Sociobiology 60(4): 397-404 (2013) DOI: 10.13102/sociobiology.v60i4.397-404

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Parasitoids of *Acromyrmex* (Hymenoptera: Formicidae) Leaf-Cutting Ants in Continuous and Fragmented Atlantic Forest

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Article History
Edited by:
Qiuying Huang, HAU, China
Received 29 July 2013
Initial acceptance 18 August 2013
Final acceptance 17 October 2013

Keywords
Habitat fragmentation, Phoridae, species richness, host-parasitoid interactions, *Apocephalus*, *Myrmosicarius*

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Abstract

Fragmentation of the habitat is a major threat to biodiversity in the Atlantic forest. Parasitoids seem to be particularly susceptible to habitat fragmentation. This study evaluated whether habitat fragmentation affected the interactions between phorid parasitoids and their *Acromyrmex* leaf-cutting ant host. Host density, and parasitoid species richness, abundance and proportion of nests with phorids were compared for a fragmented landscape and a well-preserved continuous forest in the Atlantic forest of southeast Brazil. Five *Acromyrmex* species and seven species of phorid parasitoids were found, most of them attacking exclusively *Acromyrmex niger* (Smith). Host nest density was similar in continuous and fragmented forests, and host species density was higher in fragmented forest. Parasitoid species richness, abundance and proportion of ant nests with phorids were higher in the continuous forest. This work showed for the first time the negative effect that forest fragmentation has on parasitoid species of *Acromyrmex* ants, apparently due to phorid inability to reach fragments. However, even when phorid abundance was considerably reduced in forest fragments, phorids of some species were able to parasitize ants there. In addition, the quantitative interactions among *Acromyrmex* ants and their parasitoids in Atlantic forest are described for the first time.

Introduction

Fragmentation of the habitat is a major threat to global biodiversity (Kruess & Tscharntke, 1994; Foley et al., 2005). Habitat fragmentation due to anthropogenic activity results in landscapes composed of a mosaic of remnant habitats surrounded by a more or less hostile agricultural or pasture land for cattle, called the matrix. The Atlantic forest, once the largest forest in America, is an ecosystem severely affected by habitat fragmentation. Most of the remaining Atlantic forest exists as small fragments (<100 ha; Ranta et al., 1998), that are composed of second-growth forests in early to intermediate stages of succession (Metzger et al., 2009), and the few large fragments are located in steep terrain that made human occupation difficult (Silva et al., 2007). Most of the original forest is fragmented and 80% of the fragments are <50 ha, and together with intermediate secondary forests, correspond to approximately 32–40% of what remains (Ribeiro et al., 2009).

In fragmented landscapes, population structure can be altered by several endogenous and exogenous processes (Tscharntke et al., 2002), and species are differentially affected, with some being very sensitive while others can even increase their population sizes (see Fahrig, 2003 for a review). Because community structure, interspecific interactions, and ecological functions are also affected, the magnitude and direction of the changes due to habitat fragmentation are sometimes unpredictable, especially if there is not enough information about natural history of the taxa in question. Some general responses to habitat fragmentation had been elucidated, however (Tscharntke et al., 2002; Ewers & Didham, 2006). One general response is that the effect of habitat fragmentation is more severe for species in higher trophic levels (Kruess & Tscharntke, 2000; Tscharntke et al., 2002; Montoya et al., 2006). Parasitoids, insects that deposit eggs inside a host from which a carnivorous larva emerges and feeds on it, occupy higher trophic levels in food webs. Several studies have shown the negative effect that habitat

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

fragmentation has on parasitoids, both in tropical and non-tropical areas (see Tscharntke et al., 2002 for a review; Cagnolo et al., 2009). In addition, parasitoids will be more susceptible to habitat fragmentation because of their narrow host range, as most of them are specialist, developing on few hosts only (Godfray, 1994). It has been proposed that species with narrower niches are more affected than generalists by fragmentation of their habitat (Henle et al., 2004; Cagnolo et al., 2009).

Leaf-cutting ants in the genera *Acromyrmex* and *Atta* are emblematic organisms in the Atlantic forest. These ants are generalist herbivores, and cut leaves of a wide array of plants that carry back to their nests to feed a fungus (Hölldobler & Wilson, 1990). While they are outside their nests, workers are attacked by dipteran parasitoids that belong to the family Phoridae. These parasitoids oviposit in adult workers of leaf-cutting ants while they are foraging, cutting leaves or removing wastes (Elizalde & Folgarait, 2012). Two lines of evidence suggest that these phorid parasitoids may be negatively affected by habitat fragmentation. First, many of these phorids are specialists (Elizalde & Folgarait, 2011). Second, phorid flies that attack leaf-cutting ants have small body sizes (Elizalde & Folgarait, 2011). Because body size correlates positively with dispersal abilities (Blackburn et al., 1999) and adult phorid parasitoids, which are the dispersal stage, do not have special long-dispersal means, it is possible that dispersal throughout a hostile matrix might imply a risky task. There is some evidence that phorid parasitoids of *Atta* leaf-cutting ants, are negatively affected by habitat fragmentation. In fact, release of these natural enemies has been proposed as one of the explanations of the high abundance of some species of *Atta* ants in small forest fragments and forest edges (Rao, 2000; Almeida et al., 2008). However, the focus of this work is on *Acromyrmex* ant hosts, which do not share phorid parasitoid species with *Atta* (Elizalde & Folgarait, 2011).

This study aims to provide evidence on whether habitat fragmentation is a negative factor affecting the interactions between phorid parasitoids and their *Acromyrmex* leaf-cutting ant hosts. We first tested whether *Acromyrmex* species are affected by forest fragmentation in the Atlantic forest of southeast Brazil. Then, we compared parasitoid species richness, abundance and proportion of nests with parasitoids in fragmented and well-preserved forests. We also described for the first time the quantitative interactions among *Acromyrmex* ants and their parasitoids in Atlantic forest.

Materials and Methods

Study sites. The study was conducted in two areas within the Atlantic forest of Rio de Janeiro state, southeast Brazil, which were chosen based on their different degree of fragmentation (Fig. 1). The Vassouras-Barra do Piraí

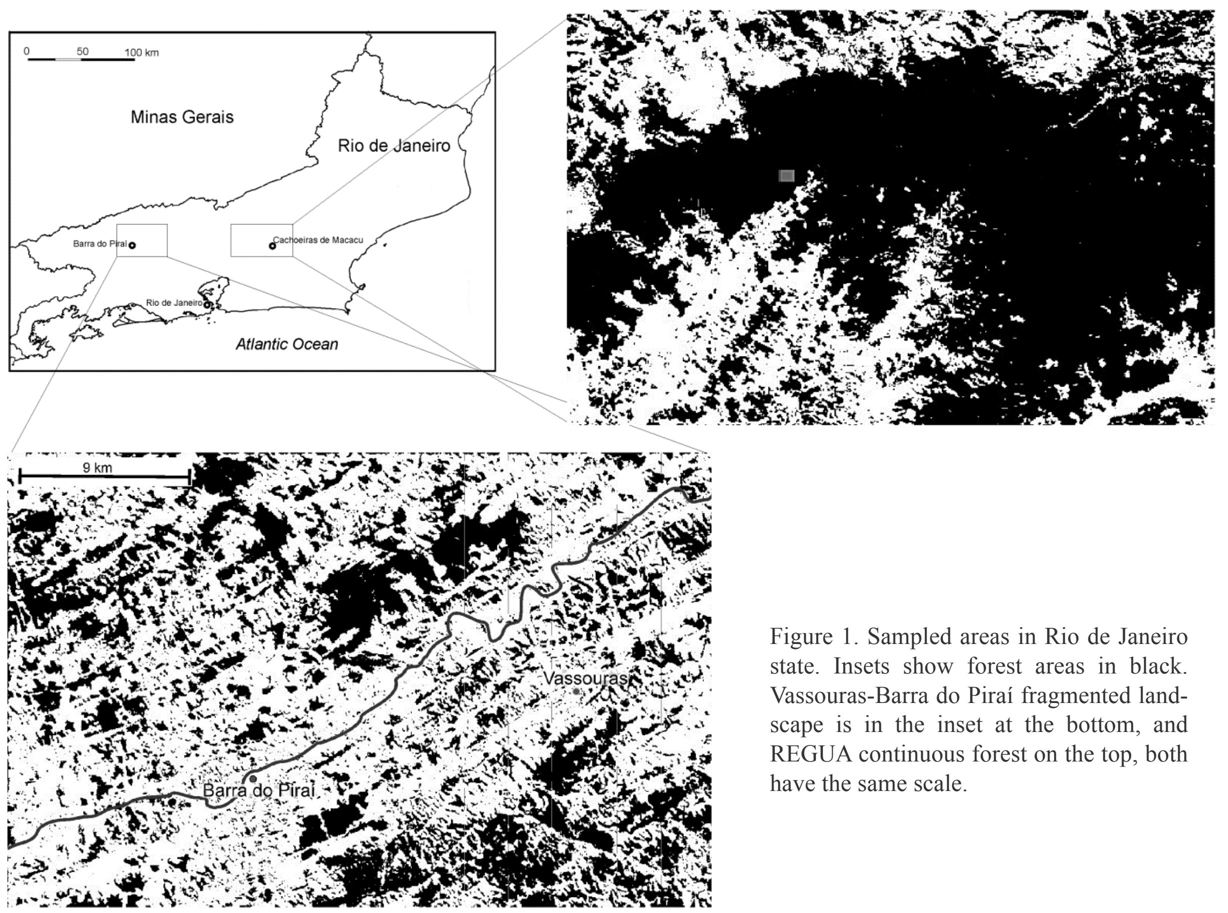

Figure 1. Sampled areas in Rio de Janeiro state. Insets show forest areas in black. Vassouras-Barra do Piraí fragmented landscape is in the inset at the bottom, and REGUA continuous forest on the top, both have the same scale.

area (22º 24'S, 43º 40'W) was selected as the highly fragmented forest. In the area, forest remains as small–medium sized fragments surrounded by a deforested matrix, which is mainly used as pasture for cattle ranching, but once was used for coffee plantations (Francelino et al., 2012). Forest remnants in the Atlantic forest of Rio de Janeiro represent only a 15.7% of the vegetation cover of the area, and are mainly secondary lowland and submontane semi-deciduous forests (Oliveira-Filho & Fontes, 2000; Francelino et al., 2012). Mean annual temperature is 20°C, and annual rainfall is 1,196 mm (Francelino et al., 2012).

The continuous forest is located in a NGO reserve, Reserva Ecológica de Guapiaçu—REGUA (22º 25'S, 42º 44'W), located in the municipality of Cachoeiras de Macacu. The area is a well preserved forest and vegetation type can be classified as a lowland and submontane rain forest of the coastal mountain range of the Rio de Janeiro state (Oliveira-Filho & Fontes, 2000). Late successional forest was selected to sample in this area (Fig. 1). The mean annual temperature is 20°C, and annual rainfall is 2,010 mm (Massera da Hora & Gonçalves Costa, 2010).

The regional climate is characterized by a hot and rainy season from October to March and a cooler and drier season from April to September (Francelino et al., 2012). Thus, we sampled during the wet season, in February and March 2012, to reduce differences in precipitation between areas (170 vs. 193 mm mean monthly precipitation in February for the fragmented forest and the continuous forest, respectively; Record-Meteo, 2007; Massera da Hora & Gonçalves Costa, 2010), although leaf-cutting ant phorids do not seem to be especially susceptible to low precipitation (Bragança et al., 2006). The areas were 100 km apart. Although the first site is a semi-deciduous forest and the other is a rain forest, they had similar elevation, distance to the ocean, mean temperature, ant species composition and ant nest density (2 more taxa were found in the fragmented forest, see Results). Host diversity was a more important factor than environmental variables to account for leaf-cutting ant parasitoid species richness (Elizalde & Folgarait, 2010).

In the Vassouras-Barra do Piraí area, 11 fragments were selected, with a range of size variation of 0.1-10.6 km2 (mean 3.4 km2), spanned over an area of 726 km2 (22º 13'–22º 30' latitude, 43º 38'–43º 51' longitude; Fig. 1). In the REGUA reserve two areas of the continuous forest were selected, separated by 2 km, and covering an area of 9 km2 (Fig. 1).

Ant and parasitoid sampling. In each selected fragment in Vassouras-Barra do Piraí area and in the two areas in the continuous forest in REGUA reserve, *Acromyrmex* nests were searched for while walking along transects. Because nests of some *Acromyrmex* species in the area are subterranean and not easily found (Gonçalves, 1961), the only evidence for nest presence are foraging trails. Thus, we walked the transects during periods of ant activity to also record foraging trails. We followed each foraging trail until it became subterranean and we counted it as a nest (unless two trail openings of the same ant species were closer than 30 m, in which case they were considered as belonging to the same nest). Transect length ranged from 250 m in the smallest forest fragments to 4km in continuous forest (mean length = 1.29 km, *SE* = 0.40, *n* = 13). Transect length in the fragmented area depended on fragment size because we extended each transect as to reach the center of the fragment. In continuous forest, transect length depended on trails already established. When a nest was found, we collected 5-10 major ants for later identification. Phorids attacking ants were collected using an aspirator for five minutes in a section of 2 m length of the foraging trail, near nest entrance, where most phorid parasitoids look for leaf-cutting ants hosts (Elizalde & Folgarait, 2012). In the few instances when nest entrance was not located, parasitoids were searched for in the most proximal portion of the foraging trail to the nest where it was possible to access, also in a section of 2 m of the trail. Ants and parasitoids collected at the same nest were kept in vials appropriately labeled as to later associate ants and phorids with each nest. Insects were identified with the available keys (for ants: Gonçalves, 1961; for parasitoids: Brown, 1997; Disney et al., 2006; 2008; 2009; Brown et al., 2010), and reference specimens were deposited in the Museum de Zoologia, Universidade de São Paulo, Brazil.

We determined ant species density by dividing the number of ant species in each transect by its area. Ant nest density was calculated dividing the number of nests from all *Acromyrmex* species. We compared ant species density and nest density per transect in fragmented and continuous forests using Mann-Whitney tests.

To evaluate the effect of forest fragmentation on parasitoids, interactions involving only *A. niger* were used. The dependent variables measured were phorid species richness, phorid abundance over each nest, and the proportion of nests with parasitoids. Because more *A. niger* nests were sampled in the continuous forest, parasitoid species richness and abundance were rarified to the same number of nests sampled in the fragmented forest using EstimateS v. 8.2 (Colwell, 2006). The effect of forest type, i.e. continuous or fragmented, on parasitoid abundance over nests was compared using Kruskal-Wallis tests, and the proportion of nests with phorids was compared with $\chi 2$-tests (with Yates correction for continuity).

Results

Acromyrmex-parasitoid interactions.

We found five *Acromyrmex* species. *Acromyrmex niger* was by far the most abundant species (Table 1). The other species collected were *A. subterraneus* (Forel), with three subspecies (*A. s. brunneus*, *A. s. molestans*, *A. s. subterra-*

neus), *A. coronatus* (Fabricius), *A. aspersus* (Smith), and *A. disciger* (Mayr) (Table 1).

Table 1. Mean (SE) relative abundance (%) for *Acromyrmex* taxa in fragmented and continuous forests in Rio de Janeiro, Brazil. Number of transects and total transect length for each forest type are indicated in square brackets. In the last column, total number of nests sampled for phorids, pooling all *Acromyrmex* species (and for *A. niger* only between parenthesis).

Taxa	Forest type	
	Fragmented [11; 8018 m]	Continuous [2; 8370 m]
A. niger	54.31 (11.19)	82.92 (0.42)
A. subterraneus	29.96 (5.70)	12.20 (0.30)
A.s. brunneus	15.61 (4.69)	9.82 (2.68)
A. s. subterraneus	4.03 (3.62)	2.38 (2.28)
A. s.molestans	3.12 (2.13)	0
A. disciger	6.83 (4.71)	0
A. coronatus	3.86 (2.80)	3.69 (1.31)
A. aspersus	0.40 (0.40)	1.19 (1.19)
Number of nests sampled	111 (59)	82 (68)

Seven species of phorid parasitoids were found, with five of them attacking exclusively *A. niger* (Table 2). Only one phorid species was attacking *A. disciger* and another was attacking *A. coronatus* only (Table 2). None of the subspecies of *A. subterraneus* nor *A. aspersus* were found to be attacked by phorids. The parasitoids *Apocephalus lutheihalteratus* Borgmeier and *Myrmosicarius catharinensis* Borgmeier were the most abundant species, and they used *A. niger* as host. The other parasitoid species had very low abundance (Table 2).

Only five nests in the continuous forest, all belonging to *A. niger*, had more than one phorid species attacking at the same time, with *Ap. lutheihalteratus* and *M. catharinensis* found together in four nests and in the other nest *Ap. lutheihalteratus* and *Neodorhniphora similis* Prado were attacking ants in the same trail.

Effect of forest fragmentation on ant-phorid interactions

All *Acromyrmex* species were present in the fragmented forest when all fragments were pooled, and only *A. disciger* and *A. s. molestans* were not collected in the continuous forest (Table 1). In fact, ant species density was higher in the fragmented forest ($U = 20$, $p = 0.03$; mean = 4.6×10^{-4} species/m^2, $SE = 0.7 \times 10^{-4}$, $n = 11$ for fragmented forest; mean = 0.9×10^{-4} species/m^2, $SE = 0.1 \times 10^{-4}$, $n = 2$ for continuous forest). However, nest density of all *Acromyrmex* species did not differ between forest types, and neither did nest density of *A. niger* ($U = 18$, $p = 0.12$; mean = 1.5×10^{-3} *Acromyrmex* nests/m^2, $SE = 0.2 \times 10^{-3}$, $n = 11$ for fragmented forest; mean = 0.8×10^{-3} *Acromyrmex* nests/m^2, $SE = 0.1 \times 10^{-3}$, $n = 2$ for continuous forest; $U = 12$, $p = 0.75$; mean = 0.7×10^{-3} *A. niger* nests/m^2, $SE = 0.2 \times 10^{-3}$, $n = 11$ for fragmented forest; mean = 0.6×10^{-3} *A. niger* nests/m^2, $SE = 0.1 \times 10^{-3}$, $n = 2$ for continuous forest).

In only 37.5% of the fragments where *A. niger* was present ($n = 8$) were there phorids attacking it (considering all *Acromyrmex* there were 45% of the 11 fragments with phorids). The rarefied phorid species richness in continuous forest was 4.81 (lower 95% confidence interval = 3.51), higher than the three species gathered over *A. niger* in the fragmented forest (Table 3). In addition, parasitoid abundance over nests was higher than that found in fragmented forest (Kruskal-Wallis $\chi^2_1 = 12.9$, $p = 0.0003$; Table 3), and the same pattern was shown by rarefied total parasitoid abundance (51.5 and 5 phorids in the continuous vs. fragmented forest, respectively). Continuous forests also had a higher proportion of *A. niger* nests with parasitoids than fragmented forest ($\chi^2_1 = 7.06$, $p = 0.008$; Table 3). In fact, phorids attacking ants were collected only in 3 out of 8 forest fragments sampled, where *A. niger* was present.

Only two phorid species were abundant enough for comparisons at phorid species level, *Ap. lutheihalteratus* and *M. catharinensis*. The first species was not present in the fragmented forest, and in the continuous forest 17.3% of the

Table 2. Interactions between *Acromyrmex* and phorid parasitoid species in two localities (+: presence; -: absence), percentage relative abundance for parasitoid species over each host (between parentheses, pooled number of parasitoids gathered in both forest types).

Ant species	Phorid species	Forest type		% relative abundance over each host
		Fragmented	Continuous	
Acromyrmex coronatus	*Myrmosicarius persecutor*	+	+	100 (2)
Acromyrmex disciger	*Neodohrniphora acromyrmecis*	+	-	100 (1)
Acromyrmex niger	*Apocephalus lutheihalteratus*	-	+	32 (21)
	Myrmosicarius catharinensis	+	+	47 (31)
	Myrmosicarius simplex	-	+	3 (2)
	Myrmosicarius tarsipennis	+	+	11 (7)
	Neodohrniphora similis	+	+	7 (5)

Table 3. Parasitoid species richness, total (and average) abundance over nests, and the proportion of *Acromyrmex niger* nests with phorids attacking in fragmented vs. continuous forests.

	Forest type	
	Fragmented	Continuous
Species richness	3	5
Abundance	5 (1)	61 (2.17)
% of nests with phorids	6	26

A. niger nests sampled had this species attacking, with most of these nests having only one *Ap. lutheihalteratus* attacking (except one nest that had three and another where 11 phorids were attacking). Meanwhile, *M. catharinensis* in the continuous forest was present in 26.9% of the *A. niger* nests sampled, and typically two phorids were attacking per trail (two phorids in median, range 1-6); however, in the fragmented forest only 5.9% of the nests had phorids of this species and in all cases only one individual was attacking ants.

Discussion

Habitat fragmentation at the Atlantic forest of southeast Brazil had a negative effect on phorids that are parasitoids of *Acromyrmex*, mainly affecting abundance. However, their ant hosts were not noticeably affected by forest fragmentation. The effect on phorids was particularly evident for the number of adult parasitoids attacking ants and the proportion of nests with parasitoids. Although species richness was also lower in the fragmented forest, the difference was due to two species, one of them with low abundance (*Myrmosicarius simplex*). There is no clear information on whether historically higher anthropogenic use in the fragmented forest area, which is a covariate always present in forest fragmentation processes, would have an important influence in our data. However, across the Atlantic forest recent history, the human intervention is very similar, with conversion of forests to crop fields and pastures after (Dean, 1997). Thus, our results adds to the body of knowledge that posit parasitoids as very susceptible animals to this type disturbance (Kruess & Tscharntke, 2000; Cagnolo et al., 2009).

Two differences between these parasitoids and their hosts seem to make phorids more affected by habitat fragmentation than their ant hosts. The first one is related to dispersal abilities. Leaf-cutting ants disperse mainly during the nuptial flight, when male and female alates fly out their parental nest to find mates, and later establish a new nest (Hölldobler & Wilson, 1990). Although it is not known how long the *Acromyrmex* studied here can disperse, *Atta* species can disperse for several kilometers (Helmkampf et al., 2008). This exceeds the distance among neighbor forest fragments in the study area (Fig. 1). Meanwhile phorids are not known to disperse much from their hosts' nests. Nothing is known of the dispersion ability of leaf-cutting ants' phorids, but other phorids that attack fire ant are able to fly up to 650 m from their hosts nests (Morrison et al., 1999) and phorid activity was much lower in areas without nearby hosts (Philpott et al., 2009). Thus, it seems plausible that flying through a matrix with pasture where hosts are rarely present (personal observation) may complicate parasitoid arrival to forest fragments. This is supported by the fact that only 37.5% of the fragments had phorids attacking *A. niger*.

The second trait that can theoretically increase susceptibility to habitat fragmentation is specialization. Leaf-cutting ants are generalist herbivores that can use several food resources, while phorids collected here were only attacking one host species. Specialists may be at greater risk in fragmented habitats mainly because resources will become scarcer and difficult to find (Tscharntke at al., 2002). Because we did not find differences in resource availability for phorids, i.e. host nest density, specializing in one host species for these phorids did not mediate the abundance reduction detected in fragmented forest. In addition, most phorid species collected during this study are reported to attack other *Acromyrmex* species (Borgmeier, 1928; 1929; Brown, 1997), which were not present in the area sampled. This suggests that even when these parasitoids were acting locally as specialists, they might have the flexibility to use other hosts in the case that they need to.

Two previous studies reported a negative effect of habitat fragmentation on the abundance of phorid parasitoids of *Atta* leaf-cutting ants (Rao, 2000; Almeida et al., 2008). One showed that the proportion of nests with phorids was lower in small forested islands compared to large islands or the mainland with continuous forest (Rao, 2000). The other study showed lower phorid abundance and attack rates in nests that were located on the edge of the fragment compared to nests that were more than 200 m from the edge (Almeida et al., 2008). This negative effect was explained by unfavorable climatic conditions at the edge forest, such as higher temperature, lower humidity and greater variation of these variables (Almeida et al., 2008). However, phorid species that are parasitoids of ants differ in their climatic tolerances and microclimate preferences (Folgarait et al., 2005; 2007; Elizalde & Folgarait, 2010, Gomes et al., 2013).

Moreover, in other host-parasitoid system, some parasitoid species showed a higher population size in continuous forest area, but other species were more abundant in the fragmented forest (Roland & Taylor, 1997). These facts highlight the importance of testing the effect of habitat fragmentation at the species level. In our study, the two most frequently collected phorid species were less abundant or not collected at all in the fragmented forest. Therefore, the negative effect of habitat fragmentation seems to be general for phorid species attacking *Acromyrmex niger* in the Atlantic forest of Rio de Janeiro.

Phorid parasitoids attacking *Atta* are well-known, especially in Brazil (Tonhasca, 1996; Erthal & Tonhasca, 2000; Tonhasca et al., 2001; Bragança et al., 2002; 2003; 2009; Bragança & Medeiros, 2006). However, parasitoids attacking *Acromyrmex* are poorly studied, and all work done remounts to studies of Frey Borgmeier around 1930 (Borgmeier, 1928; Borgmeier, 1929) and studies in Argentina (Elizalde & Folgarait, 2011; 2012). Because phorid species attacking *Atta* are different from those attacking *Acromyrmex* (Elizalde & Folgarait, 2011), the information gathered for *Atta*–phorid system cannot be extrapolated to *Acromyrmex*–phorid system. Thus, this study contributes to the knowledge of phorids using *Acromyrmex* hosts. Seven phorid species were found attacking *Acromyrmex*, most of them over *A. niger*. In the continuous forest, *A. niger* had a very high parasitoid load compared to what is frequently found in leaf-cutting ant-phorid parasitoid assemblages (Elizalde & Folgarait, 2011; Elizalde et al., in rev.). All phorid species reported to attack *Acromyrmex* in the region (Borgmeier, 1928; 1929) were collected during this work, suggesting that our sampling was enough. The only exception was *Ap. lamellatus*, which was recorded in association with *A. niger* (Borgmeier, 1926; as cited in Brown, 1997), although it is not known whether this is a parasitoid of that ant species. Few nests had two or more phorid species attacking ants at the same time, and that only occurred in the continuous forest. This low overlap of phorid species in nests, coupled with the very low abundance of phorids attacking ants in each nest in forest fragments, ruled out an effect of interactions among phorid species influencing the observed phorid abundance pattern.

Our work also showed that even when phorid abundance is considerably reduced in forest fragments, possibly because of their inability to reach fragments, phorids of some species are able to live there. Because leaf-cutting ants are agricultural pests, and agricultural activities are among the main drivers of habitat fragmentation (Foley et al., 2005), it is necessary to understand how leaf-cutting ants' natural enemies such as phorids are affected by forest fragmentation. An important management tool to control pests in agricultural croplands is to leave fragments of native forest around crops, which function as refuges for natural enemies (Bragança et al., 1998; Zanetti et al., 2000). Since some phorid parasitoids were able to live on fragments, more studies on the population dynamics of these phorids on fragmented landscapes are necessary to understand if and how forest fragments could function as reservoirs for parasitoids of leaf-cutting ants.

Acknowledgments

We are grateful to Fábio Souto Almeida and Luana Priscila de Carvalho Pereira for their help in the fieldwork. Special thanks to Nicholas and Raquel Locke, from REGUA, for providing invaluable logistical support. Farmers from Vassouras-Barra do Piraí region kindly authorized our fieldwork in the forest fragments. FAPERJ granted JMQ a scholarship (Proc.101.472/2010). LE thanks Fundación Bunge y Born (Argentina). Ants and parasitoids were collected under permit number SISBIO-14674.

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