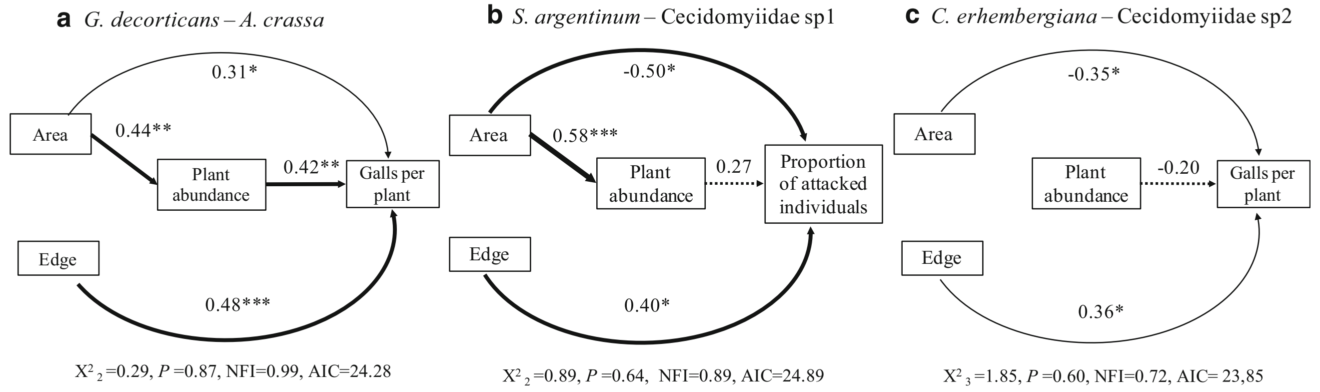

Fig. 2 Structural equation models examining the direct and indirect effects of fragment area (log transformed) and interior/edge location on number of galls per plant (log) or proportion of galled plants in *G. decorticans* (**a**), *S. argentinum* (**b**) and *C. ehrenbergiana* (**c**). Non significant ($p > 0.1$) direct paths to herbivory are represented by *dashed lines*. *Arrow* thickness indicates the standardized magnitude of each effect, *asterisks* denote significant factors: ***$p < 0.005$; **$p < 0.05$; *$p < 0.1$. The location variable is presented as ''Edge'' effect. *NFI* non-normed fit index, *AIC* Akaike criterium of goodness-of-fit

expected for such specialized herbivores from the resource concentration hypothesis (Root 1973). On the other hand, *S. argentinum* plants being rarer in smaller forests did not explain the larger proportion of those plants bearing Cecidomyiidae sp 1 galls. A dilution effect, with fewer plants being exploited as their availability increases (Power 1987) might be involved in the latter case or, as suggested above, the expansion of edge microclimatic conditions.

In conclusion, our study supports a tendency for galling insects to benefit from edge conditions, and less consistent changes with regard to forest size. Our results also suggest a very limited role for plant availability as a mechanism mediating fragmentation effects on herbivory by galling insects. Finally, the assessment of individual galling species allowed the detection of a possible indicator of forest quality, *A. cordobensis*, prevailing under the more pristine interior conditions. Further studies employing mechanistic approaches and dealing with specific responses in multi-species systems, are prerequisites for the comprehension and conservation of galling insects and their herbivore–plant interactions in increasingly fragmented landscapes.

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