The flower flies and the unknown diversity of Drosophilidae (Diptera): a biodiversity inventory in the Brazilian fauna

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Abstract

Diptera is a megadiverse order, reaching its peak of diversity in Neotropics, although our knowledge of dipteran fauna of this region is grossly deficient. This applies even for the most studied families, as Drosophilidae. Despite its position of evidence, most aspects of the biology of these insects are still poorly understood, especially those linked to natural communities. Field studies on drosophilids are highly biased to fruit-breeders species. Flower-breeding drosophilids, however, are worldwide distributed, especially in tropical regions, although being mostly neglected. The present paper shows results of a biodiversity inventory of flower-breeding drosophilids carried out in Brazil, based on samples of 125 plant species, from 47 families. Drosophilids were found in flowers of 56 plant species, of 18 families. The fauna discovered showed to be highly unknown, comprising 28 species, 12 of them (>40%) still undescribed. Not taking in account opportunist species, two thirds of the diversity exclusive from flowers were undescribed. The *bromeliae* group of *Drosophila* was the most representative taxon, with eight species (six undescribed), including four polyphagous and four *Solanum*-specialised species. Different, although morphologically and ecologically similar species were found from northern and southern localities. Other taxa of restrict flower-breeding drosophilids were the subgenus *Phloridosa* of *Drosophila* and the genus *Zygothrica*. Some specimens of the genera *Cladochaeta*, *Rhinoleucophenga* and *Scaptomyza* were found, but its relation to flowers is unclear. Additionally, ten species of ample niche was found using flowers opportunistically. Localities and host plants are recorded for all species collected.

Key words: Arthropoda, flower-breeding drosophilids, host plants, Insecta, Neotropical Region, new localities, specialisation

INTRODUCTION

Dealing with the huge diversity of living forms are one of the major challenges for biological sciences. Estimates range from three to 100 millions species, 5-10 millions being the more plausible

ones, and a great portion of this biodiversity is experiencing high levels of human-caused threats (Myers *et al.*, 2000; May, 2010). The invertebrate, and especially, insect diversity account for a great proportion of the total biodiversity. Almost one million species of insects are formally described worldwide and Brazil, with a huge territory and an outstanding environmental heterogeneity, is a key country in this context, housing the highest insect diversity of the world Estimates indicate that Brazilian fauna harbours 500 thousands to one million insect species, around 10% of the insect diversity of the Earth (Rafael *et al.*, 2009).

Diptera is one of the megadiverse orders, comprising alone about 10% of the world's biodiversity. Neotropics appear to be the most diverse region in these insects, although our knowledge of Neotropical dipteran fauna remains grossly deficient (Brown, 2005). This is not untrue even for the most studied families, as Drosophilidae. For more than one century, species of this family are largely used as model organisms for a variety of studies, especially in genetical research. This undoubtedly has brought an exceptional attention for this group of organisms, stimulating early studies on taxonomy and natural history of the family (Sturtevant, 1916, 1921; Duda, 1925, 1927). In spite of this position of evidence, most aspects of the biology of these insects are poorly understood, especially those linked to natural communities.

The diversity of the family is also barely assessed. This family is one of the larger in Diptera, possessing more than 4,000 described species (Bächli, 2010), besides a great number waiting for recognition. The Brazilian fauna of drosophilids has for long being researched (Dobzhansky & Pavan, 1943, 1950; Pavan & Cunha, 1947). The number of drosophilid species currently recorded for Brazil is 304 (Gottschalk *et al.*, 2008). Although a big number, it represents, therefore, an underestimate of the total diversity. Records of drosophilids in Brazilian territory are strikingly concentrated to some regions, and inventories for most regions are still lacking (Chaves & Tidon, 2008; Gottschalk *et al.*, 2008). Furthermore, samples are greatly biased to fruit-breeders and species attracted to banana-baited traps.

Brncic (1983) listed 140 species of drosophilids associated to flowers in some manner worldwide. This number includes from very generalist species, which use flowers opportunistically, to specialised species, which depend on the flowers in all stages of life cycle. These last species are rarely detected in the traditional samples taken with fruit baits. In Neotropics, the best well-studied flower-specialised species belong to the *flavopilosa* group of *Drosophila* Fallén, 1823 (Brncic, 1962, 1966; 1978; Hofmann & Napp, 1984; Sepel *et al.*, 2000; Santos & Vilela, 2005), restrict to flowers of plants of the genus *Cestrum*. Other notable flower-breeding taxa in Neotropical Region are the groups *bromeliae*, *onychophora*, *xanthopallescens* and the subgenus *Phloridosa* Sturtevant, 1942, all belonging to the genus *Drosophila* (Pipkin, 1964; Hunter, 1979; Chassagnard & Tsacas, 1992; Val & Marques, 1996; Silva & Martins, 2004). Flower-breeding drosophilids, therefore, are

present worldwide, especially in tropical regions. Other noteworthy examples are the *aterrima* group of *Scaptodrosophila* Duda, 1923, in Africa (Tsacas *et al.*, 1988), the subgenus *Exalloscaptomyza* Hardy, 1965 of *Scaptomyza* Hardy, 1949, in Hawaii (Montague & Kaneshiro, 1982; Starmer & Bowles, 1994), *Scaptodrosophila hibisci* (Bock, 1977) and *S. aclinata* (McEvey & Barker, 2001), in Australia (Cook *et al.*, 1977; McEvey & Barker, 2001), the *elegans* subgroup of the *melanogaster* group of *Drosophila* (Sultana *et al.*, 1999; Suwito *et al.*, 2002), the genus *Colocasiomyia* de Meijere, 1924 (Carson & Okada, 1980; Okada, 1986; Sultana *et al.*, 2006) and the genus *Arengomyia* Yafuso and Toda, 2008 (Yafuso *et al.*, 2008), in Asia.

Flower-breeding species are greatly neglected by the investigations in Neotropical Region and represent a good example of the still unknown fauna of drosophilids. So, we report here, a diversity inventory of the Brazilian drosophilid fauna associated with flowers, based on an ample sampling effort on a variety of plants, providing information on host plants, localities, including many new records, and the discovery of a highly unknown diversity, comprising mainly undescribed species.

MATERIAL AND METHODS

This survey was conducted in several localities throughout the Brazilian territory (Figure 1). Most of the collections were carried out in the states of Rio Grande do Sul and Santa Catarina, the two southernmost Brazilian states. Additional samples were taken from the states of Paraná, São Paulo, Minas Gerais, Bahia, Pernambuco and Pará.

Flowers of 125 species of plants, from 47 families, were collected. They were detached during anthesis directly from the plants, or collected as recently fallen flowers in the ground. They were put in plastic bags and taken to laboratory, where they were transferred to vials with vermiculite, closed with foam stoppers and kept at 25ºC, being inspected for the emergence of drosophilid imagines. In this case, the specimens were aspirated, aged for few days in standard culture medium and identified by external morphology and terminalia, consulting specialised literature. For analysis of terminalia, postabdomens were prepared following Bächli *et al.* (2004), with minor modifications. Voucher specimens will be pinned (double-mounted) and deposited in the Museu de Ciências Naturais (MCNZ), Porto Alegre, RS, Brazil.

Plant species were identified after Souza and Lorenzi (2005) and other specialised literature. Eventually, some plants were identified by specialists. The taxonomic classification follows APG II (2003), Souza and Lorenzi (2005) and other literature, when appropriate.

RESULTS

Fauna and flora

From the 125 species of plants sampled, 56 proved to be host for flower-breeding drosophilids, spread in 18 botanical families. Plant species with no emergence of drosophilids in our collections are listed in Appendix S1 in Supporting Information.

All over, 28 species of drosophilids were found. The species found were divided, *grosso modo*, in three categories: (1) “restrict” - species which were caught repeatedly and seems to use living flowers as an exclusive or at least constant breeding site (Table 1); (2) “uncertain biology” - species of genera with obscure or unknown biology and collected only occasionally (Table 2); and (3) “opportunists” - species known to be mainly fruit-breeders, using flowers only incidentally or as a secondary resource, and preferentially fallen flowers (Table 3).

Localities

The localities where which species was found are listed below. They are given from North to South, in the following format: State: Municipality, Locality (coordinates).

(1) “Restrict” flower-breeding species

bromeliae* group of *Drosophila

***D. bromeliae* Sturtevant, 1921.** Pará: Belém, Reserva do Mocambo (01º26'34.35”S; 48º24'35.59”W, 40m); Pernambuco: Recife, UFPE campus (08º03'14”S; 34º57'00”W); Recife, UFRPE campus (08º00'45”S; 34º56'57”W); Vitória de Santo Antão, IFPE/Campus Vitória (08º06'04.1”S; 35º17'41.3”W; 152m).

***D. bromelioides* Pavan and Cunha, 1947.** São Paulo: Águas de Lindóia, Morro do Cruzeiro (22º28'43”S; 46º37'34”W); Paraná: Guarapuava, Parque do Lago (25º24'9.099”S; 51º28'30.82”W); Santa Catarina: Governador Celso Ramos, Anhatomirim Island (27º25'38.09”S; 48º33'53.89”W); Florianópolis, Ratones Grande Island (27º28'20.20”S; 48º33'43.00”W); Antônio Carlos, Centro (27º31'03.373”S; 48º46'18.23”W); Florianópolis, Ponta do Coral (27º34'23”S; 48º31'41”W); Florianópolis, Santa Mônica (27º35'34”; 48º30'53”W); Florianópolis, Morro da Lagoa da Conceição (27º35'40.9”S; 48º28'41.6”); Florianópolis, UFSC campus (27º36'08.127”S; 48º31'30.39”W); Florianópolis, Joaquina (27º36'43.9”S; 48º26'36.3”W); Rio Grande do Sul: Caxias do Sul, Grupo de Escoteiros Saint Hilaire (29º09'38.2”S; 51º08'31.7”W, 706m); Caxias do Sul, Marcopolo/BR-116 road (29º11'06.4”S; 51º10'23.8”W, 695m); Porto Alegre, Parque Farroupilha (30º02'13.0”S; 51º13'06.0”W); Porto Alegre, Parque Maurício Sirotsky Sobrinho (30º02'34”; 51º13'55”W); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W); Porto Alegre, Parque Gabriel Knijnick (30º06'12”S; 51º12'08”W); Pelotas, Balneário dos Prazeres (31º43'28.4”S; 52º11'59.5”W; 15m, and 31º44'06.5”S; 52º12'54.1”W; 21m); Pelotas, near Laranjal (31º45'28.4”S; 52º15'42.8”W; 15m); Pelotas, Fragata (31º45'18.3”; 52º23'01.1”W; 62m); Pelotas, Fragata, near Arroio Fragata (31º45'29.5”S; 52º24'05.05”W; 62m).

Type III. Santa Catarina: Antônio Carlos, Rachadel (27º29’52.8”S; 48º47’38.6”W); Rio Grande do

Sul: Porto Alegre, Parque Marinha do Brasil (30º03'16.3”S; 51º13'57.8”W); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W); Pelotas, Balneário dos Prazeres (31º43'28.4”S; 52º11'59.5”W; 15m).

Type III'. Pernambuco: Recife, UFPE campus (08º03'14”S; 34º57'00”W).

Type IV. Santa Catarina: Florianópolis, Córrego Grande (27º35'37.6”S; 48º29'37.0”W); Rio Grande do Sul: Cruz Alta, CEPPA (28º34'11"S; 53º36'53"W) (*D.* type IV of Hochmüller *et al.*, submitted); Flores da Cunha, RS-122 road (29º01'27.9”S; 51º11'41.0”W; 729m, and 29º01'37.4”S; 51º11'43.7”W; 733m); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

Type IV'. Bahia: Itaparica, Itaparica Island, (12º54’18”S; 38º40’01”W); Minas Gerais: Monte Sião, Centro (22º25'36.16”S; 46º34'10.43”W); São Paulo: Águas de Lindóia, Morro do Cruzeiro (22º28'43”S; 46º37'34”W); Paraná: São José dos Pinhais, Águas Belas (25º32'09.71”S; 49º10'52.87”W); Santa Catarina: Antônio Carlos, Rachadel (27º29'48.02”S; 48º47'39.70”W).

Type V. Santa Catarina: Florianópolis, Córrego Grande (27º35'37.6”S; 48º29'37.0”W); Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W); Pelotas, Balneário dos Prazeres (31º43'28.4”S; 52º11'59.5”W; 15m, and 31º44'06.5”S; 52º12'54.1”W; 21m).

Type VI. Pará: Belém, Reserva do Mocambo (01º26'34.35”S; 48º24'35.59”W, 40m).

Subgenus *Phloridosa* Sturtevant, 1942 (*Drosophila*)

***D. denieri* Blanchard, 1938.** Santa Catarina: Antônio Carlos, Centro (27º31'03.373”S; 48º46'18.23”W); Florianópolis, Ponta do Coral (27º34'23”S; 48º31'41”W); Rio Grande do Sul: Caxias do Sul, Marcopolo/BR-116 road (29º11'01.3”S; 51º10'14.4”W, 701m, and 29º11'06.4”S; 51º10'23.8”W, 695m); Porto Alegre, Parque Maurício Sirotsky Sobrinho (30º02'34”; 51º13'55”W); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W); Pelotas, Fragata (31º45'18.3”; 52º23'01.1”W; 62m); Pelotas, Fragata, near Arroio Fragata (31º45'29.5”S; 52º24'05.05”W; 62m).

***D. lutzii* Sturtevant, 1916.** São Paulo: Águas de Lindóia, Centro (22º28'17”S; 46º37'36”W); Águas de Lindóia, Morro do Cruzeiro (22º28'43”S; 46º37'34”W); Paraná: Guarapuava, Parque do Lago (25º24'9.099”S; 51º28'30.82”W); Santa Catarina: Governador Celso Ramos, Anhatomirim Island (27º25'38.09”S; 48º33'53.89”W); Florianópolis, UFSC campus (27º36'08.127”S; 48º31'30.39”W); Rio Grande do Sul, Caxias do Sul, Marcopolo/BR-116 road (29º11'01.3”S; 51º10'14.4”W, 701m); Rio Grande do Sul: Porto Alegre, Parque Maurício Sirotsky Sobrinho (30º02'34”; 51º13'55”W); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

Genus *Zygothrica* Wiedemann, 1830

***Z. dispar* (Wiedemann, 1830).** Santa Catarina: Florianópolis, Morro da Lagoa da Conceição (27º35'40.9”S; 48º28'41.6”W, 200m); Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***Z.* sp.1.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

(2) “Uncertain biology”

***Cladochaeta bupeo* Grimaldi and Nguyen, 1999.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***Cladochaeta* sp.1.** Rio Grande do Sul: Porto Alegre, Parque Farroupilha (30º02'13.0”S; 51º13'06.0”W).

***Rhinoleucophenga joaquina* Schmitz *et al.*, 2009.** Santa Catarina: Florianópolis, Parque Municipal das Dunas da Lagoa da Conceição, Joaquina (27º38'S; 48º28'W).

***Scaptomyza* sp.1.** Rio Grande do Sul: Porto Alegre, Parque da Marinha (30º03'40.75”S; 51º13'40.75”W); Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***Scaptomyza* sp.2.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***Scaptomyza* sp.2.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

(3) “Opportunists”

***D. cardinoides* Dobzhansky and Pavan, 1943.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. griseolineata* Duda, 1927.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. mediostriata* Duda, 1925.** Santa Catarina: Florianópolis, Ponta do Coral (27º34'23”S; 48º31'41”W).

***D. mediovittata* Frota-Pessoa, 1954.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. melanogaster* Meigen, 1830.** Pernambuco: Recife, UFPE campus (08º03'14”S; 34º57'00”W); Santa Catarina: Florianópolis, UFSC campus (27º36'08.127”S; 48º31'30.39”W).

***D. paulistorum* Dobzhansky and Pavan, 1949.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. simulans* Sturtevant, 1919.** Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. sticta* Wheeler, 1957.** Santa Catarina: Antônio Carlos, Centro (27º31'03.373”S; 48º46'18.23”W); Rio Grande do Sul: Porto Alegre, UFRGS/Campus do Vale (30º04’12.4”S; 51º07’06.9”W).

***D. tripunctata* group sp.1.** Rio Grande do Sul: Porto Alegre, Parque Farroupilha (30º02'13.0”S; 51º13'06.0”W).

***Zaprionus indianus* Gupta, 1970.** Rio Grande do Sul: Porto Alegre, Parque Farroupilha (30º02'13.0”S; 51º13'06.0”W).

DISCUSSION

The flower-breeding drosophilid fauna of Brazil proved to be strikingly unknown. From the 28 species found, 12 were still undescribed at the moment of collection, *i. e.*, > 40%. The ignorance in respect to this fauna is still more pronounced if one takes by side the opportunist fruit-breeders species and considers only the exclusive fauna of the flowers (our "restrict" and "uncertain biology" categories): 12 undescribed species out of 18, *i. e.*, two thirds of them. Undescribed species of drosophilids in Brazilian fauna are not uncommon, even in surveys based on banana-baited traps. Medeiros and Klaczko (2004) estimated that half of the *Drosophila* species of the state of São Paulo, the best sampled Brazilian state, was still undescribed. A high number of undescribed species was also collected in Santa Catarina, other relatively well-studied state, by Gottschalk *et al.* (2007) and Döge *et al.* (2008). The diversity of flower-breeding drosophilids, although clearly lower than that associated to fruits, appears to be still more unknown. This is especially astonishing considering that Drosophilidae is one of the most studied taxa of Diptera. Brown (2005) estimated that for the largest Diptera families, the rate of new described species is only 7.6 per year in the Neotropical region, and more than 1,000 years would be necessary to describe all species of Diptera in the world. Furthermore, a described species does not mean necessarily a well-known species: several described species found in the present survey are recorded for the first time in some Brazilian states or even in South America. In fact, drosophilid records in Brazil are strongly biased towards fruit-feeding species of *Drosophila*, especially in southeastern and southern localities (more exactly, near the main universities); moreover, about one third of the species recorded in Brazil are known for a single locality (Gottschalk *et al.*, 2008).

The restrict flower-breeding species

The species included here are thought to breed exclusively or preferentially in flowers. They are never or rarely attracted to fruit-baited traps. The most representative taxon in this category was the *bromeliae* group of *Drosophila*.

bromeliae group

This group showed to be the most speciose, with the greatest number of individuals and widespread, found in all sites surveyed (Figure 1). Altogether, eight species were found, with marked differences in geographical distribution (Figure 2) and host species (Table 1), from very generalist to ecologically specialised species. All this species are cryptic in respect to external morphology, but can be clearly discriminated by aedeagus morphology. Individuals of the polyphagous species start to emerge from flowers around 10-13 days after the field collection. The *Solanum*-specialised species takes a little longer, around 13-16 days.

Drosophila bromelioides was the most conspicuous species and proved to be widely

generalist, recorded in 42 host species, from 16 botanical families. Although rarely, this species is sometimes caught at low numbers even in banana-baited traps (De Toni *et al.*, 2007; Gottschalk *et al.*, 2007; Schmitz *et al.*, 2007) and under constant attention can be reared in banana-agar medium in laboratory. However, living flowers are clearly its preferred breeding site. It presented a southern distribution, in the states of Rio Grande do Sul (new southernmost locality in Pelotas), Santa Catarina, Paraná (first record) and São Paulo. Other studies have recorded it also in Goiás, Minas Gerais and Bahia (Vilela & Mori, 1999; Chaves & Tidon, 2008; Roque & Tidon, 2008). A morphologically similar species, *D. bromeliae*, was found in northern localities (Pernambuco and Pará states, first record to both) and seems to have also a similar ecology. Previously it was known only for Central America, Colombia and the Brazilian state of Mato Grosso (*Drosophila* sp.1 of Blauth & Gottschalk, 2007). It showed to be a polyphagous species, found in five host species, of five families, and also can be reared in banana-agar medium. As our sampling effort in northern Brazilian regions was lower, these numbers can not be directly compared to those of *D. bromelioides*. Future samplings in the region are necessary to clear the extent of the niche breadth of this species. It is probable that various other hosts can be found.

The other six species of the *bromeliae* group found were undescribed, and are mentioned herein as types III, III', IV, IV', V and VI.

Based on morphology, types III and III' are thought to be related species. The type III was found in the southern states of Rio Grande do Sul and Santa Catarina, while the type III' was found in the northeastern state of Pernambuco. Although also polyphagous, being found in six host species from five families, the type III exploits a very less variety of host plants comparing to the sympatric *D. bromelioides*. In turn, the type III' was found in only one host species, being more restrict that the sympatric species *D. bromeliae*. However, future sampling probably must find other host plants for it, as *Thunbergia grandiflora* is a cultivated exotic plant. Presumably, it may occupy a similar niche to its southern sibling type III, *i. e.*, polyphagous but not so generalist as *D. bromelioides* and *D. bromeliae*. Both types III and III' can be reared, although difficultly, from banana-agar medium in laboratory.

In southern localities, *D. bromelioides* and type III can occur is some hosts both sympatrically and synchronically, although seemingly with some different preferences. A great number of type III specimens were reared from *Brugmansia suaveolens*, where it generally outnumbered *D. bromelioides*. *Ipomoea alba* was an exception in its genus for apparently representing an important host for type III, whereas other species of the genus host almost exclusively *D. bromelioides*. The type III' was also find co-occurring with the more generalist *D. bromeliae* in *Thunbergia grandiflora* flowers in Pernambuco. All four species showed to be able to exploit exotic elements, suggesting that host shifts are commonplace in this group.

Contrasting to their more generalist siblings, four monophagous species complete the group, all of them using exclusively species of *Solanum* as host species. Despite some effort, no one of these species could be reared in artificial culture media in laboratory, even when some kind of *Solanum* flower juice was added to the medium. These species are being called here as types IV, IV', V and VI.

The types IV and IV' are morphologically similar and presented a north/south pattern of distribution. Despite *Solanum* sampling in northern states, the type IV was found only in the southern states of Rio Grande do Sul and Santa Catarina. Northwards, the type IV' seems to occupy its place, being found in Bahia, Minas Gerais, São Paulo, Paraná and Santa Catarina. Santa Catarina state may represent a contact zone between the two species, where they occur sympatrically or at least parapatrically. The two localities where each species were found are distant from each other just 31,5 kilometers.

Additionally, the type V was found in the southern states of Rio Grande do Sul and Santa Catarina. This species share some hosts with type IV, although the two species seem to have some different host preferences. Both species exploits *Solanum paniculatum*, separately or together; in the other hand, type IV occurs solely in *S. mauritianum*, while type V is the only found in *S. sisymbriifolium*. Other *Solanum* species were less sampled, but they also shared *S. sanctaecatharinae*. The type V showed to have a niche slightly more ample, being found in six species of *Solanum*, while the type IV was found in three species. Some specimens of the generalist *D. bromelioides* was reared from *Solanum* flowers, but in a few occasions and at low numbers, suggesting that these genus does not represent a main host for it. Finally, in a sample taken in the northern state of Pará, other species was found, the type VI. Its host plant, *S. stramoniifolium* does not occur in southern Brazil.

Solanum is a large and worldwide distributed genus, especially in tropical and subtropical regions (Mentz & Oliveira, 2004). Species sampled in the present survey are native from Neotropics and are mostly ruderal plants, occurring in pioneer types of vegetation, in roadsides, field and forest borders. However, no equivalent *Solanum*-specialised drosophilid is known in other parts of the world. The only literature record known by us is on the occurrence of *Scaptodrosophila minimeta* in flowers of *S. torvum* and *S. mauritianum* in Australia (Bock & Parson, 1981), but the ecology of this species is poorly known. It can be supposed that this species uses other natural resource, as both species of S*olanum* are native from Neotropics and introduced in Australia.

Figure 2 summarises the known geographical distribution of the species treated here and illustrates the north/south pattern of distribution presented by pairs of morphologically and ecologically similar species (*D. bromeliae* and *D. bromelioides*, types III and III', types IV and IV', respectively with a northern and a southern distribution).

Phloridosa

This small subgenus comprises only Neotropical flower-breeding species. Two species were represented in our samples, *D. denieri* and *D. lutzii*. Their time for emergence of adults was around 10-13 days after the flowers were collected. *Drosophila lutzii* are widespread in Southern United States, Mexico, Central America (Sturtevant, 1921; Chassagnard & Tsacas, 1992), and introduced in Hawaii (Montague & Kaneshiro, 1982), but only scattered sampled in South America (Pilares & Suyo, 1982, in Peru; Vilela, 1984, in Argentina; Acurio & Rafael, 2009, in Ecuador). It was recorded in Brazil for the first time only recently, by Schmitz and Hofmann (2005), in the southern states of Rio Grande do Sul and Santa Catarina, followed by Roque and Tidon (2008) in the states of Mato Grosso and Goiás, in central Brazil. In the present survey it is recorded for the first time in the states of São Paulo and Paraná. In turn, *D. denieri* seems to be restrict to South America, being referred for northern Argentina (Blanchard, 1938), Uruguay (Goñi *et al.*, 1998) and in the Brazilian states of Rio Grande do Sul, Santa Catarina (Schmitz & Hofmann, 2005), Rio de Janeiro (Frota-Pessoa, 1952) and Mato Grosso (Blauth & Gottschalk, 2007). Both species are polyphagous. In the present survey, while *D. deneri* occurred in a wider variety of botanical families, including exotic elements, most specimens of *D. lutzii* occurred in *Ipomoea*. However, this species is also recorded for different botanical families (Chassagnard & Tsacas, 1992; Roque & Tidon, 2008). The two species co-occurred in *Brugmansia suaveolens*, but generally *D. denieri* was the most common species in this plant. In the other hand, *D. lutzii* was the most common species found in all species of *Ipomoea*, except *I. alba*. Interestingly, in Pelotas, the southern locality surveyed by us, *D. lutzii* was absent, and *D. denieri* apparently took its place, occurring in *I. cairica* and *I. indica* with higher numbers of individuals when compared to localities closely northwards (Porto Alegre, Florianópolis), when it was only rarely found in such hosts. These two species, wherever found, almost always shared their host plants with species of the *bromeliae* group.

Zygothrica

It is reported that great numbers of adult flies of this genus can be found over bracket fungi in rainforests, but is questionable the kind of relation between flies and fungi. Undoubtedly, fungi actually represent breeding sites for some *Zygothrica* species (Grimaldi, 1987; Roque *et al.*, 2006; Gottschalk *et al.*, 2009), but Grimaldi (1987) suggested that in many cases they are used only as rendezvous sites. Indeed, most records for breeding sites in the genus are flowers, although they are reported only for a few species (Grimaldi, 1987). *Zygothrica dispar* is a good example of this behaviour: Burla (1954) stated that flies of this species were caught by sweeping a net over numerous fungi, but Frota-Pessoa (1952), Malogolowkin (1952) and Santos and Vilela (2005) reared the species from flowers. It was suggested before (Malogolowkin, 1952; Santos & Vilela, 2005) that this species is mainly a ground-feeder, using fallen flowers opportunistically. Contrarily,

in our samples it was reared mainly in living flowers. Time for emergence was around 15-18 days. It demonstrated a preference for forested environments, being, in fact, the principal flower-breeding species in the area of Atlantic Forest of Morro da Lagoa da Conceição, Florianópolis. The other species, *Z.* sp.1, was reared only from *Solanum* flowers. Interestingly, this situation is analogous with that found in the *bromeliae* group of *Drosophila*, with *Solanum* again requiring a specialised performance.

Species of uncertain biology

The nature of the interaction between the species included in the category "uncertain biology" and flowers of the host plants recorded in this survey is doubtful. These species are absent in the baited trap-based surveys carried out by our research team in Southern Brazil (De Toni *et al.*, 2007; Gottschalk *et al.*, 2007; Schmitz *et al.*, 2007; Döge *et al.*, 2008; and others). In the other hand, they were found only occasionally in our flower samples. If they are not specialised breeders in flowers, they may occupy still another unknown niche.

Both species of *Cladochaeta* Coquillett, 1900 found belong to the *nebulosa* group. *Cladochaeta bupeo* was known previously only by a few individuals from Panama, collected during the decades of 1950s and 1960s (Grimaldi & Nguyen, 1999). This finding represents, therefore, its first record in South America and its new southernmost locality (Porto Alegre, Rio Grande do Sul). The other species, *C.* sp.1, certainly is a related species, although undescribed. Grimaldi & Nguyen (1999), in an extensive revision of the genus, stressed the huge gap existing in the knowledge of *Cladochaeta* in the Neotropical Region, regarding especially to the situation in Brazil. The authors expect that many species of this genus remain to be recorded or described from Brazilian territory. From the 124 described species of *Cladochaeta*, only four were recorded from Brazil (Gottschalk *et al.*, 2008). The ecology of this genus is another issue that remains obscure. They are reported to be associated with spittlebug nymphs (Hemiptera, Cercopidae). The possibility that the specimens from Porto Alegre were associated with spittlebugs elsewhere in the larval stage and reached flowers to pupate can not be discarded. However, only 10-12 species have a Cercopidae host known (Grimaldi & Nguyen, 1999), and a few cases of association between *Cladochaeta* and flowers that seems not involve Cercopidae hosts are reported: between *C. floridana* (Malloch, 1924) and *Bidens pilosa* (Asteraceae) in Florida, USA, between *C. psychotria* Grimaldi & Nguyen, 1999 and *Psychotria chiriquiensis* (Rubiaceae) in Costa Rica (Grimaldi & Nguyen, 1999), and between *C.* aff. *paradoxa* and *Cestrum sendtnerianum* (Solanaceae) in São Paulo, Brazil (Santos & Vilela, 2005). The two species found in Porto Alegre were represented only by two and three individuals, which emerged 12-13 days after flowers were collected, and were not found again in subsequent samples from the same plants.

The genus *Rhinoleucophenga* Hendel, 1917 was represented by one species found in

Florianópolis, still undescribed in the occasion. Based on the seven specimens caught, it was subsequently described as *R. joaquina* (Schmitz *et al*., 2009). Its life cycle is considerably longer than other drosophilids reported here, as imagines took 20-21 days to emerge after the field collection of the flowers. The natural history of this genus is poorly understood. Some reports associate them as predators of coccids and mealybugs (Hemiptera, Coccoidea) in larval stage (Ashburner, 1981; Culik & Ventura, 2009), or as breeders in cacti (Wheeler, 1952). The presence of *Rhinoleucophenga* in flowers were never reported before. A subsequent attempt to collect it from the same plant and locality was unsuccessful.

Although being one of the larger genera of Drosophilidae, with 262 described species, *Scaptomyza* is virtually ignored in Brazil, with just three described species recorded (Gottschalk *et al.*, 2008). Three species were found in Porto Alegre and probably represent undescribed species. The time for emergence of imagines after collection ranged from 11-14 days for all species. *Scaptomyza* sp.1 (36 specimens) and *S.* sp.3 (15 specimens) belong to subgenus *Mesoscaptomyza* Hackman, 1959, while *S.* sp.2 (26 specimens) belongs to the genus *Parascaptomyza* Duda, 1924. This last subgenus was never reported for Brazil before. Specimens of this genus were mainly found during late winter of 2006, in the flowering period of some Bignoniaceae, but were not found thereafter. Although the biology of the genus is not wholly understood, some species of *Scaptomyza* are known to be important flower breeders, especially in Hawaii (Montague & Kaneshiro, 1982; Magnacca *et al.*, 2008). In Brazil, Santos and Vilela (2005) reported one individual of *Scaptomyza* sp. from *Cestrum sendtnerianum* (Solanaceae), in São Paulo.

Opportunist species

Several species found in the present survey are not supposed to present ecological niches strictly linked to flowers. Most of them are common members of the Neotropical fruit assemblages of drosophilids (De Toni *et al.*, 2001; Silva *et al.*, 2005) and are usually attracted to fruit baited traps (Tidon, 2006; De Toni *et al.*, 2007; Gottschalk *et al.*, 2007; Garcia *et al.*, 2008), as *D. cardinoides*, *D. griseolineata*, *D. mediostriata*, *D. paulistorum*, *D. melanogaster*, *D. simulans* and *Zaprionus indianus*, the last three being exotic species. The only specimen classified as *D. tripunctata* gr. sp.1 was a female from *tripunctata* group, not identified at species level, but probably also fits this situation. Except for *D. melanogaster* and *D. paulistorum*, all of these species were reared exclusively from fallen flowers. Fallen flowers constitute a substrate very distinct from living flowers, requiring a less specialised performance (Brncic, 1983), giving opportunities for generalist species, what Pipkin *et al.* (1966) called “ground-feeders”. Furthermore, the specimens of *D. paulistorum* reared from living flowers of *Allamanda polyantha* presented a strikingly reduced body size, suggesting that they passed the preadult stage at suboptimal conditions. Interestingly, specimens of *D. melanogaster* reared from living flowers of *Thunbergia grandiflora* (from Recife)

presented a *brown*-like phenotype. If this natural mutation is result of the unusual and possibly stressful breeding site is an open question. Other evidence that suggests that these species use flowers only as a secondary or incidental host is the fact that they were not found repeatedly in such hosts. *Drosophila cardinoides* was abundantly reared (n>100) from fallen flowers of *Ceiba speciosa* in late Summer of 2007, which demonstrates its ability to exploit such resource, but no other individual were found in subsequent samples of the same tree, even in the same site, indicating that this association is not constant. Other species were found in lower numbers (normally n<10). The only species found repeatedly in a host plant was *D. mediostriata* in fallen flowers of *Hibiscus pernambucensis*. This species is, nevertheless, also reared from fruits (Heed, 1957; De Toni *et al.*, 2001), although its presence in flowers was already reported (Dobzhansky & Pavan, 1950; Pikin *et al.*, 1966). Unusually, Schmitz *et al.* (2007) found this species abundantly in banana baited traps at mangrove forests of Santa Catarina Island, southern Brazil, contrasting to very lower abundances in similar surveys in other environments of the same region (De Toni *et al.*, 2007; Gottschalk *et al.*, 2007; Bizzo *et al.*, in press). *Hibiscus pernambucensis* is one of the main floristic components of peripheral areas of the mangroves in southern Brazil. However, *D. mediostriata* oviposits exclusively in fallen flowers, since only *D. bromelioides* was reared from samples of living flowers, showing a clear niche separation of the two species in the flowers of this plant.

The remaining two species are less common in diversity surveys. *Drosophila mediovitatta* was known only for Rio de Janeiro, Brazil (Frota-Pessoa, 1952), Rocha, Uruguay (Goñi *et al.*, 1998) and Rio Grande do Sul, Brazil (Gottschalk *et al.*, 2009). It was already reported from flowers before (Goñi *et al.*, 1998), but also from rotten cladodes (Goñi *et al.*, 1998) and from fungi (Gottschalk *et al.*, 2009), this last record in the same locality of the present study. Finally, *D. sticta* was already recorded from flowers before (Pipkin *et al.*, 1966; Santos & Vilela, 2005), but also in banana-baited traps (Medeiros & Klaczko, 2004). This species, found previously from El Salvador to Colombia and in the Brazilian state of São Paulo, is recorded for the first time in the states of Santa Catarina and Rio Grande do Sul (new southernmost locality in Porto Alegre). It was found again in Porto Alegre, soon after, in banana-baited traps (Carolina F. Garcia, unpubl. data, 2009).

Future directions

Our sampling was far to be exhaustive, and biased to southern localities. The huge territorial extension of Brazil and the extremely high spatial heterogeneity and diversity of flora make a complete assessment of the flower-breeding diversity of drosophilids a challenging task. So, there is a high demand for new efforts in searching for flower-breeding drosophilids in Brazil and Neotropical Region as a whole, widening both the range of geographical localities and the diversity of flora surveyed as potential hosts. Several other Drosophilidae taxa not sampled in the present

survey are known to be flower-breeding in Neotropical region, as the *onychophora* and *xanthopallescens* groups of *Drosophila* and additional species of the *bromeliae* group and the subgenus *Phloridosa* of *Drosophila*. They all share the condition of being very poorly known. Even the *flavopilosa* group of *Drosophila*, a comparatively better studied taxon, still requires better understanding. Surveys of Drosophilidae diversity are highly needed, and alternative methods of sampling must be considered besides the traditional banana-baited traps and fallen fruits. Collecting drosophilids from flowers is a relatively simple and cheap method, so it is not difficult to be included in diversity inventories. It is quite certain that many Neotropical flower-breeding species still wait for being discovered. The lack of taxonomic knowledge on this fauna may be the most prohibitive challenge that a researcher may find in dealing with its samples. The small number of taxonomists and the low value and support currently given for taxonomy is undoubtedly a major impediment, but more efforts in this area are urgently needed.

Identifying properly the taxa linked to flowers in a satisfactory biogeographical and ecological framework is a prerequisite to elucidate episodes of host shifts and the repeated evolution of flower-breeding habits within family Drosophilidae. Understanding the natural history of these insects may provide important highlights on the evolution of specialisation to host plants. The nature of the insect/plant interaction remains to be unveiled: parasitism, mutualism or just inquilinism?. Reliable information on what exactly the larvae and adults feed would be welcome. Literature reports on larvae or adults feeding on plant tissues or fluids, pollen or yeasts are more conjectural that empirical. Other issues to be addressed are the role of potentially toxic plant secondary compounds as selective factors for the adaptive process of colonizing a new host species, besides the chemosensory mechanisms related to the insect recognition of hosts. A multi-disciplinary approach would be essential for giving a light to these questions.

The occurrence of species with a broad range of generalist/specialist ecology in the *bromeliae* group of *Drosophila*, as well as evidences of marked differences in the geographical distribution of the species, provides an interesting opportunity to study events of speciation, involving potentially biogeographical or ecological factors.

Studies on tropical assemblages of drosophilids normally are challenged by the huge diversity and complexity of such associations. The study of flower-breeding drosophilids is an opportunity to study the species coexistence through a relatively simpler model. Other ecological, genetic and evolutionary mechanisms could be better understood. As Brncic (1983) stated many years ago, the study of species with restricted niches like the flower-breeding forms is advantageous because it is possible to relate their genetic structure with the ecology under simpler variables, so allowing a better understanding of the evolutionary process of the members of the family Drosophilidae as a whole.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Plant species with no emergence of drosophilids.

Table 1: Host plants for Brazilian restrict flower-breeding species of drosophilids found in the present survey.

	bromeliae group								Subgenus *Phloridosa*		*Zygothrica*	
	D. bromeliae	*D. bromelioides*	type III	type III'	type IV	type IV'	type V	type VI	*D. denieri*	*D. lutzii*	*Z. dispar*	*Z.* sp.1
Acanthaceae												
Justicia carnea											x	
Thunbergia alata *		x										
Thunbergia grandiflora *	x	x	x	x							x	
Apocynaceae												
Allamanda cathartica			x									
Allamanda polyantha		x										
Aristolochiaceae												
Aristolochia gigantea		x										
Asparagaceae												
Yucca guatemalensis		x										
Bignoniaceae												
Distictella cuneifolia	x											
Jacaranda mimosifolia #		x										
Jacaranda sp. #		x									x	
Macfadyena unguis-cati		x										
Pyrostegia venusta		x										
*Spathodea campanulata** #		x										
Tabebuia alba #		x										
Tabebuia heptaphylla #		x										
Tecoma stans		x										
Convolvulaceae												
Ipomoea alba		x	x						x			
Ipomoea asarifolia	x											
Ipomoea batatas		x								x		
Ipomoea cairica		x							x	x	x	
Ipomoea carnea fistulosa		x	x							x		
Ipomoea aff. *chiliantha*		x								x		
Ipomoea indica		x							x	x		

Ipomoea pes-caprae		x							x		
Cucurbitaceae											
Cucurbita pepo *		x						x			
Fabaceae											
Bauhinia variegata *		x									
Erythrina crista-galli #		x									
Wisteria floribunda #		x									
sp.1		x									
Hypericaceae											
Hypericum sp.1		x									
Iridaceae											
Dietes bicolor *		x									
Malvaceae											
Abutilon sp.		x									
Ceiba speciosa #		x	x								
Dombeya wallichii *		x									
Hibiscus rosa-sinensis *	x	x									
Hibiscus pernambucensis		x									
Hibiscus tiliaceus *		x						x			
Malvaviscus penduliflorus		x									
Melastomataceae											
Tibouchina sp.1		x									
Musaceae											
sp.1	x										
Passifloraceae											
Passiflora alata		x									
Passiflora edulis		x						x			
Solanaceae											
Brugmansia suaveolens		x	x					x	x	x	
Brunfelsia uniflora										x	
Solanum mauritianum				x	x						
Solanum paniculatum		x		x	x	x					
Solanum sisymbriifolium						x					
Solanum stramoniifolium							x				
Solanum sanctaecatharinae				x		x					x
Solanum sp.2						x					
Solanum sp.3		x				x					

Tropaeolaceae	
Tropaeolum majus	x
Zingiberaceae	
Hedychium coronarium *	x

* exotic species in Neotropic; # fallen flowers

Table 2: Host plants for Brazilian species of drosophilids of uncertain biology found in flowers in the present survey.

	C. bupeo	*C.* sp.1	*R. joaquina*	*S.* sp.1	*S.* sp.2	*S.* sp.3
Bignoniaceae						
Pyrostegia venusta	x			x		
Tabebuia alba #				x		
Tabebuia heptaphylla #				x	x	x
Bromeliaceae						
Dyckia encholirioides			x			
Malvaceae						
Dombeya wallichii *				x		
Dombeya tiliacea *		x				

* exotic species in Neotropic; # fallen flowers

Table 3: Host plants for Brazilian opportunist species of drosophilids found in flowers in the present survey.

	D. cardinoides	*D. griseolineata*	*D. mediostriata*	*D. mediovittata*	*D. melanogaster*	*D. paulistorum*	*D. simulans*	*D. sticta*	*D. tripunctata* gr. sp.1	*Z. indianus*
Acanthaceae										
Thunbergia grandiflora *					x					
Apocynaceae										
Allamanda polyantha						x				
Aristolochiacaea										
Aristolochia gigantea					x					
Asparagaceae										
Yucca guatemalensis #							x			x
Bignoniaceae										
Tabebuia alba #		x						x		
Tabebuia heptaphylla #				x			x			
Fabaceae										
Erythrina speciosa #									x	
Malvaceae										
Ceiba speciosa #	x							x		
Hibiscus pernambucensis #			x							

* exotic species in Neotropic; # fallen flowers

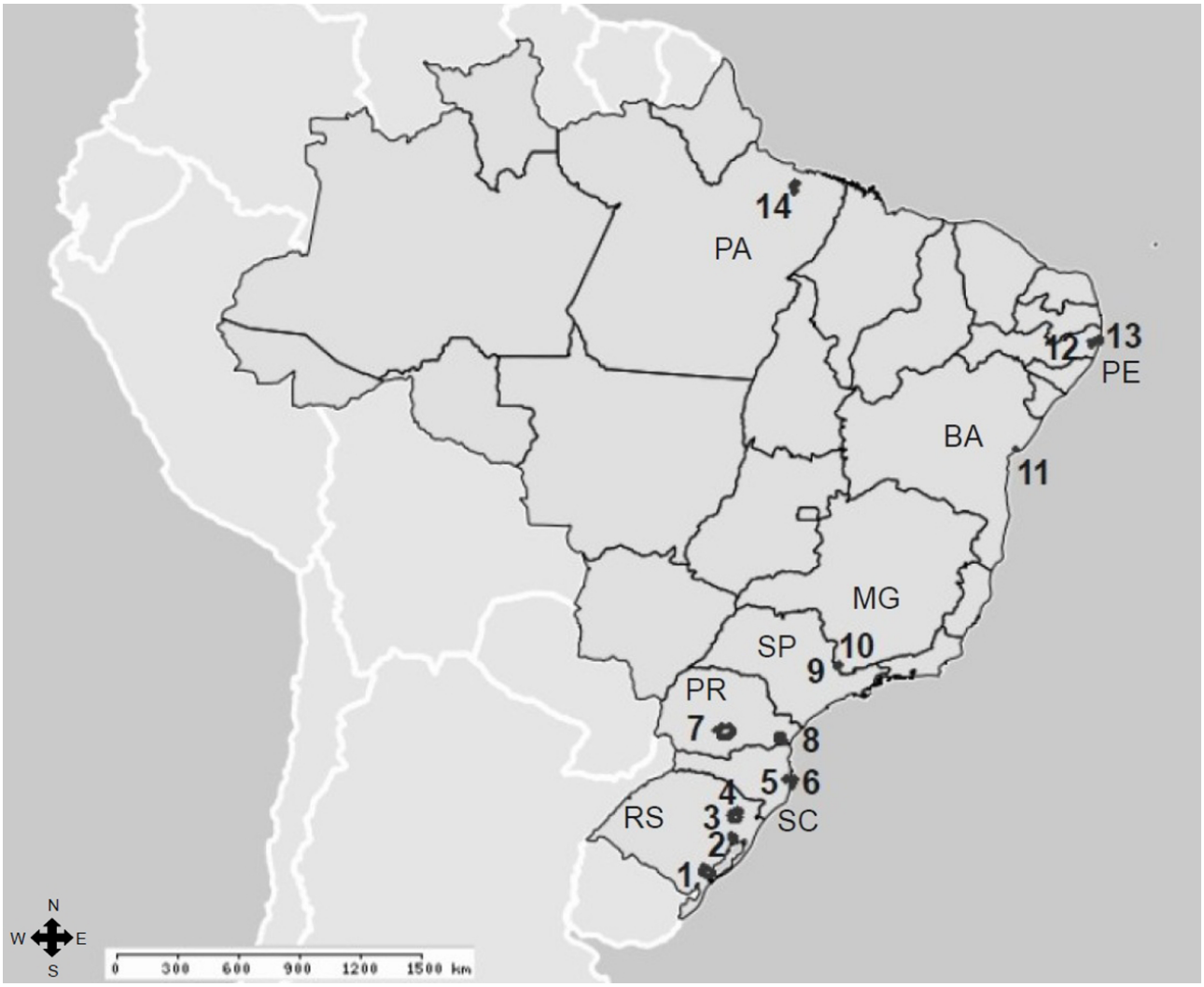

Figure 1: Map of Brazil showing the states and municipalities where samples of this study were taken: RS – Rio Grande do Sul: 1. Pelotas, 2. Porto Alegre, 3. Caxias do Sul, 4. Flores da Cunha; SC – Santa Catarina: 5. Antônio Carlos, 6. Florianópolis; PR – Paraná: 7. Guarapuava, 8. São José dos Pinhais; SP – São Paulo: 9. Águas de Lindóia; MG – Minas Gerais: 10. Monte Sião; BA – Bahia: 11. Itaparica; PE – Pernambuco: 12. Vitória de Santo Antão, 13. Recife; PA – Pará: 14. Belém.

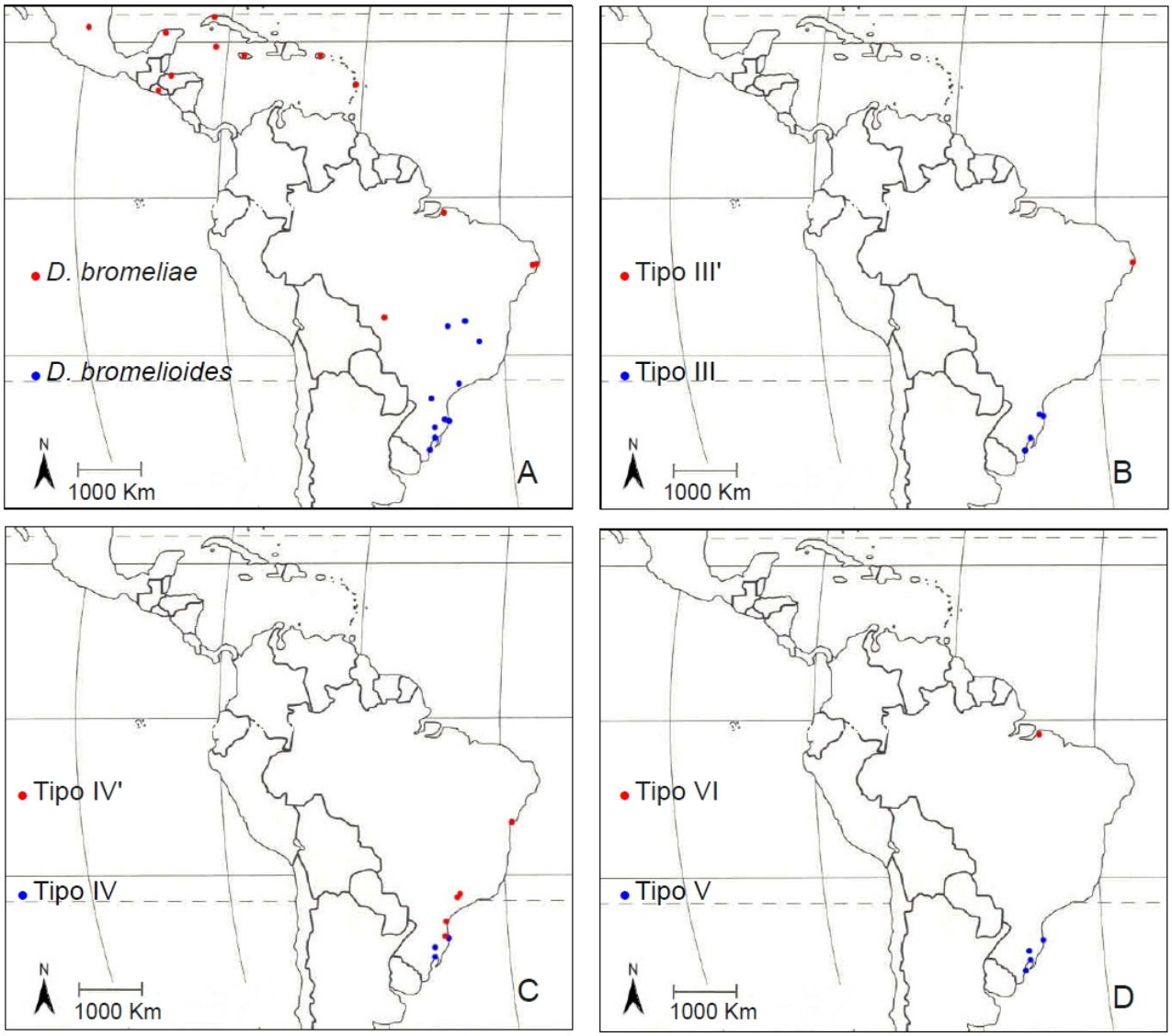

Figure 2: Geographical distribution of the species belonging to *bromeliae* group of *Drosophila* found in this study. A. *D. bromeliae* and *D. bromelioides*, includes additional literature records (Sturtevant, 1921; Frota-Pessoa, 1952; Clayton & Wasserman, 1957; Heed, 1957; Petersen, 1960; Wheeler, 1970; David, 1973; Vilela & Mori, 1999; Lachance *et al.*, 2001; Blauth & Gottschalk, 2007; Chaves & Tidon, 2008; Roque & Tidon, 2008); B. Types III and III'. C. Types IV and IV'. D. Types V and VI.

Supporting Information

Appendix S1: List of plant species with no emergence of drosophilid specimens in the present survey.

Acanthaceae	*Justicia floribunda*
	Sanchezia nobilis
	Odontonema strictum
	sp.1
Alliaceae	*Agapanthus africanus*
Asteraceae	*Mikania cordifolia*
	Senecio brasiliensis
Apocynaceae	*Allamanda blanchetii*
	Nerium oleander
	Tabernaemontana catharinensis
	Thevetia peruviana
Araceae	sp.1
Balsaminaceae	*Impatiens walleriana*
Begoniaceae	*Begonia coccinea*
Bignoniaceae	*Memora schomburgkii*
	Podranea ricasoliana
Cactaceae	*Nopalea cochenillifera*
Cannaceae	*Canna denudata*
	Canna limbata
Capparaceae	*Cleome hassleriana*
Convolvulaceae	*Ipomoea imperati*
Commelinaceae	*Tradescantia* sp.
Cucurbitaceae	*Momordica charantia*
Ericaceae	*Gaylussacia brasiliensis*
	Rhododendron simsii
Escalloniaceae	*Escallonia bifida*
Euphorbiaceae	*Euphorbia pulcherrima*
Fabaceae	*Bauhinia forficata*
	Delonix regia
	Lupinus sp.
	Macroptilium lathyroides
	Peltophorum dubium
	Schizolobium parahyba
Geraniaceae	*Pelargonium hortorum*

Heliconiaceae	*Heliconia velloziana*
Iridaceae	*Gladiolus hortulanum*
Lamiaceae	*Salvia coccinea*
Liliaceae	*Lilium regale*
	Lilium sp.1
Lythraceae	*Lagerstroemia indica*
	Punica granatum
Magnoliaceae	*Magnolia liliflora*
Malvaceae	*Abelmoschus esculentus*
	Brachychiton populneus
	Hibiscus schizopetalum
	Luehea divaricata
Melastomataceae	*Tibouchina urvilleana*
Musaceae	*Musa ornata*
Nymphaeaceae	*Nymphaea ampla*
Oleaceae	*Jasminum mesnyi*
Onagraceae	*Ludwigia* sp.
Orchidaceae	*Epidendrum fulgens*
	sp.1
Oxalidaceae	*Oxalis corniculata*
	Oxalis latifolia
Piperaceae	*Piper* sp.
Plantaginaceae	*Russelia equisetiformis*
	sp.1
Proteaceae	*Grevillea banksii*
Rosaceae	*Rosa grandiflora*
Solanaceae	*Datura stramonium*
	Petunia littoralis
	Petunia sp.
	Solanum juripeba
	Streptosolen jamesonii
Urticaceae	*Cecropia pachystachya*
Verbenaceae	*Lantana camara*
	Petrea subserrata
Zingiberaceae	*Renealmia* cf. *petasites*