Neotropical Entomology

ISSN: 1519-566X

journal homepage: www.scielo.br/ne

ECOLOGY, BEHAVIOR AND BIONOMICS

Geographical Transition Zone of *Solenopsis* Fire Ants (Hymenoptera: Formicidae) and *Pseudacteon* Fly Parasitoids (Diptera: Phoridae) in the State of São Paulo, Brazil

MA Pesquero[1], AMPM Dias[2]

[1]Univ Estadual de Goiás, UnU de Morrinhos, Morrinhos, GO, Brasil
[2]Univ Federal de São Carlos, Depto de Ecologia e Biologia Evolutiva, São Carlos, SP, Brasil

Keywords
Host selection, community, biological control

Correspondence
Marcos A Pesquero, Rua 14, nº 625, Jardim América, Morrinhos, 75650-000, GO, Brasil; mapesq@ueg.br

Edited by Fernando L Cônsoli – ESALQ/USP

Received 07 February 2011 and accepted 12 July 2011

Abstract

Solenopsis saevissima (Smith) and *Solenopsis invicta* Buren are the most abundant and widely distributed fire ants in Brazil. The occurrence of the two fire ant species and of their parasitoids *Pseudacteon* spp. is described for a climatic and phytophysiognomic transition area in the state of São Paulo. Both fire ant species have a parapatric distribution, apparently determined by the climate: *S. saevissima* predominates in the north part of São Paulo (Aw climate), while *S. invicta* in the south (Cfa climate). A sympatric area is observed between the latitudes 21ºS and 23ºS. Two different communities of parasitic decapitating flies were associated with *S. saevissima* in the north and with *S. invicta* in the south, with a sympatric area in the municipality of São Carlos (21°58'S 47°53'W). The possible causes of this biogeographic pattern are discussed. Preference tests with *Pseudacteon* flies challenge the association of *P. litoralis* Borgmeier, *P. curvatus* Borgmeier, *P. wasmanni* Schmitz, *P. pradei* Borgmeier and *P. obtusus* Borgmeier with *S. saevissima*, and *P. dentiger* Borgmeier, *P. disneyi* Pesquero and *P. lenkoi* Borgmeier & Prado with *S. invicta*.

Introduction

Previous research has resulted in considerable knowledge about the taxonomy and geographic distribution of *Pseudacteon* decapitating flies in South America (Patrock *et al* 2009, Plowes *et al* 2009). Due to the high species richness of fire ants and the natural occurrence of parasitoids in South America, the host specificity is an important aspect to be considered when selecting natural enemies for fire ant biological control in the US (Vazquez *et al* 2004, Folgarait *et al* 2005b). Moreover, the ecological differentiation among parasitoid species such as daily activity (Pesquero *et al* 1996, Folgarait *et al* 2007a), attack place (Pesquero *et al* 1993, Orr *et al* 1997, Folgarait *et al* 2007b) and host size (Williams & Banks 1987, Campiolo *et al* 1994, Morrison *et al* 1997) has also been demonstrated to be important in species composition of local communities.

Solenopsis saevissima (Smith) and *S. invicta* Buren are the most common fire ants species in Brazil. *Solenopsis saevissima* occupies a large central area where the Brazilian savannah dominates, extending to the north, northeast and southeast regions of Brazil (Ross *et al* 2010). *Solenopsis invicta* also has a wide distribution, including Paraguay, a great extension in Bolivia, in northeastern Argentina, north of Uruguay and a north-south band of Brazil that goes from the state of Rondônia to the state of Rio Grande do Sul. Both *S. invicta* and *S. saevissima* are parapatric in Brazil, with known zones of contact in the states of Mato Grosso do Sul, São Paulo and

Paraná (Porter *et al* 1992, MacKay *et al* 1994, Shoemaker *et al* 2006).

Of the 36 described *Pseudacteon* species that parasitize fire ants in the Neotropical region, 19 are associated with *S. saevissima* and *S. invicta* in South America, and 16 are listed as common to both species of fire ants (Patrock *et al* 2009). However, 11 of these species have ranges that are mostly limited to one species or another. Only five species of parasitoids (*P. borgmeieri* Schmitz, *P. cultellatus* Borgmeier, *P. nudicornis* Borgmeier, *P. solenopsidis* Schmitz and *P. tricuspis* Borgmeier) have ranges that broadly overlap with both fire ant species (Patrock *et al* 2009). Furthermore, the oviscape of *P. nudicornis*, *P. cultellatus*, and *P. tricuspis* shows intraspecific variation (Porter & Pesquero 2001), suggesting the occurrence of populations in process of reproductive isolation. Here we describe the occurrence of *Pseudacteon* parasitoid species and their fire ant hosts in a transition zone between two different described communities for Brazil (Pesquero 1997). We have also conducted tests to determine the preference of *Pseudacteon* species for *S. saevissima* and *S. invicta* in the field.

Material and Methods

Field work was carried out in six municipalities situated in the state of São Paulo: Anhembi (AN: 22°47'S, 48°7'W), Itirapina (IT: 22°24'S, 47°54'W), São Carlos (SC: 21°58'S, 7°53'W), Rincão (RI: 21°35'S, 47°57'W), Barrinha (BA: 21°12'S, 48°10'W) and Sales Oliveira (SO: 20°52'S, 47°53'W). The region has transition characteristics of the Brazilian savanna and the Atlantic Forest (Fig 1a), and is located between the two main climatic zones according to the Köppen's classification, "Aw" to the north and "Cfa" to the south of the state (Fig 1b). Two pasture areas (0.2 ha) 5-10 km apart, located near to a river, stream or lake were demarcated in each municipality to estimate the richness and abundance of species of *Solenopsis* and *Pseudacteon*. All colonies found in the areas were disturbed with the aid of a small shovel to encourage the exit of ants and to attract the parasitoids.

A sample of fire ant workers was removed from each colony for species identification (Trager 1991). Flies were collected during the first seven hours from sunrise, a period that includes the peak of activity of all the species found in the wider region (Pesquero 1997). Flies that approached the colonies and hovered over fire ant workers in attack mode (Porter 1998) were collected with an aspirator. A cooler (circa 12°C) was used to store the flies prior to species identification (Porter & Pesquero 2001) with a hand lens (20x). Voucher specimens of *Solenopsis* and *Pseudacteon* were retained by the authors and deposited in the Museu de Zoologia, Universidade de São Paulo, state of São Paulo, Brazil.

One colony identified as *S. invicta* and another as *S. saevissima*, collected in Anhembi and Sales Oliveira, respectively, were separated from soil particles by flotation (Jouvenaz *et al* 1977), transferred to white plastic trays (35 x 40 x 10 cm) coated internally with Fluon (ACG Chemicals Americas Incorporation, Bayonne, NJ) and fed with insects, water and sugar water during

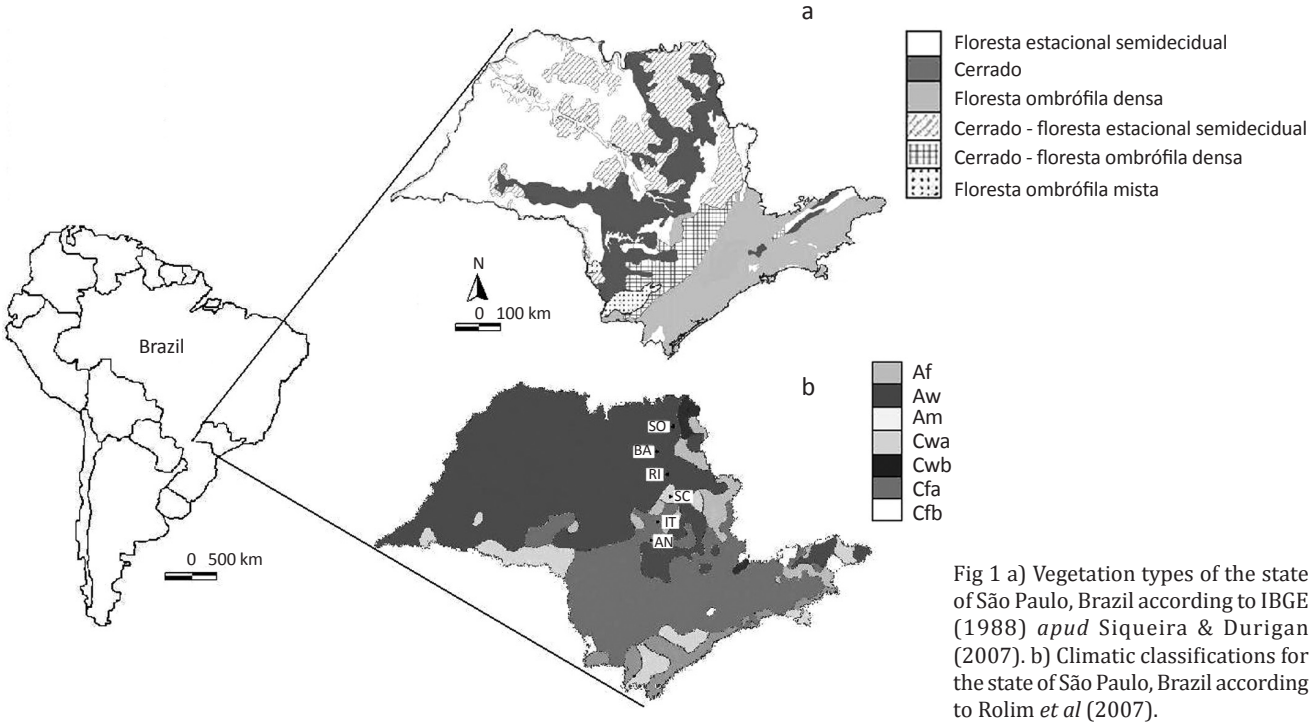

Fig 1 a) Vegetation types of the state of São Paulo, Brazil according to IBGE (1988) *apud* Siqueira & Durigan (2007). b) Climatic classifications for the state of São Paulo, Brazil according to Rolim *et al* (2007).

the study. These trays of fire ants were used in the host selection assays. In each sampling place a test of host choice was established, where the parasitoid flies could choose between the nest of *S. saevissima* or *S. invicta* simultaneously.

Trays were 10 m apart one from another to reduce mutual interference in the attraction of parasitoids, and were transferred to another distant point 50 m from the previous one at 1h intervals. The flies captured were stored and identified as described previously and released before dusk. Rates of attack, parasitoid pupation and emergence were not observed. Data on the preference of species of *Pseudacteon* for the two species of *Solenopsis* was analyzed by Wilcoxon matched pairs test with the Systat program (Systat Incorporation 2010).

Results

A total of 84 colonies of fire ants with estimates of densities varying between 10 and 70 colonies/ha (38.2 ± 6.44, n = 12) was found at the sampling sites. *Solenopsis saevissima* was dominant in the sites to the north of SC (RI, BA, SO), with 92% of the 27 colonies, while *S. invicta* was dominant in the sites to the south of SC (IT, AN), with 70% of the 20 colonies. Only *S. saevissima* colonies were found below IT to the south, and only *S. invicta* colonies were found above RI to the north. In SC, 27% of the 37 colonies belonged to *S. invicta* and 38% to *S. saevissima*, with 19% having ambiguous characteristics between both species and six colonies seemed to belong to two other fire ants species.

A total of 186 unidentified males and 398 females of *Pseudacteon* were collected. Fifteen species of *Pseudacteon* were observed in the whole sampling sites. Two communities of parasitoids were recognized: a northern community with nine species (5.11 ± 0.32, n = 6) associated with *S. saevissima*, and a southern community with eight species (4.68 ± 0.84, n = 4) associated with *S. invicta* (Fig 2). A mixture of *Pseudacteon* species of the two communities (13 species, 9 ± 0, n = 2) was observed in SC. *Pseudacteon tricuspis*, *P. nudicornis* and *P. solenopsidis* occurred in territories of both species of fire ants, and *P. borgmeieri* occurred only in SC associated with a single unidentified fire ant species. The most abundant species in the southern community were *P. wasmanni* Schmitz, *P. tricuspis*, *P. litoralis* and *P. pradei* Borgmeier, and in the northern were *P. cultellatus*, *P. affinis* Borgmeier, *P. disneyi* Pesquero, *P. fowleri* Pesquero and *P. dentiger* Borgmeier (Table 1).

A total of 106 males and 195 females belonging to 14 species of *Pseudacteon* were observed on the two trays of fire ants (Table 2). The two communities of *Pseudacteon* flies recognized the dominant *Solenopsis* species at the sampling sites (z = 3.29, n = 14, P < 0.001). In an analysis restricted to the species of parasitoids that were simultaneously attracted to the colonies of *S. invicta* and *S. saevissima* (*P. affinis*, *P. disney*, *P. dentiger*, *P. tricuspis*, *P. pradei* and *P. wasmanni*), the preference for the local host ant remained significant (z = 2.20, n = 6, P < 0.03).

Discussion

The average density of fire ant colonies in the region (38.18 ± 6.44, n=12) was intermediate if compared with the values found for *S. invicta* (30 ± 37 and 55 ± 8 colonies/ha) in surveys carried out in South America by Porter *et al* (1992, 1997). *Solenopsis saevissima* and *S. invicta* had a narrow latitudinal sympatric band in the study region situated between 22°24' and 21°35'S. However, records of *S. saevissima* in the state of Paraná

Fig 2 Distribution of *Pseudacteon* spp. according to sampling sites in the state of São Paulo, Brazil. The north and south communities are associated with *Solenopsis saevissima* and *Solenopsis invicta*, respectively. The species around São Carlos were found at sites both to the north and to the south.

Table 1 Abundance of *Pseudacteon* species in selected municipalities in the state of São Paulo, Brazil. IT+AN = sites where *Solenopsis invicta* predominates. RI+BA+SO = sites where *Solenopsis saevissima* predominates. SC = site where both species of fire ants are similarly abundant.

Pseudacteon	IT+AN	SC	RI+BA+SO	Total
Southern community				
curvatus	1	6		7
litoralis	26	5		31
nudicornis	1	2		3
obtusus[1]	12	6		18
pradei	24	2		26
solenopsidis	2	1		3
tricuspis	28	9		37
wasmanni	16	42		58
Northern community				
affinis		10	8	18
borgmeieri		5		5
cultellatus		61	36	97
dentiger		5	14	19
disneyi		24	13	37
fowleri		17	10	27
lenkoi			6	6
nudicornis			3	3
solenopsidis			1	1
tricuspis[1]			2	2
Total	110	195	93	398

[1]These biotypes are smaller and have distinctive morphological differences when compared to type specimens.

Table 2 Abundance of *Pseudacteon* on the trays of *Solenopsis invicta* and *Solenopsis saevissima* in all sampling sites (AN, IT, SC, RI, BA, SO) in the state of São Paulo, Brazil.

Pseudacteon	Fire ant species		Total
	S. saevissima	*S. invicta*	
Northern community			
affinis	6	2	8
cultellatus	36	0	36
dentiger	14	1	15
disneyi	7	1	8
fowleri	10	0	10
lenkoi	6	0	6
nudicornis	3	0	3
tricuspis[1]	2	0	2
Males	38	8	46
Southern community			
curvatus	0	1	1
litoralis	0	26	26
obtusus[1]	0	12	12
pradei	4	20	24
tricuspis	4	24	28
wasmanni	1	15	16
Males	3	68	71
Total	134	178	312

[1]These biotypes are smaller and have distinctive morphological differences when compared to type specimens.

expand its distribution area by approximately 420 km to the south of the study region into the *S. invicta* territory (Shoemaker *et al* 2006). It is possible that the climatic conditions are a limiting factor to the distribution of these ants, although the two zones have similar average annual rainfall (circa 1500 mm^3). In the north area of the state of São Paulo, characterizing the climate "Aw", the temperature, potential evaporation and hydric deficiency are higher than those of the south "Cfa" climate area (Rolim *et al* 2007). However, the occurrence of *S. invicta* in lower latitudes (Porto Velho 8°36'S, 63°54'W) (Lofgren *et al* 1975) and the high latitudinal overlap between the two fire ant species (circa 17° of difference between the most northern occurrence of *S. invicta*) (Lofgren *et al* 1975) and the most southern occurrence of *S. saevissima* (Shoemaker *et al* 2006) require more studies, including examination of competitive exclusion. The high recruitment response and dominance abilities of *S. invicta* reinforce this hypothesis (Cacaterra *et al* 2008).

The species of *Pseudacteon* observed here represent 75% of all known species of this group associated with fire ants of *S. saevissima* group in South America. The southern community corresponded to flies previously described for the region of Rio Claro (SP) (22°24'S, 47°33'W) on *S. invicta*, while the northern community corresponded to flies found in Goiânia (GO) (16°42'S, 49°15'W) on *S. saevissima* (Pesquero 1997). Populations of *P. tricuspis* and *P. nudicornis* found in the territories of *S. saevissima* and *S. invicta* have the biotypes previously described for the state of Goiás and São Paulo, respectively (Porter & Pesquero 2001). *Pseudacteon affinis* and *P. cultellatus* were identified as the biotypes found in the state of Goiás, and *P. curvatus* Borgmeier in the state of São Paulo (Porter & Pesquero 2001).

The territories of the two communities studied here were abruptly interrupted in São Carlos (SC), indicating strong environment changes. Three non-exclusive hypotheses may contribute to this geographic distribution pattern. The first hypothesis is that parasitoids can be

species specific to the fire ants and, therefore, follow the distribution of their host. Although the development of *Pseudacteon* flies on non-host fire ants species is possible under laboratory conditions, the approach and attack rates are reduced compared with local fire ant species (Folgarait *et al* 2002, Folgarait *et al* 2005b). Ecological and behavioral factors are considered as so or more important as physiological and taxonomic limitations in the determination of the host range in other groups of parasitoids (Whitfield & Wagner 1988, Morehead & Feener Jr 2000, Stireman & Singer 2003).

Although the reduced number of fire ant species colonies (n = 1) can underestimate intercolonial variation, assays for host selection demonstrated the preference of the *Pseudacteon* fly communities for the local fire ants species. However, *P. affinis*, *P. dentiger*, *P. disneyi*, *P. pradei*, *P. tricuspis* and *P. wasmanni* were attracted by the two fire ants species (Table 2). Of these parasitoids, *P. tricuspis* and *P. disneyi* have regional biotypes and attack different *Solenopsis* species (Pesquero 1997, Calcaterra *et al* 2005); *P. pradei* and *P. wasmanni* occur in areas having an association with more than one fire ant host species (Patrock *et al* 2009), but *P. affinis* and *P. dentiger* seem to be limited to the distribution area of *S. saevissima* (Pesquero 1997, Patrock *et al* 2009).

In our second hypothesis, the climatic differences between the northern and the southern areas can enforce important physiological restrictions regarding to body temperature and water balance for these small insects (Porter & Gates 1969). Indeed, Folgarait *et al* (2005a) found a significant association between climatic variables (mainly temperature and precipitation) and groupings of *Pseudacteon* species in South America. However, the limiting factors for the regional climatic variations can be overcome by acclimatization of these species. Evaluating the period of daily activity of two communities of *Pseudacteon* in places with different climates in Brazil, Pesquero (1997) reported that the majority of species in the community located in tropical climate with dry winters had crepuscular activity, while those species situated in humid climate with hot summers were active during the warmest hours of the day.

In our last hypothesis, we assume that communities can be saturated, making difficult the introduction of a new species (Ricklefs 1987). This subject is little explored in communities of *Pseudacteon*, but the predominance (84%) of local assemblies with a lower richness (up to four species) as compared with the richness observed for regional assemblies in South America (Patrock *et al* 2009), and the convergence of structure between two regional communities in Brazil (Pesquero 1997) suggest the role of competition in the community structure of these insects.

This study represents the first register of geographic transition zone between populations of fire ants *S. invicta* and *S. saevissima*, and between communities of *Pseudacteon* parasitoid flies supported by these ants in Brazil. The distribution of parasitoid flies seems to be determined by host specificity, while fire ants distribution seems to result from climatic influence. However, data on change of niche of *Pseudacteon* (Pesquero 1997) and dominance of *Solenopsis* (Calcaterra *et al* 2008) indicate that interespecific competition must also be taken into consideration in the inquiry of this phenomenon.

Acknowledgments

Nivaldo D Oliveira assisted during field collections. Rafael F Juliano (UEG - UnU Morrinhos) and two anonymous reviewers of the manuscript provided a number of helpful suggestions. This study was supported by a research assistantship provided by FAPESP.

References

Calcaterra LA, Livore JP, Delgado A, Briano JA (2008) Ecological dominance of the red imported fire ant, *Solenopsis invicta*, in its native range. Oecologia 156: 411-421.

Calcaterra LA, Porter SD, Briano JA (2005) Distribution and abundance of fire ant decapitating flies (Diptera: Phoridae: *Pseudacteon*) in three regions of southern South America. Ann Entomol Soc Am 98: 85-95.

Campiolo S, Pesquero MA, Fowler HG (1994) Size-selective oviposition by phorid (Diptera: Phoridae) parasitoids on workers of the fire ant, *Solenopsis saevissima* (Hymenoptera: Formicidae). Etologia 4: 85-86.

Folgarait PJ, Bruzzone OA, Patrock RJW, Gilbert LE (2002) Developmental rates and host specificity for *Pseudacteon* parasitoids (Diptera: Phoridae) of fire ants (Hymenoptera: Formicidae) in Argentina. J Econ Entomol 95: 1151-1158.

Folgarait PJ, Bruzzone OA, Porter SD, Pesquero MA, Gilbert LE (2005a) Biogeography and macroecology of phorid flies that attack fire ants in southeastern Brazil and Argentina. J Biogeogr 32: 353-367.

Folgarait PJ, Chirino MG, Patrock RJW, Gilbert LE (2005b) Development of *Pseudacteon obtusus* (Diptera: Phoridae) on *Solenopsis invicta* and *Solenopsis richteri* fire ants (Hymenoptera: Formicidae). Environ Entomol 34: 308-316.

Folgarait PJ, Patrock RJW, Gilbert LE (2007a) The influence of ambient conditions and space on the phenological patterns of a *Solenopsis* phorid guild in an arid environment. Biol Control 42: 262-273.

Folgarait PJ, Patrock RJW, Gilbert LE (2007b) Associations of fire ant phorids and microhabitats. Environ Entomol 36: 731-742.

Jouvenaz DP, Allen GE, Banks WA, Wojcik DP (1977) A survey for pathogens in fire ants, *Solenopsis* spp., in the Southeastern United States. Fla Entomol 60: 275-279.

Lofgren CS, Banks WA, Glancey BM (1975) Biology and control of imported fire ants. Annu Rev Entomol 20: 1-30.

MacKay WP, Porter SD, Fowler HG, Vinson SB (1994) A distribuição das formigas lava-pés (*Solenopsis* spp.) no estado de Mato Grosso do Sul, Brasil (Hymenoptera: Formicidae). Sociobiology 24: 307-312.

Morehead SA, Feener Jr DH (2000) An experimental test of potential host range in the ant parasitoid *Apocephalus paraponerae*. Ecol Entomol 25: 332-340.

Morrison LW, Dall'Aglio-Holvorcem CG, Gilbert LE (1997) Oviposition behavior and development of *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). Environ Entomol 26: 716-724.

Orr MR, Seike SH, Gilbert LE (1997) Foraging ecology and patterns of diversification in dipteran parasitoids of fire ants in south Brazil. Ecol Entomol 22: 305-314.

Patrock RJW, Porter SD, Gilbert LE, Folgarait PJ (2009) Distributional patterns of *Pseudacteon* associated with the *Solenopsis saevissima* complex in South America. 17p. J Insect Sc 9:60, available online: insectscience.org/9.60.

Pesquero MA (1997) Estrutura de comunidades de *Pseudacteon* spp (Diptera: Phoridae) parasitóides de *Solenopsis* spp. (Hymenoptera: Formicidae). Tese de doutorado, UNESP, Campus de Botucatu, Botucatu, 56p.

Pesquero MA, Campiolo S, Fowler HG (1993) Phorids (Diptera: Phoridae) associated with mating swarms of *Solenopsis saevissima* (Hymenoptera: Formicidae). Fla Entomol 76: 179-181.

Pesquero MA, Campiolo S, Fowler HG, Porter SD (1996) Diurnal pattern of ovipositional activity in two *Pseudacteon* fly parasitoids (Diptera: Phoridae) of *Solenopsis* fire ants (Hymenoptera: Formicidae). Fla Entomol 79: 455-457.

Plowes RM, Lebrun EG, Brown BV, Gilbert LE (2009) A review of *Pseudacteon* (Diptera: Phoridae) that parasitize ants of the *Solenopsis geminata* Complex (Hymenoptera: Formicidae). Ann Entomol Soc Am 102: 937-958.

Porter SD, Fowler HG, MacKay WP (1992) Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). J Econ Entomol. 85: 1154-1161.

Porter WP, Gates DM (1969) Thermodynamic equilibria of animals with environment. Ecol Monogr 39: 227-244.

Porter SD, Pesquero MA (2001) Illustrated key to *Pseudacteon* decapitating flies (Diptera: Phoridae) that attack *Solenopsis saevissima* complex fire ants in South America. Fla Entomol 84: 691-699.

Porter SD, Williams DF, Patterson RS, Fowler HG (1997) Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): Escape from natural enemies? Environ Entomol 26: 373-384.

Ricklefs RE (1987) Community diversity: relative roles of local and regional process. Science 235: 167-171.

Rolim GS, Camargo MBP, Lania DG, Moraes JFL (2007) Classificação climática de Köppen e de Thornthwaite e sua aplicabilidade na determinação de zonas agroclimáticas para o estado de São Paulo. Bragantia 66: 711-720.

Ross KG, Gotzek D, Ascunce MS, Shoemaker DD (2010) Species delimitation: a case study in a problematic ant taxon. Syst Biol 59: 162-184.

Shoemaker DD, Ahrens ME, Ross KG (2006) Molecular phylogeny of fire ants of the *Solenopsis saevissima* species-group based on mtDNA sequences. Mol Phylogenet Evol 38: 200-215.

Siqueira MF, Durigan G (2007) Modelagem da distribuição geográfica de espécies lenhosas de cerrado no estado de São Paulo. Rev Bras Bot 30: 233-243.

Stireman JO, Singer MS (2003) What determines host range in parasitoids? An analysis of a tachinid parasitoid community. Oecologia 135: 629-638.

Trager JC (1991) A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). J N Y Entomol Soc 99: 141-198.

Vazquez RJ, Porter SD, Briano JA (2004) Host specificity of a biotype of the fire ant decapitating fly *Pseudacteon curvatus* (Diptera: Phoridae) from northern Argentina. Environ Entomol 33: 1436-1441.

Whitfield JB, Wagner DL (1988) Patterns in host range within the Nearctic species of the parasitoid genus *Pholetesor* Mason (Hymenoptera: Braconidae). Environ Entomol 17: 608-615.

Williams DF, Banks WA (1987) *Pseudacteon obtusus* (Diptera: Phoridae) attacking *Solenopsis invicta* (Hymenoptera: Formicidae) in Brazil. Psyche 94: 9-13.