



Ants associate with microlepidoptera galleries in leaves of *Acrostichum danaeifolium* Langsd. & Fisch.

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ABSTRACT

Acrostichum danaeifolium, a Neotropical fern, occurs preferentially in marshy areas or at the margins of lakes and mangroves. Microlepidoptera larvae burrow through the petioles of the fern, preferentially on the non-expanded leaves. The galleries in the petiole create a new microhabitat, harboring a rich fauna of arthropods. The aim of the present study was to assess the richness of ants associated with its petiole. The study was conducted in a population of *A. danaeifolium* from the Atlantic Forest in Rio de Janeiro state, Southeastern Brazil. Six collections were carried out every two months (2009-2010), three in the dry and three in the rainy season. The leaves were divided into three development stages: non-expanded leaves (NEL), expanded leaves (EL) and senescent leaves (SL). Seven leaves from each phase were randomly collected from seven individuals. A total of fifteen ant species were recorded. The species with the highest frequency and density in fern petioles were *Camponotus crassus* and *Crematogaster curvispinosa*. The highest ant richness and abundance was found in senescent leaves. The high number of ants found in the petioles of *Acrostichum danaeifolium* qualifies it as a potential key species in the marshes and flooded areas where it occurs.

Introduction

Since ferns have no flowers, most researchers have long ignored the potential of fern-animal interactions (Watkins Junior et al., 2008). However, these interactions may occur via herbivory (Mehlreter, 2010), with the presence of domatia (Gómez-Pignataro, 1974), leaf nectaries (Koptur et al., 1982), crypticity (Santos and Wolff, 2015) and galls (Santos et al., 2019a). Mutualistic (Jermy and Walker, 1975; Gómez-Pignataro, 1977; Walker, 1986; Gay, 1993), antagonistic (Farias et al., 2018) and commensal interactions (Mehlreter et al., 2003; Santos et al., 2019b) have been recorded between ferns and ants. The ants have also established poorly understood relationships with fern leaf nectaries (Page, 1982; Koptur et al., 1982, 1998; Tempel, 1983; Heads and Lawton, 1984, 1985).

In ferns, there are few records of ants using the cavities produced by microlepidoptera larvae on leaf petioles as shelter (Mehlreter et al., 2003; Santos and Mayhé-Nunes, 2007), as well as on senescent galls after the inducing insect hatch (Santos et al., 2019b). Despite their

scarcity, studies demonstrate the importance of cavities and galleries in the stems and petioles of plants, and fallen twigs on the soil as a source of shelter and expansion for ant colonies (Fernandes et al., 2019).

Acrostichum danaeifolium Langsd. & Fisch. (Pteridaceae) (Figure 1a) is a fern species that occupy primarily marshy areas, margins of lakes and mangroves, floodable fields and clay and brackish soils, forming sparse to dense populations (Tryon and Tryon, 1982). Studies in a Mexican mangrove recorded an average density of 5,555 plants ha⁻¹ of *A. danaeifolium*, with a clumped distribution pattern (Mehlreter and Palacios-Rios, 2003). So, it can be a focal species for the establishment of ants and other arthropod species in the marshes and flooded areas where it occurs. Mehlreter et al. (2003) reported that these ferns were infested with the larvae of a non-identified species of microlepidoptera, which produced galleries in the petioles of the fern leaves, thereby forming a microhabitat that could be subsequently colonized by ants and other organisms. The authors observed that ant colonies move from dead to young leaves of the same or another *A. danaeifolium* individual, though they do not present data on ant richness and abundance in the different leaf phases.

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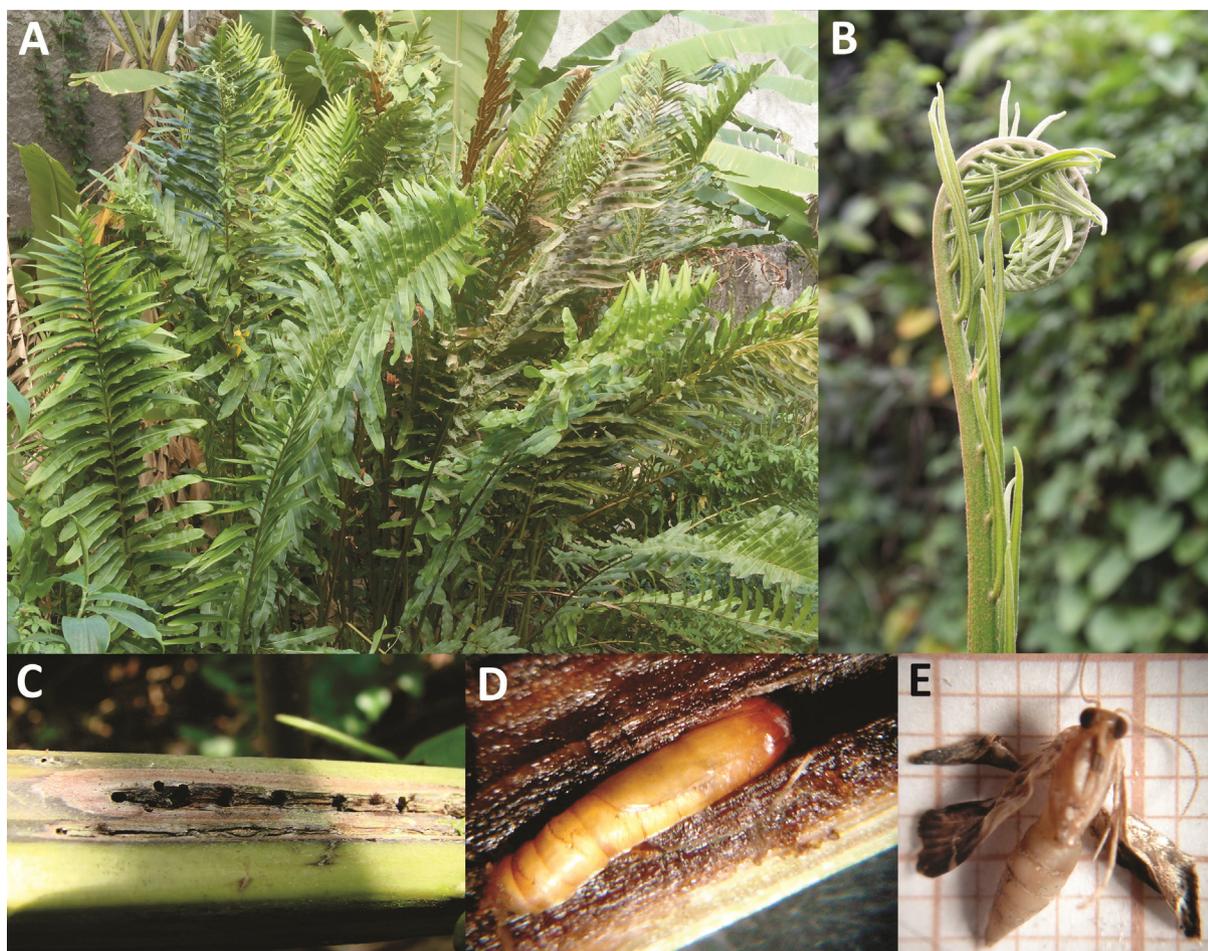


Figure 1 A- The fern species *Acrostichum danaeifolium*, habit. B- Crozier (non-expanded leaf). C- Petiole of the fern leaf with holes and galleries excavated by the microlepidoptera larvae. D- Longitudinal section of the petiole showing the microlepidoptera pupa inside. E- Microlepidoptera adult.

The present study aimed to analyze ant richness and abundance associated with the petiole of a Brazilian population of the fern *A. danaeifolium*, at different leaf phases (non-expanded, expanded, and senescent) and seasons of the year (rainy and dry) in order to test ant use regarding leaf stage and periodicity.

Material and methods

Study area

The study was based on a population of *A. danaeifolium* in a marsh belonging to the Engenho Pequeno Environmental Protection Area (APAEP), municipality of São Gonçalo, Rio de Janeiro state, Brazil (22° 50' 55.74"S 43° 2' 25.73"W). The APAEP encompasses several Atlantic Forest fragments, at an altitude above 75m and different stages of ecological succession, with a total area of 10.05 km² (Santos and Pinto, 2006). According to the classification of Veloso et al. (1991) and subsequent analysis by the Brazilian Institute of Geography and Statistics (IBGE, 2012), this area is classified as a submontane dense ombrophilous forest. The climate is type AW, with the driest period between May and October and the rainy season occurring from November to April. Average annual temperature, relative humidity and precipitation are around 26°C, 74% and 1,060mm, respectively (Bertolino et al., 2016).

Collection and laboratory procedures

Collections were carried out every two months in different individuals of the same population, between March 2009 and January 2010, totaling six collections, divided into the dry (May, July and September) and rainy (November, January and March) seasons. Leaves of *A. danaeifolium* were divided into three development stages: non-expanded leaves (NEL), that is, those with the rachis fully expanded, but the pinnae still curled; expanded (EL) and senescent leaves (SL) that are characterized as dry, albeit still attached to the plant (Figure 1AB). Seven leaves from each phase were randomly collected from seven individuals, totaling 126 leaves. The number of non-expanded leaves (crozier and expanding leaves) of each fern was accounted and inspected for traces of microlepidoptera herbivory (galleries and cavities). All non-expanded leaves with signs of microlepidoptera herbivory were also counted.

Leaves sclerophylly or toughness is as important trait to evaluate the preference of the herbivorous in leaf attack (Coley, 1983). The petiole sclerophylly was quantified by the specific dry leaf weight per unit area (Choong et al., 1992). Petiole samples with 4cm long of NEL and EL leaves were taken. The volume (unit area in cm³) was calculated by the following equation: $\pi r^2 h$, where r = petiole radius and h = petiole height. After that the petioles were oven dried and their weight (g) noted. The petiole sclerophylly (S) was expressed by g/cm³.

Leaves (NEL, EL, SL) were packed in plastic bags and the material was screened in the laboratory. Petioles were carefully cut with razor blades

in the search for microlepidoptera (larva and pupa) and ants. All ants were euthanized and fixed in 70°GL alcohol. They were identified by Dr. Rodrigo M. Feitosa, in the Laboratory of Ant Systematics and Biology at Universidade Federal do Paraná. Botanical vouchers were deposited in the herbarium of the Faculdade de Formação de Professores da Universidade do Estado do Rio de Janeiro (RFFP) and zoological vouchers in the Padre Jesus Santiago Moure Entomological Collection, Universidade Federal do Paraná, Department of Zoology (DZUP).

Statistical analyses

Data distribution was examined using the Shapiro-Wilk test. The Kruskal-Wallis and Dunn's post hoc tests were applied to investigate the following relations: production of non-expanded leaves and seasons; non-expanded leaves with traces of microlepidoptera herbivory and seasons; and sclerophylly of the petiole of non-expanded and expanded leaves. For frequency data of abundance and richness of ants in the petioles, the Pearson's χ^2 test was applied. Principal Coordinates Analysis (PCoA) ordination was performed based on presence and absence of the ants in leaves into different development stages (NEL, EL, SL) and seasons (dry and rainy), using the Sørensen similarity index. The expected richness of ants was performed using the estimators Chao 2, Jackknife 1, Jackknife 2 and Bootstrap. The statistical tests were conducted applying the PAST (PAleontological STatistics) program, version 3.10.

Results

The petioles of *A. danaeifolium* are excavated by the larvae of a non-identified species of microlepidoptera (Figure 1). These larvae were most frequent on non-expanded leaves (Table 1). These leaves displayed less sclerophylly than expanded leaves in the dry and rainy seasons (Kruskal-Wallis H test, $\chi^2=17.8$, $P=0.001$, $N=14$ - Figure 2). There was no significant difference in microlepidoptera herbivory in the period analyzed ($\chi^2=8.05$, $P=0.076$ - Figure 3A). However, there was a significant difference in the production of non-expanded leaves ($\chi^2=29.51$, $P=0.001$), with leaf production greater in September 2009 (end of the dry season), and November (2009) and January (2010), both in the rainy season (Figure 3B).

The tunnels excavated by microlepidoptera larvae in the petioles of fern leaves (Figure 1CD) provide a suitable microhabitat occupied by a rich ant fauna (Table 2). Fifteen ant species, belonging to nine genera and three subfamilies were recorded (Table 2). Except for *Camponotus* sp. 1, *Camponotus* sp. 2, *Cephalotes minutus* (Fabricius, 1804), *Cephalotes pinelii* (Guérin-Méneville, 1844), *Monomorium floricola* (Jerdon, 1851) and *Solenopsis* sp. 1, all the ant species established nests inside the fern petioles. Among ant colonies found, four species were recorded in only one leaf, while *Crematogaster curvispinosa* Mayr, 1862 was reported in 10 leaves, *Camponotus crassus* Mayr, 1862 in eight, *Brachymyrmex* sp. 1 in six, *Pheidole* sp. 1 in five and *Brachymyrmex* sp. 2 in three leaves (Table 2).

The species with the highest frequency and density in fern petioles were *Camponotus crassus* and *Crematogaster curvispinosa* (Table 2). Most ants (10 species) were recorded exclusively inside senescent leaves. Only *Pheidole* sp. 1 was found in all leaf phases (Table 2). Ants

were found on twenty senescent leaves, nine expanded leaves and one non-expanded leaves. The highest ant richness and abundance also was found on senescent leaves (Table 3). There was a significant difference in ant abundance between the dry and rainy seasons, with the dry season exhibiting the highest abundance ($\chi^2=7.629$; $P=0.022$). This difference was not found for ant richness ($\chi^2=1.790$; $P=0.408$) (Table 3). The observed and estimated richness were similar in four indicators (Table 3).

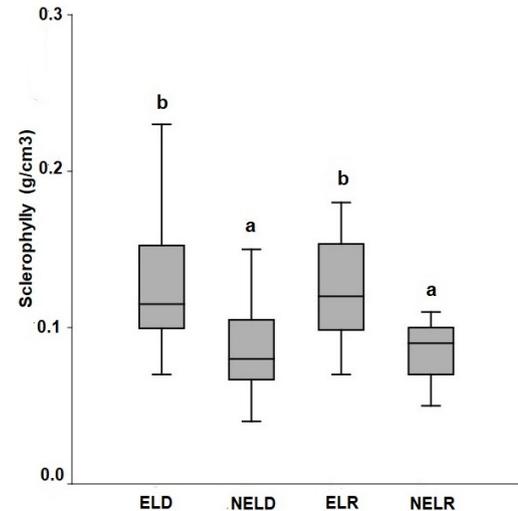


Figure 2 Sclerophylly ($S=g/cm^3$) of the petiole of non-expanded and expanded leaves of *Acrostichum danaeifolium* in the dry and rainy seasons. NELR=non-expanded leaves of rainy season; NELD=non-expanded leaves of dry season; ELD=expanded leaves of dry season; ELR=expanded leaves of rainy season. Values with the same letter do not differ ($P<0.05$) according to the Kruskal-Wallis and Dunn's post hoc tests.

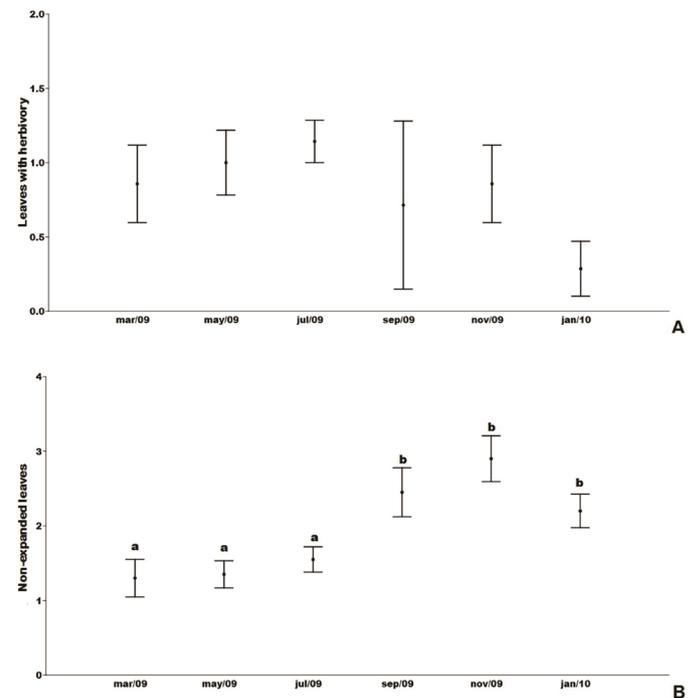


Figure 3 A- Non-expanded leaves of *Acrostichum danaeifolium* with traces of microlepidoptera herbivory. There is no significant difference between sample medians according to the Kruskal-Wallis H test ($\chi^2=8.05$ and $P=0.076$). B- Non-expanded leaf production (crozier and expanding leaves) of *A. danaeifolium*. Values with the same letter do not differ ($P<0.05$) according to the Kruskal-Wallis and Dunn's post hoc tests.

Table 1 Microlepidoptera larval and pupal abundance in each leaf phase by season. NEL= Non-expanded leaves; EL=Expanded leaves; SL=Senescent leaves. (N=126 leaves).

Microlepidoptera	Dry Season			Rainy Season		
	NEL	EL	SL	NEL	EL	SL
Larva	7	0	2	3	0	0
Pupa	5	0	0	2	0	0

Table 2 Ants associated with the petioles of *Acrostichum danaeifolium* leaves. NEL=Non-expanded leaves; EL=Expanded leaves; SL=Senescent leaves. Number of leaves analyzed (N= 126). Number of leaves with ants (30). Number of ants (N=1893).

Subfamilies	Species	Leaf phase	Occurrence (No. of leaves)	Absolute frequency (%)	Relative frequency (%)	Number of ants per leaf	Absolute density	Relative density (%)	Colonies	Season
Formicinae	<i>Brachymyrmex</i> sp.1	EL/SL	6	4.76	14.29	13.5±37.11	81	4.28	Yes (larvae and pupae)	Rainy Dry
	<i>Brachymyrmex</i> sp.2	EL/SL	3	2.38	7.15	23.67±29.02	71	3.75	Yes (pupae)	Rainy Dry
	<i>Camponotus crassus</i> Mayr, 1862	SL	8	6.35	19.07	108.63±162.99	869	45.91	Yes (eggs, immature and sexual individuals)	Rainy Dry
	<i>Camponotus (Myrmaphaenus)</i> sp. 1	SL	1	0.79	2.37	1	1	0.05	No	Dry
	<i>Camponotus</i> sp. 2	SL	1	0.79	2.37	1	1	0.05	No	Dry
	<i>Camponotus sexguttatus</i> (Fabricius, 1793)	SL	1	0.79	2.37	118	118	6.23	Yes (Eggs and sexual individuals)	Rainy
	<i>Nylanderia</i> sp.	SL	1	0.79	2.37	67	67	3.54	Yes (sexual individuals)	Dry
Myrmicinae	<i>Cephalotes minutus</i> (Fabricius, 1804)	SL	1	0.79	2.37	1	1	0.05	No	Rainy
	<i>Cephalotes pinelii</i> (Guérin-Méneville, 1844)	SL	1	0.79	2.37	2	2	0.11	No	Dry
	<i>Crematogaster curvispinosa</i> Mayr, 1862	SL/EL	10	7.94	23.84	47.20±95.18	472	24.93	Yes (Eggs, pupae and sexual individuals)	Rainy Dry
	<i>Monomorium floricola</i> (Jerdon, 1851)	SL	1	0.79	2.37	36	36	1.9	No	Rainy
	<i>Pheidole</i> sp. 1	NEL/EL/SL	5	3.97	11.92	6.80±6.19	34	1.8	Yes (Larvae and pupae)	Rainy Dry
	<i>Pheidole</i> sp. 2	SL	1	0.79	2.37	112	112	5.92	Yes (Larvae)	Rainy
	<i>Solenopsis</i> sp. 1	EL	1	0.79	2.37	1	1	0.05	No	Dry
Pseudomyrmecinae	<i>Pseudomyrmex phyllophilus</i> (Smith, F., 1858)	SL	1	0.79	2.37	27	27	1.43	Yes (Eggs and sexual individuals)	Rainy

Table 3 Abundance, richness and estimated richness of ants in the petioles of *Acrostichum danaeifolium* leaves. NEL=Non-expanded leaves; EL=Expanded leaves; SL=Senescent leaves. n=21 leaves of each phase by season. (N=126 leaves).

	Dry			Rainy			χ^2 (DF=2)
	NEL	EL	SL	NEL	EL	SL	
Abundance	5	158	914	0	95	721	7.629 ($P=0.022$)
Richness	1	4	9	0	4	8	1.790 ($P=0.408$)
Chao 2	0.6±0.4	3.3±1.6	8.4±2.8	0	3.5±1.3	7.5±3.4	
Jackknife 1	1.0±0.8	4.0±1.6	9.3±2.2	0	4.2±1.4	8.1±2.3	
Jackknife 2	1.2±1.3	4.5±2.6	10.4±3.6	0	4.4±2.4	9.2±3.9	
Bootstrap	1.3±0.6	3.5±1.1	8.2±1.6	0	5.1±1.0	5.6±1.6	

In accord with the ant community in leaves of different development stages (NEL, EL, SL) and seasons (dry and rainy), three groups were generated. One group composed by expanded leaves in the dry season (ELD), expanded leaves in the rainy season (ELR), senescent leaves in the dry season (SLD). A second group formed by non-expanded leaves in the dry season (NELD) and non-expanded leaves in the rainy season NELR. Finally, a third group formed by senescent leaves in the rainy season (SLR). In the PCoA, the axis 1 explains 55.3% and the axis 2 27.9% of the variance (total=83.2%) (Figure 4).

Discussion

In our analyses, we recorded larvae and pupae of a non-identified microlepidoptera species in petioles of *A. danaeifolium*. Many fern species may have their tissues foraged by moth borer larvae (Balick et al.,

1978; Mehlreter et al., 2003). This moth larvae attack seems to be correlated with the nutritional composition of the tissues, the presence of secondary defense metabolites and the diameter and age of the rhizomes and the petiole. According to Portugal (2011), the petiole tissues of *A. danaeifolium* are rich in mucilage, a rich source of carbohydrates.

The microlepidoptera larvae were found mostly in petioles of non-expanded leaves (Table 1), which exhibit less sclerophylly (Figure 2). Young leaves with low toughness have high rates of herbivory (Kursar and Coley, 2003). Despite the fact that larvae were found on senescent leaves, the largest number was observed on their non-expanded leaves. Similar results were found by other authors, which observed a preference of herbivores for recently expanded fern leaves or those in the expanding stage (Mehlreter et al., 2003; Schmitt and Windisch, 2005).

The leaf production of *A. danaeifolium* was greater in the end of dry season and the rainy season (Figure 3B), and crozier and senescent

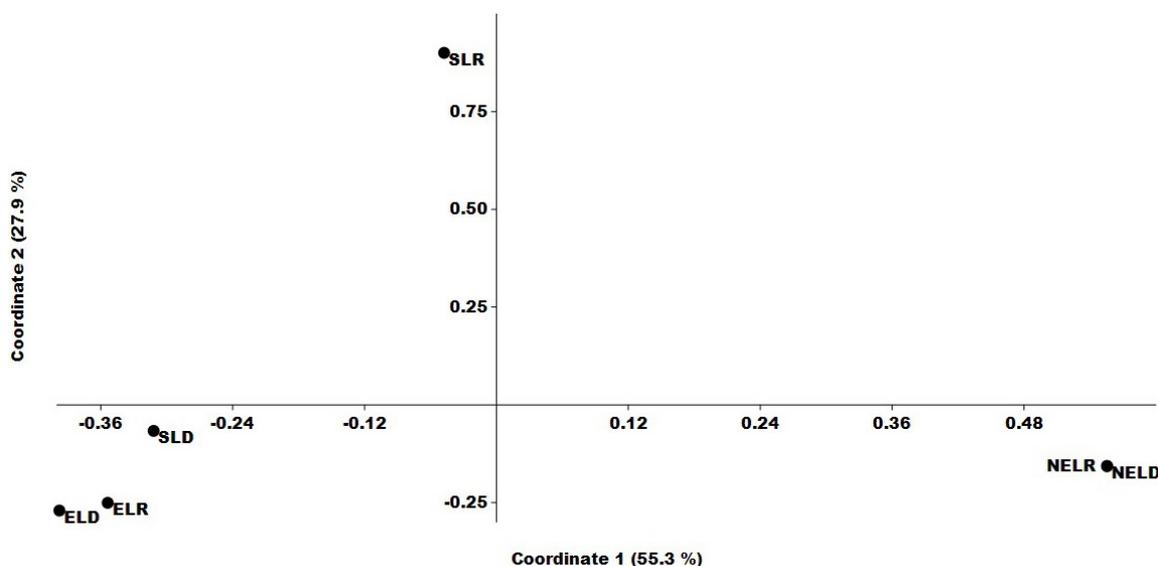


Figure 4 PCoA (Principal Coordinates Analysis) ordination diagram for the presence and absence of the ants in the different leaf stages of *Acrostichum danaeifolium* collected in the dry and rainy seasons. NELD=non-expanded leaves of dry season; NELR=non-expanded leaves of rainy season; ELD=expanded leaves of dry season; ELR=expanded leaves of rainy season; SLD=senescent leaves of dry season; SLR=senescent leaves of rainy season.

leaves were present in all the seasons of the year. Similar results were found on phenology studies of *A. danaeifolium* growing in Mexican mangrove (Mehlreter and Palacios-Rios, 2003), and Brazilian Atlantic Rain Forest (Farias and Xavier, 2011). Thus, microlepidoptera activity and the subsequent colonization of empty galleries by ants and other arthropods are recurrent in all seasons. After microlepidoptera herbivory, the non-expanded leaves survive and develop. Thus, the holes and galleries excavated by the microlepidoptera larvae could be visualized, and their presence confirmed leaf herbivory. In our study, petioles with traces of microlepidoptera herbivory, ants and other arthropods were observed during the entire observation period (Figure 3A), in line with Mehlreter et al. (2003). These authors also reported that the maximum size of *A. danaeifolium* leaves attacked or not by moth larvae was not significantly different, indicating that the damage to the petiole may not have been harmful to the fern.

Fifteen ant species, belonging to nine genera were recorded in the tunnels excavated by microlepidoptera larvae in the petioles of *Acrostichum danaeifolium*. From these, nine species established colonies inside the fern petioles, five of them with high frequency of colonies in *A. danaeifolium* leaves, as *Crematogaster curvispinosa*, *Camponotus crassus*, *Brachymyrmex* sp. 1, *Pheidole* sp. 1 and *Brachymyrmex* sp. 2 (Table 2). Even though species of *Crematogaster* used nesting in cavities of standing plants, most species of the referred genera are well-known for being extremely generalist regarding their nesting strategies, with colonies found from the soil to the canopy of tropical environments (Baccaro et al., 2015). Future studies could answer if these nests are polydomic or monodomic, because the two patterns can be identified in tropical ants of these genera (Pfeiffer and Linsenmair, 1998; Nakano et al., 2013). In comparison to the 15 ant species found here, Mehlreter et al. (2003) recorded 10 species belonging 10 genera of ants in the petioles of *A. danaeifolium* in Mexico, in most cases forming colonies.

Ants occurred on all leaf types; however, the highest ant richness and abundance was found on senescent leaves (Table 2, 3), differing from the results obtained by Mehlreter et al. (2003), where ants transferred from one old dry leaf to another younger leaf on the same or another plant. This result refutes the hypothesis that ants prefer the young leaf stages of *A. danaeifolium*.

The ant community of the SLR was different of the others leaf stages by presenting the exclusive ant species *Camponotus sexguttatus* (Fabricius, 1793), *Cephalotes minutus*, *Monomorium floricola*, *Pheidole* sp. 2, and *Pseudomyrmex phyllophilus* (Smith, F., 1858) (Figure 4, Table 2). The senescent leaves of rainy season were characterized by the highest abundance of the ant species *Crematogaster curvispinosa*, *Camponotus sexguttatus*, and *Pheidole* sp. 2. On the other hand, in senescent leaves of dry season, the more abundant species was *Camponotus crassus* (Table 2). The fertile leaves of this fern species last for approximately four months and sterile leaves 10 months (Mehlreter and Palacios-Rios, 2003). However, there are no data about how long the senescent leaves of *A. danaeifolium* persist on the environment as nesting resources for the ants, and neither why they prefer the senescent leaves. Fernandes et al. (2019) pointed that the twig morphology (length and diameter) and the presence and size of its holes can structure the occupation of twigs by ants. A similar process could be involved in ant occupation of *A. danaeifolium* leaves.

Although there was a higher abundance in the dry season, ant richness did not differ between the dry and rainy seasons (Table 3). In the dry season there are fewer plant structures that act as shelter, foraging or nidification areas, which increases visitation and ant establishment in the few plants that provide these resources (Belchior et al., 2016).

This work approached the system formed by fern (*Acrostichum danaeifolium*), microlepidoptera (non-identified species) and ants (fifteen species). We can conclude that *A. danaeifolium*, a fern species that occurs in floodable fields, has an elevated richness of ants associate with microlepidoptera galleries in the petiole of its leaves, especially in senescent ones. Battirola et al. (2004) report the importance of some key plant species in floodable systems, as refuge and breeding ground for different groups of arthropods. The high densities of *A. danaeifolium* populations (Mehlreter and Palacios-Rios, 2003), and the elevated number of ants found in its petioles could qualify it as a key species in the marshes and flooded areas where *A. danaeifolium* occurs.

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