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Article

Ants associated with fronds of the tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum*

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Abstract: *Pteridium* is a cosmopolitan genus of ferns that possess nectaries on its fronds (fern leaves), thereby attracting ants. Foliar (or extrafloral) nectaries are nectar-producing glands that are not related to pollination, but rather attract ants and other arthropods. Foliar nectaries are found in 101 fern species, belonging to 11 genera and six families. The aim of the study is to characterize the community of ants that visit the fronds of *Pteridium esculentum* subsp. *arachnoideum*, as well as daily and seasonal ant abundance in different frond development stages. The study was conducted in the Atlantic Forest of Rio de Janeiro state, Brazil. Bimonthly collections were established, where 30 expanding fronds and 30 fully expanded fronds were randomly marked. In each 1-hour shift starting at 8:30 am and ending at 5:30 pm, the fronds were observed for the presence of ants. Thirty three ant species were recorded on the *Pteridium esculentum* subsp. *arachnoideum* fronds, distributed into six subfamilies and 13 genera. The most abundant species were *Solenopsis* sp.1 and *Ectatomma tuberculatum.* Eight ant species were observed foraging the nectaries of tropical bracken fern fronds. *Ectatomma tuberculatum* has been observed feeding on the nectaries and patrolling the fronds. Ant activity peak was on mid-day during the rainy season. The tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum* has a rich (the highest recorded until now on *Pteridium* species) and diverse ant community on its fronds, mainly on the expanding fronds. The presence of generalist predatory ants (*Ectatomma tuberculatum* and *Solenopsis* sp.1) during the entire study period suggests a positive interaction between ants and *Pteridium esculentum* subsp. *arachnoideum*.
Keywords: *ant-plant interactions; Atlantic Forest; behavioral ecology; foliar nectaries; pteridophytes.*

Formigas associadas às frondes da samambaia *Pteridium esculentum* subsp. *arachnoideum*

Resumo: *Pteridium* é um gênero cosmopolita de samambaias que possui nectários em suas frondes (folhas de samambaias), atraindo formigas. Nectários foliares (ou extraflorais) são glândulas produtoras de néctar que não estão relacionadas com a polinização, mas podem atrair formigas e outros artrópodes. Nectários foliares já foram registrados em 101 espécies de samambaias, pertencentes a 11 gêneros e seis famílias. O objetivo do estudo é caracterizar a comunidade de formigas que visitam as frondes de *Pteridium esculentum* subsp. *arachnoideum,* bem como a abundância diária e sazonal das formigas em diferentes estágios foliares. O estudo foi realizado na Mata Atlântica do estado do Rio de Janeiro, Brasil. Foram estabelecidas coletas bimestrais, onde foram marcadas aleatoriamente 30 frondes em expansão e 30 frondes totalmente expandidas. Em cada turno de 1 hora com início às 8h30 e término às 17h30, as frondes marcadas foram observadas quanto à presença de formigas. Trinta e três espécies de formigas foram registradas nas frondes do *Pteridium esculentum* subsp. *arachnoideum*, distribuídas em seis subfamílias e 13 gêneros. As espécies mais abundantes foram *Solenopsis* sp.1 e *Ectatomma tuberculatum*. Foram registradas oito espécies de formigas forrageando os nectários foliares da samambaia. *Ectatomma tuberculatum* foi observada se alimentando nos nectários e patrulhando as frondes. As formigas tiveram o pico de atividade

ao meio-dia e na estação chuvosa. A samambaia tropical *Pteridium esculentum* subsp. *arachnoideum* tem uma elevada riqueza (a maior já registrada até o momento para espécies de *Pteridium*) e diversidade de formigas em suas frondes, com maior frequência nas frondes não totalmente expandidas. A presença de formigas predadoras generalistas (*Ectatomma tuberculatum* e *Solenopsis* sp.1) durante todo o período de estudo sugere uma interação positiva entre as formigas e *Pteridium esculentum* subsp. *arachnoideum*.
Palavras-chave: *interações formiga-planta; Mata Atlântica; ecologia comportamental; nectários foliares; pteridófitas.*

Introduction

Pteridium (bracken fern) is a fern genus distributed world-wide. The circumscription of species is widely discussed in the literature, about 20 morphotypes have been recognized, and several infra-specific ranks have been adopted (PPG I 2016, Thomson 2016, Schwartsburd et al. 2018). While some authors recognize only two species: *Pteridium aquilinum* (L.) Kuhn and *P. esculentum* (G. Forst.) Cockayne along their infraspecies (Thomson 2016). All the species of the genus have nectaries on their fronds (fern leaves) (Tryon & Tryon 1982), and the oldest record of nectaries in ferns was reported by Francis Darwin in 1877 for *Pteridium aquilinum* (L.) Kuhn (Lloyd 1901).

Foliar (or extrafloral) nectaries are nectar-producing glands that are not related to pollination, but rather attract ants and other arthropods (Koptur et al. 2013). Fern nectars contain a variety of amino acids and a large amount of sugar, particularly sucrose, fructose and glucose (Koptur 1992, Mehltreter et al. 2022). Foliar nectaries are found in 101 fern species, belonging to 11 genera and six families (Lloyd 1901, Koptur et al. 1982, White & Turner 2012, Mehltreter et al. 2022). Some authors believe that the nectaries promote interactions between ferns and ants (Koptur et al. 1982, 1998, Page 1982).

There are many records of ants and bees associated with the bracken fern nectaries (Page 1982, Tempel 1983, Heads & Lawton 1984, 1985, Olesen 1988; Rashbrook et al. 1992, White & Turner 2012), though some authors reported no ants on the *Pteridium* nectaries for some bracken populations (Rumpf et al. 1994). The function of nectaries remains controversial (Cooper-Driver 1990); some studies reported no benefits from ants that visited the foliar nectaries for *Pteridium* species (Tempel 1983, Heads & Lawton 1984, Rashbrook et al. 1992), while others related benefits for ants and plants (Heads 1986, Jones & Paine 2012). The highest density and frequency rates of ants have been observed on young fronds of *Pteridium* species in the rainy season (Tempel 1983, Rashbrook et al. 1992).

Many studies have characterized arthropod fauna associated with *Pteridium* spp. fronds (Lawton 1976, Balick et al. 1978, Hendrix 1980, Winterbourn 1987), while others have reported ants visiting their nectaries (Lawton 1976, Balick et al. 1978, Page 1982) and assessed the interactions between these two organisms (Page 1982, Tempel 1983, Heads & Lawton 1984, 1985, Rashbrook et al. 1992). However, few of these characterized the entire ant community present on the fronds of this fern (Douglas 1983, Tempel 1983, Heads & Lawton 1984, 1985). These studies evaluated *Pteridium* species of USA, England, Scotland, South Africa, and New Zealand. For the Neotropical Region, Ávila & Otero (2013) recorded five ant species visiting the nectaries of the croziers of *Pteridium caudatum* from Venezuela [*Brachymyrmex* sp., *Camponotus rufipes* (Fabricius, 1775), *Linepithema* sp. *Pheidole* sp., and *Solenopsis geminata* (Fabricius, 1804)]. Martins et al. (1995) recorded one species (*Atta sexdens rubropilosa* Forel, 1908) cutting pinnae and rachis of the bracken fern fronds. Santos and Mayhé-Nunes (2007) reported a single ant species [*Dolichoderus attelaboides* (Fabricius, 1775)] associated with the nectaries of *P. arachnoideum* [*Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) Thomson].

Pteridium esculentum subsp. *arachnoideum* (Kaulf.) Thomson is a tropical bracken species widely distributed in South and Central America. Despite being a native species in these regions, it has a high invasive potential and can cause several environmental problems in natural and anthropic areas (Schwartsburd et al. 2017, Oliveira et al. 2018). The present study aims to characterize the ant community on fronds of *Pteridium esculentum* subsp. *arachnoideum* (tropical bracken fern), a Neotropical fern species, as well as daily and seasonal ant abundance in different frond development stages.

Materials and Methods

1. Study area

The study was conducted in a population of *Pteridium esculentum* subsp. *arachnoideum* located in the Restinga (coastal sandy plain) of the Maricá Environmental Protection Area, in the municipality of Maricá, Rio de Janeiro state, Southeastern Brazil (22° 57' 41.05"S, 42° 53' 20.22" W). Restinga is a type of vegetation associated with the Atlantic Forest. Nimer (1972) classified Maricá's climate as hot tropical and super humid, with short dry periods. Studies that characterized Maricá's climate between 1989 and 2000 indicate that the minimum temperature is lower in winter (8.6 °C to 15.2 °C), with July as the coldest month (always below 15 °C), while the highest temperatures are recorded in summer, with means between 29.2 °C and 37.3 °C, and February being the hottest month (temperatures always above 33 °C, reaching 37.7 °C) (Pereira et al. 2001). In the study area there are only two seasons. According to Barbieri (2005), the rainy season in Southeastern Brazil occurs between October and March and the dry season between April and September.

2. Collection and laboratory procedures

Tempel (1983) divided the frond development of *Pteridium* into 6 stages. In this study, the fronds in stages 1 to 5 were considered expanding fronds, and those in stage 6 fully expanded fronds (Figure 1). Since *P. arachnoideum* has subterraneous rhizomes, the fronds were used as a sampling unit. Thirty expanding fronds and thirty fully expanded fronds were randomly marked with red ribbon, at least 2m apart to each other. Throughout the day (8:30 am–5:30 pm), the fronds were inspected during each 1-hour shift and all ants on bracken fronds collected with an entomological aspirator, to obtain the abundance of each species. The ants which were feeding on the bracken fern nectaries were recorded. Collections were carried out every two months for one year, one day (without rain) per month, between February 2009 and

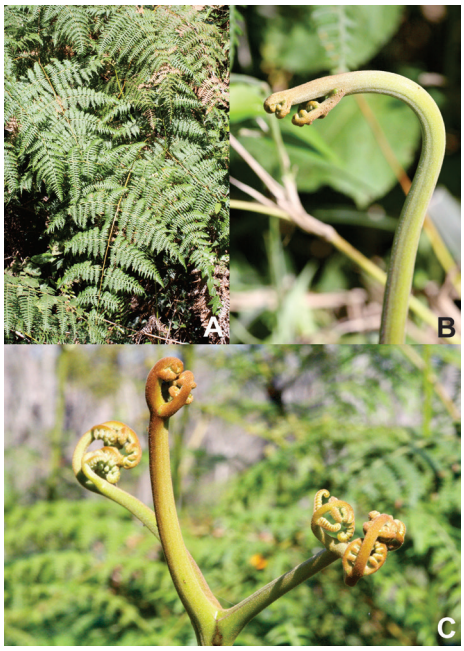

Figure 1. Frond stages of *Pteridium esculentum* subsp. *arachnoideum*. A: Fully expanded frond. B-C: Expanding frond. All photos: Marcelo Guerra Santos.

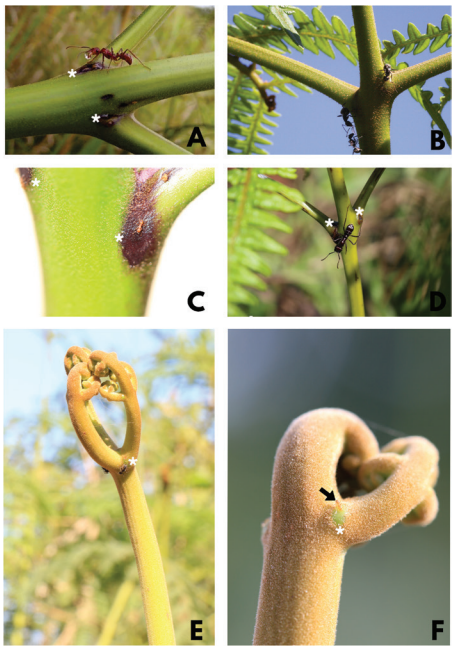

Figure 2. Ants on frond nectaries of *Pteridium esculentum* subsp. *arachnoideum*. A: *Ectatomma tuberculatum* feeding on the nectary. It's possible to see a nectar droplet in their open jaws. B: *Camponotus crassus*. C: *Wasmannia auropunctata*. D: *Ectatomma brunneum*. E: *Pheidole* sp. F: *Brachymyrmex* sp. (arrow). *Nectaries. Photo A: Isabella Rodrigues Lancellotti. Photos B, C, E, F: Marcelo Guerra Santos. Photo D: Camille Santos Carraco.

February 2010. The ants were preserved in 70% alcohol, mounted in entomological boxes (Lattke 2003), and identified by Dr. Antônio Mayhé-Nunes and Dr. Rodrigo M. Feitosa. Vouchers were deposited in the herbarium of the Faculdade de Formação de Professores da Universidade do Estado do Rio de Janeiro (RFFP 20.281) and the Padre Jesus Santiago Moure Entomological Collection, Universidade Federal do Paraná, Department of Zoology (DZUP).

3. Statistical analyses

To detect differences in ant frequencies (number of observations) between expanding and fully expanded fronds (categorical variables), we performed a Pearson's chi-squared test (Gotelli and Ellison 2011). The expected richness of ants on bracken fronds was calculated using the estimator Chao 2. It provides a minimum estimate of richness in homogeneous samples using presence and absence (incidence) data, in just one or two samples (Magurran 2013). The statistical tests were conducted in PAST (PAleontological STatistics), version 3.10 (Hammer et al. 2001).

Circular statistics were used to estimate the month of highest incidence of the ant species, time of intensity peak on fern fronds. Furthermore, the mean angle, Rayleigh test (p), and length of mean vector (r) were calculated. The program Oriana was used for the calculations of circular statistics (Kovach 2009).

Results

A total of 599 ants were observed on the fronds of *Pteridium esculentum* subsp. *arachnoideum*. Of this total, we managed to collect only 529 ants, and all were identified at least to the generic level. We recorded 33 ant species on the tropical bracken fern fronds, distributed among six subfamilies and 13 genera (Table 1). The observed richness was similar to the richness estimated by Chao 2 = 33.8 ± 6.0. Eight ant species were observed foraging the nectaries of tropical bracken fern fronds, *Brachymyrmex* sp.1 (Figure 2F), *Camponotus crassus* Mayr, 1862 (Figure 2B), *Camponotus* sp.1, *Ectatomma tuberculatum* (Olivier, 1792) (Figure 2A), *Ectatomma brunneum* (Fr. Smith, 1858) (Figure 2D), *Pheidole* sp.1 (Figure 2E), *Solenopsis* sp.1, and *Wasmannia auropunctata* (Roger, 1863) (Figure 2C). *Ectatomma tuberculatum* has also been observed patrolling the fronds.

The subfamilies with the highest ant richness were Formicinae and Myrmicinae (both with nine species). The species with the greatest abundance were *Solenopsis* sp.1 (165 individuals) and *Ectatomma tuberculatum* (151 individuals) (Figure 2A), and those with intermediate abundance were *Brachymyrmex* sp.1 (65 individuals), *Camponotus* sp.1 (26 individuals), and *Wasmannia auropunctata* (21 individuals). All other 28 ant species had an abundance of less than 10 individuals (Table 1).

The chi-squared test (X^2) demonstrated a significant difference for ant abundance between the analyzed months ($X^2 = 397.17$, DF = 6, $P < 0.000001$), with the higher abundance in October (100 individuals) and December (226 individuals), both in the beginning of the rainy season (Table 1). October and December are the months most likely to find 25 of the 33 species recorded, among them the species with the highest abundance, *Ectatomma tuberculatum* and *Solenopsis* sp.1 (October and December respectively). April, June, and August (dry season), and February (end of the rainy season) are the months with the lowest probability of finding ant species on *Pteridium esculentum* subsp. *arachnoideum* (Table 1).

There was a significant difference in the frequency of ants (number of observations) visiting the expanding and fully expanded fronds of *Pteridium esculentum* subsp. *arachnoideum* in all the months observed, with ants showing a preference for the former (Table 2). Most ants (19 species) have their highest visitation intensity peak between 10:30 am and 1:30 pm, including the species with the highest abundance, *Solenopsis* sp.1 and *Ectatomma tuberculatum* (Table 3).

Table 1. Abundance and circular statistical tests (month of highest incidence of the species and Rayleigh test (*p*) of ant species collected on the fronds of *Pteridium esculentum* subsp. *arachnoideum*, between February 2009 and February 2010, in the Restinga of Maricá, Rio de Janeiro state, Brazil. Rainy season (between October and March) and dry season (between April and September) (Barbieri 2005).

Subfamily	Ant species	Month								Relative abundance (%)	Month of highest incidence	Rayleigh test (*p*)
		Feb 9	Apr 9	Jun 9	Aug 9	Oct 9	Dec 9	Feb 10	Abundance			
Dolichoderinae	*Dorymyrmex brunneus* (Forel, 1908)	1	0	0	0	2	0	1	4	0,76	December	0,137
	Dorymyrmex sp.	2	0	0	0	1	0	0	3	0,57	Janaury	0,137
	Linepithema iniquum (Mayr, 1870)	0	0	0	1	0	0	0	1	0,19	February	< 1E-12
	Linepithema sp.	0	0	0	3	0	0	2	5	0,95	August	0,137
	Tapinoma atriceps Emery, 1888	0	0	0	1	1	1	0	3	0,57	October	0,512
	Tapinoma melanocephalum (Fabricius, 1793)	0	1	1	4	4	0	0	10	2,08	October	0,512
	Tapinoma sp.1	0	0	0	1	0	0	0	1	0,19	August	0,512
	Tapinoma sp.2	0	0	0	0	2	1	0	3	0,57	October	0,137
Ectatomminae	*Ectatomma brunneum* (Fr. Smith, 1858)	0	0	0	0	8	0	0	8	1,51	October	< 1E-12
	Ectatomma tuberculatum (Olivier, 1792)	33	9	28	4	40	32	5	151	28,54	December	< 1E-12
Formicinae	*Brachymyrmex* sp.1	0	4	4	14	13	11	19	65	12,29	December	0,895
	Brachymyrmex sp.2	0	0	0	1	1	3	0	5	0,95	October	0,512
	Camponotus crassus Mayr, 1862	1	0	0	1	1	0	1	4	0,76	August	0,512
	Camponotus leydigi Forel, 1886	0	1	0	0	1	0	0	2	0,38	October	0,512
	Camponotus sexguttatus (Fabricius, 1793)	0	0	0	1	0	0	0	1	0,19	August	0,512
	Camponotus sp.1	–	5	–	5	10	4	2	26	4,91	October	0,137
	Camponotus sp.2	0	0	0	0	8	0	0	8	1,51	October	< 1E-12
	Camponotus sp.3	0	1	0	0	0	0	0	1	0,19	April	0,512
	Camponotus sp.4	0	0	1	0	2	1	0	4	0,76	November	0,512
Myrmicinae	*Cephalotes minutus* (Fabricius, 1804)	0	0	0	0	0	1	0	1	0,19	December	0,512
	Cephalotes pusillus (Klug, 1824)	0	0	0	0	1	9	0	10	1,89	December	0,512
	Cephalotes sp.1	0	0	0	0	0	1	0	1	0,19	December	0,512
	Nylanderia sp.	0	0	0	0	0	2	0	2	0,38	October	0,137
	Pheidole sp.1	1	0	2	0	0	2	0	5	0,95	February	0,512
	Pheidole sp.2	0	0	1	0	0	2	0	3	0,57	December	0,512
	Solenopsis sp.1	1	0	0	8	1	154	1	165	31,19	December	< 1E-12
	Solenopsis sp.2	1	0	0	0	0	2	0	3	0,57	December	0,137
	Wasmannia auropunctata (Roger, 1863)	0	4	0	15	2	0	0	21	3,97	August	0,137
Ponerinae	*Neoponera villosa* (Fabricius, 1804)	*0*	*0*	2	0	0	0	0	2	0,38	August	0,137
Pseudomyrmecinae	*Pseudomyrmex gracilis* (Fabricius, 1804)	0	1	0	0	1	0	0	2	0,38	June	0,512
	Pseudomyrmex pallidus (Fr. Smith, 1855)	1	0	0	0	0	0	0	1	0,19	February	0,512
	Pseudomyrmex sp.1	3	0	0	0	0	0	0	3	0,57	February	0,033
	Pseudomyrmex sp.2	3	0	1	0	1	0	0	5	0,95	February	0,512
Abundance		**47**	**26**	**40**	**59**	**100**	**226**	**31**	**529**			

Table 2. Ant frequency (number of observations) on *Pteridium esculentum* subsp. *arachnoideum* fronds at different stages of development in the Restinga of Maricá, Rio de Janeiro state, Brazil.

Month/year	Expanding fronds	Fully expanded fronds	Chi-squared test
February 2009	37	20	5,07, *P* = 0,024
April 2009	53	18	17,25 *P* = 3,27E-05
June 2009	42	20	7,80 *P* = 0,005
August 2009	35	18	5,45 *P* = 0,019
October 2009	82	58	4,11 *P* = 0,042
December 2009	139	20	89,06 *P* < 1,0E-06
February 2010	45	12	19,10 *P* = 1,2E-05
N	**433**	**166**	

Discussion

The record of 33 ant species belonging to 13 genera is the highest ant richness recorded on *Pteridium* fronds until now, of this total, eight were observed foraging the nectaries. Tempel (1983) listed 18 nectar feeding ants, distributed on 12 genera on *Pteridium aquilinum*, in USA. This author also found Myrmicinae as the richest subfamily (9 spp.). Douglas (1983) reported nine ant species associated with the nectaries of *P. aquilinum* in USA. Ávila and Otero (2013) recorded five ant species visiting the nectaries of the croziers of *Pteridium caudatum*, in Venezuela. Heads and Lawton (1984, 1985) reported three ant species on nectaries of *P. aquilinum* in England. In Brazil, Martins et al. (1995) reported a single ant species [*Atta sexdens* (Linnaeus, 1758)] cutting pinnae and rachis of the *Pteridium* fronds. Santos and Mayhé-Nunes (2007) recorded *Dolichoderus attelaboides* (Fabricius 1775) as the only ant species associated with the foliar nectaries of *P. arachnoideum* [*Pteridium esculentum* subsp. *arachnoideum*] in the Atlantic Forest of Rio de Janeiro state.

Vargas et al. (2010) recorded 52 ant species in the litter of the Restinga of Maricá (restinga vegetation). So, the richness found on the *P. esculentum* subsp. *arachnoideum* fronds represents 63.5% of the ants registered for this region until now. For angiosperms species with foliar nectaries in Cerrado (Brazilian savanna), 34 ant species were found on *Caryocar brasiliense* Cambess. (Caryocaraceae), 24 on *Ouratea hexasperma* (A.St.-Hil.) Baill. (Ochnaceae), and 12 on *Qualea grandiflora* Mart. (Vochysiaceae) (Oliveira & Pie 1998). In mangrove vegetation, *Taliparitipernambucense* (Arruda) Bovini (Malvaceae) was visited by 19 ant species (Cogni & Freitas, 2002).

The ant visitation on *Pteridium esculentum* subsp. *arachnoideum* fronds was greater in October and December (both in the beginning of the rainy season). Tempel (1983) conducted a study in New Jersey (EUA) and found that nectar secretion by *Pteridium aquilinum* and ant visitation were more frequent from May to August, that is, in summer, with high rates of precipitation. In South Africa, the period in which ants have the greatest impact on *Pteridium* herbivores occurs between November and December, corresponding to the rainy season in this region (Rashbrook et al. 1992). These data indicate that the change in ant visitation of bracken fronds is highly associated with the summer season.

The most abundant ant species (*Brachymyrmex* sp.1, *Camponotus* sp.1, *Ectatomma tuberculatum*, *Solenopsis* sp.1, and *Wasmannia auropunctata*) on tropical bracken fern have their highest visitation intensity peak near to mid-day, between 12:00 and 2:00 pm. According to Kaspari (2003), temperature is an important factor that regulates the activities of ant populations. Increased visitation may be attributed to the natural rise in the daily activities of ants as a function of their ectothermy and exudation of foliar nectaries. *Ectatomma tuberculatum* was one of the ant species with highest abundance, and visited the fronds of *Pteridium esculentum* during 9:30 am to 4:30 pm with the intensity peak at 1:07 pm. (Table 3). This ant species presents high activity at night, with massive exiting of workers at end of the day (sunset) and massive entry in the nest at beginning of the morning (sunrise), or high foraging activity in the morning and no mass exit at sunset (Wheeler 1986). According to Valenzuela-González et al. (1995), *E. tuberculatum* foraging was mainly nocturnal during the dry season and diurnal in the rainy season. Page (1982) reported that the foliar nectaries of *Pteridium aquilinum* were more active in the morning. Mehltreter et al. (2022), analyzing 16 fern species (*Aglaomorpha* and *Campyloneurum* genera), observed that nectar secretion occurred mainly during the night and early morning, but could continue until the afternoon, depending on air humidity conditions. In fact, in Restinga of Maricá it was possible to observe a few tropical bracken ferns secreting nectar during the period close to noon (Figure 2A). But we did not measure local climatic data in these days. The nighttime period was not assessed here and probably a different ant community may be visiting the foliar nectaries of *Pteridium esculentum* subsp. *arachnoideum* at this period. However, Tempel (1983) evaluated populations of *Pteridium aquilinum* Kuhn in New Jersey (USA) at night and found no evidence of nocturnal ant activity.

Ectatomma tuberculatum and *Solenopsis* sp.1, both generalist predator ants (Wheeler 1986, Valenzuela-González et al. 1995, Wojcik et al. 2001, see also comments by Tolofo 2011 on other *Ectatomma* species), were present during the entire period of observations, and were the most abundant species on the fronds of *Pteridium esculentum* subsp. *arachnoideum*. *E. tuberculatum* has been observed feeding on the nectaries, and patrolling the fronds, whereas *Solenopsis* sp.1 was only feeding on nectaries. However, other generalist predator ants were also present in lower abundance, as follows: *Dorymyrmex brunneus* (Forel, 1908), *Dorymyrmex* sp., *Ectatomma brunneum*, *Neoponera villosa* (Fabricius, 1804), *Pheidole* sp.1, *Pheidole* sp.2, *Pseudomyrmex* sp.1 and *Pseudomyrmex* sp.2 (Table 4). Douglas (1983) observed that *Camponotus pennsylvanicus* (De Geer, 1773), *Formica obscuriventris* (Mayr, 1870), and *Formica subsericea* (Say, 1836) defend the nectaries of the developing croziers, while other smaller species such as *Tapinoma sessile* (Say, 1836), *Temnothorax rugatulus* (Emery, 1895), *Leptothorax muscorum* (Nylander, 1846), and *Lasius alienus* (Foerster, 1850) (not predatory ant species) only utilize nectar and do not seem to defend the fern croziers. The establishing mutualistic relationship between ants and foliar nectaries seems to depend on the occurrence and abundance of large or aggressive ants visiting the plants (Koptur 1984, Heads 1986).

The frequency of ants (number of observations) was greater on expanding fronds than on fully expanded fronds of *P. esculentum* subsp. *arachnoideum*. Marquis (2012) reports that phenology is vital in determining herbivore attack intensity, since the plant life cycle can allow plants to evade attack or be exposed in its most vulnerable

Table 3. Ant species abundance per hour of visitation on *Pteridium esculentum* subsp. *arachnoideum* fronds and circular statistical tests (mean time, mean angle, and length of mean vector), between February 2009 and February 2010 (seven collections), in the Restinga of Maricá, Rio de Janeiro state, Brazil. (n = 529 ants).

Ant species	Time										Time of intensity peak	Length of mean vector (*r*)
	8:30 AM	9:30 AM	10:30 AM	11:30 AM	12:30 PM	1:30 PM	2:30 PM	3:30 PM	4:30 PM	5:30 PM		
Brachymyrmex sp.1	2	3	4	11	14	6	7	14	5	0	12:52 (193,095°)	0,859
Brachymyrmex sp.2	0	0	0	0	1	1	1	0	2	0	02:42 (220,525°)	0,914
Camponotus crassus	0	0	0	0	0	0	1	3	0	0	03:15 (228,766°)	0,994
Camponotus leydigi	0	0	0	0	2	0	0	0	0	0	12:30 (187,5°)	0,697
Camponotus sexguttatus	0	0	1	0	0	0	0	0	0	0	10:30 (157,5°)	1
Camponotus sp.1	0	0	3	4	4	6	7	2	0	0	01:37 (204,485°)	0,931
Camponotus sp.2	0	0	3	3	1	0	0	1	0	0	11:40 (175,209°)	0,921
Camponotus sp.3	0	0	0	0	0	0	0	0	1	0	04:30 (247,5°)	1
Camponotus sp.4	0	1	1	0	1	0	1	0	0	0	01:30 (202,5°)	1
Cephalotes pusillus	0	1	1	1	0	0	0	1	6	0	03:30 (232,5°)	0,377
Cephalotes minutus	0	0	0	0	1	0	0	0	0	0	12:30 (187,5°)	1
Cephalotes sp.1	0	0	0	0	0	0	0	0	1	0	01:30 (202,5°)	1
Dorymyrmex brunneus	0	0	0	1	0	1	1	1	0	0	04:30 (247,5°)	0,394
Dorymyrmex sp.	0	0	0	0	0	2	0	0	1	0	04:30 (247,5°)	0,369
Ectatomma brunneum	0	0	2	1	1	0	3	1	0	0	01:00 (195,211°)	0,883
Ectatomma tuberculatum	0	21	21	22	14	15	21	24	13	0	01:07 (196,868°)	0,438
Linepithema iniquum	0	0	0	0	1	0	0	0	0	0	08:30 (127,5°)	0,513
Linepithema sp.	0	0	0	1	2	0	1	1	0	0	02:53 (223,266°)	0,565
Nylanderia sp.	0	0	0	0	0	0	0	2	0	0	02:30 (217,5°)	1
Neoponera villosa	0	0	0	1	0	1	0	0	0	0	02:30 (217,5°)	0,72
Pheidole sp.1	0	1	3	0	0	1	0	0	0	0	09:30 (142,5°)	0,531
Pheidole sp.2	0	1	2	0	0	0	0	0	0	0	10:30 (157,5°)	0,596
Pseudomyrmex gracillis	0	0	1	1	0	0	0	0	0	0	10:30 (157,5°)	0,494

Continue...

...Continuation

Ant species	Time										Time of intensity peak	Length of mean vector (*r*)
	8:30 AM	9:30 AM	10:30 AM	11:30 AM	12:30 PM	1:30 PM	2:30 PM	3:30 PM	4:30 PM	5:30 PM		
Pseudomyrmex pallidus	0	0	0	1	0	0	0	0	0	0	11:30 (172,5°)	0,398
Pseudomyrmex sp.1	0	0	1	2	0	0	0	0	0	0	11:10 (167,513°)	0,992
Pseudomyrmex sp.2	0	1	0	2	0	0	0	1	0	0	01:02 (195,653°)	0,381
Solenopsis sp.1	0	0	0	0	0	2	1	4	3	0	12:28 (187,177°)	0,374
Solenopsis sp.2	0	1	1	0	0	0	0	1	0	0	10:00 (150°)	0,991
Tapinoma atriceps	0	0	1	0	1	0	0	0	0	0	12:30 (187,5°)	0,476
Tapinoma melanocephalum	0	0	3	2	2	0	0	0	1	0	11:30 (172,5°)	0,707
Tapinoma sp.1	0	0	0	0	0	0	1	0	0	0	02:30 (217,5°)	1
Tapinoma sp.2	0	0	1	0	2	0	0	0	0	0	01:30 (202,5°)	0,319
Wasmannia auropunctata	0	0	4	7	1	4	0	3	2	0	01:30 (202,5°)	0,638

Table 4. Genera of ants found on *Pteridium esculentum* subsp. *arachnoideum* in the Restinga of Maricá, Rio de Janeiro state and their respective feeding habits.

Genus	Feeding habit	Reference
Brachymyrmex	Most species are omnivorous, and some exploit the sugary solutions of extrafloral nectaries or trophobiont insects.	Baccaro et al. (2015); Quirán (2005)
Camponotus	Omnivorous.	Fernández (2003)
Cephalotes	Omnivorous, feed on sugary secretions produced by membracids and extrafloral nectaries, and have a preference for pollen grains.	Baccaro et al. (2015); Moretti & Ribeiro (2006)
Dorymyrmex	Hunt live insects, including alates (flying ants). Some species collect honeydew from sap-sucking insects.	Baccaro et al. (2015)
Ectatomma	Omnivorous. Prey on annelids, gastropods and a number of arthropods, including ants, wasps, bee pupae, lizards and termites. Also frequently seen collecting sugary liquids secreted by hemipterans, extrafloral nectaries and flower and fruit exudates.	Baccaro et al. (2015); Lattke (2003); Tolofo (2011)
Linepithema	Generalists. Feed on sugary solutions from extrafloral nectaries and honeydew from hemipterans, but may be opportunist predators.	Baccaro et al. (2015)
Nylanderia	Generalists, frequently visit extrafloral nectaries.	Baccaro et al. (2015); LaPolla et al. (2011)
Neoponera	Omnivorous, generalist predators or specialists. Occasionally feed on the arillus of fallen seeds on the forest floor.	Baccaro et al. (2015); Lattke (2003)
Pheidole	Omnivorous, predators and necrophagous.	Baccaro et al. (2015); Wilson (2003)
Pseudomyrmex	Omnivorous and very aggressive. Many species are associated with plants that have extrafloral nectaries.	Baccaro et al. (2015); Whitcomb et. al (1972)
Solenopsis	Predators and necrophagous. They may explore extrafloral nectaries.	Baccaro et al. (2015); Wojcik et al. (2001)
Tapinoma	Some species feed on sugary solutions produced by aphids and coccids.	Baccaro et al. (2015)
Wasmannia	Omnivorous.	Baccaro et al. (2015); Fisher & Cover (2007)

phase, when not fully mature. Tempel (1983) found that nectar secretion is significantly higher in the first developmental stages of *Pteridium aquilinum*, and becomes practically inactive in the final stages. As such, the activity pattern of ants is correlated to foliar nectar exudation. Rashbrook et al. (1992) observed a larger number of ants on young fronds, which have more active nectaries (greater nectar exudation). Thus, it can be inferred that in the most vulnerable stage (juvenile), higher nectar production acts as a lure for ants, which sometimes protect individuals that supply nectar. In the Restinga of Maricá we observed very few full expanded fronds of the tropical bracken fern secreting nectar during the day (Figure 2A). However, almost all observed fronds (expanding and full expanded) were not secreting nectar. Even though, the ants still remained scraping the nectaries (Figures 2B–F).

According to Tempel (1993), most of the significant damage to *Pteridium aquilinum* occurs before maturity, demonstrating no need for the additional protection provided by ants in the final stage of development, and in turn, the low nectar production. Furthermore, studies conducted by Santos et al. (2005) found cyanogenesis in all young *Pteridium arachnoideum* fronds but in only 9.1% of the mature fronds. Cyanogenesis is a defensive process in which the plant releases hydrocyanic acid when injured by herbivores (Vetter 2000). The levels of phenolic substances, which may also act defensively, increase significantly during the maturation of *P. esculentum* subsp. *arachnoideum* fronds (unpublished data). Furthermore, the fronds exhibit a norsesquiterpene denominated ptaquiloside, which is responsible for toxic, mutagenic and cancerigenous action in *Pteridium* species (Yamada et al. 2007).

The tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum* has a remarkedly rich (the highest recorded until now on *Pteridium* species) and diverse ant community on its fronds, mainly on the expanding fronds, which peaks at the mid of the day in the rainy season. The presence of generalist predatory ants (*Ectatomma tuberculatum* and *Solenopsis* sp.1) during the entire study period suggests that there may be a positive interaction between ants and *Pteridium esculentum* subsp. *arachnoideum*. Future studies are needed to understand the relationship between these ants and the tropical bracken fern, especially those that interact with leaf nectaries.

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Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.XB751P> and <https://data.scielo.org/dataset.xhtml?persistentId = doi:10.48331/scielodata.XB751P>.

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