



Biology, Ecology and Diversity

Spatial and temporal dynamics of drosophilid larval assemblages associated to fruits

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ABSTRACT

The study of organisms and their resources is critical to further understanding population dynamics in space and time. Although drosophilids have been widely used as biological models, their relationship with breeding and feeding sites has received little attention. Here, we investigate drosophilids breeding in fruits in the Brazilian Savanna, in two contrasting vegetation types, throughout 16 months. Specifically, larval assemblages were compared between savannas and forests, as well as between rainy and dry seasons. The relationships between resource availability and drosophilid abundance and richness were also tested. The community (4,022 drosophilids of 23 species and 2,496 fruits of 57 plant taxa) varied widely in space and time. Drosophilid assemblages experienced a strong bottleneck during the dry season, decreasing to only 0.5% of the abundance of the rainy season. Additionally, savannas displayed lower richness and higher abundance than the forests, and were dominated by exotic species. Both differences in larval assemblages throughout the year and between savannas and gallery forests are consistent with those previously seen in adults. Although the causes of this dynamic are clearly multifactorial, resource availability (richness and abundance of rotten fruits) was a good predictor of the fly assemblage structure.

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Introduction

The family Drosophilidae, which includes the genus *Drosophila*, has a cosmopolitan distribution and includes about 4,000 species (Brake and Bächli, 2008). These small flies are abundant in various types of environments, are easily manipulated, have a short life cycle, and produce a large number of offspring (Markow and O'Grady, 2008). For these reasons, some species of this family have long been used as biological models, mainly in Genetics and Molecular Biology (Brookes, 2001; Clark et al., 2007). The relationships between these organisms and their environment, however, are relatively less understood; this is unfortunate, because “surveying *Drosophila* breeding site distribution can provide the basis for testing many evolutionary ecological hypotheses” (Markow and O'Grady, 2008).

There are currently 128 nominal species of the family Drosophilidae recorded in the Brazilian savanna (Blaunch and Gottschalk, 2007; Chaves and Tidon, 2008; Mata et al., 2008; Roque and Tidon, 2008; Roque and Tidon, 2013; Valadão et al., 2010), locally known as Cerrado (see methods). The drosophilids of this biome have been

systematically studied for 15 years by capturing adults with traps, thereby generating much information toward the understanding of the organization of these insects' communities (Mata and Tidon, 2013; Roque et al., 2013; Tidon, 2006). The large, natural heterogeneity of the Cerrado is expressed in the drosophilid assemblages at both the spatial and temporal dimensions.

For example, assemblages from forest and savannas are quite different, each one having a particular set of characteristic species. The drosophilid assemblages of the gallery forests are richer in species, mainly the rare species, than those of the savannas. Indeed, the majority of rare species is exclusively from or prefers forests. The abundance of flies, on the other hand, is typically higher in the savannas, which are dominated by exotic and widespread species. During the rainy season, when many plant species produce and disperse fleshy fruits (Oliveira, 1998), the richness and abundance of flies are high. On the other hand, in the dry season the populations of these flies suffer strong bottlenecks, and many species are no longer captured (Mata and Tidon, 2013; Roque et al., 2013; Tidon, 2006). However, as the niches of immature and adult flies differ greatly during their life cycles (Powell, 1997), it is unknown if the results obtained from adults apply to the immature stages.

Drosophilids breed on different types of substrata, including fungi, flowers, leaves, and even animal carcasses (Carson, 1971). The few

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studies focusing on larvae assemblages in the Brazilian savanna, however, have indicated that drosophilids are associated more with fruits. These flies were found especially breeding in wolf apples (*Solanum lycocarpum* A.St.-Hil., Solanaceae) (Leão and Tidon, 2004), moriche palms (*Mauritia flexuosa* L.f., Arecaceae) (Valadão et al., 2010), and *Emmotum nitens* (Benth.) Miers (Icacinaeae) (Roque et al., 2009). Although these studies have revealed some aspects of the population dynamics of the larvae, they were episodic and focused on only a few focal plant species.

The aim of this study was to investigate the drosophilid larval assemblages in fruits of two contrasting vegetations of the Cerrado, savanna (*cerrado sensu stricto*) and gallery forests, across four protected areas in the Central region of Brazil, over 16 months. Based on previous adult drosophilid data, we tested six predictions derived from comparisons between dry and rainy season and between savanna and gallery forest: (1) the abundance of drosophilid larvae is higher in the rainy season; (2) the richness of drosophilid species is higher in the rainy season; (3) the fluctuation of drosophilid abundance and richness is associated with fluctuation in resource availability throughout seasons; (4) the abundance of drosophilid larvae is higher in the savanna; (5) drosophilid richness is higher in forests, and (6) the relative abundance of exotic species is higher in the savanna. Besides the original conclusions obtained from these predictions, they also allowed the determination of whether the patterns of larvae assemblages are consistent with those found in adult assemblages.

Material and methods

Area of study

This study was conducted in four protected areas of the Distrito Federal, Brazil: Estação Ecológica de Águas Emendadas - ESECAE (15°34'26" S, 47°34'58" W), Parque Nacional de Brasília - PNB (15°43'56" S, 47°55'53" W), Jardim Botânico de Brasília - JBB (15°52'42" S, 47°50'17" W), and Reserva Ecológica do IBGE (15°56'31" S, 47°52'41" W). In each protected area, two gallery forest areas and two savanna areas (*cerrado sensu stricto*), approximately 400 m² each and at least 200 m away from each other, were sampled monthly between October 2010 and January 2012.

The landscape of the Cerrado is a mosaic of vegetation types, ranging from grasslands and savannas to forests (Ratter et al., 1997). The savanna vegetation shows highly variable structure on the well-drained interfluvies, while gallery forests, or other wetland vegetation follow the watercourses (Oliveira and Marquis, 2002). There is a predominance of a savanna vegetation type, called *cerrado sensu stricto*, which harbours a unique array of drought- and fire-adapted plant species. Therefore, most gallery forests are embedded in an open vegetation matrix, and the transition between them is usually sharp.

The Cerrado climate is highly seasonal, characterized by a well-defined dry season from May to September. The average annual rainfall is 1500 mm, but the rains are heavily concentrated between November and March (Eiten, 1972). The Cerrado is, therefore, a very heterogeneous biome due to the interacting effects of seasonality, topography, and edaphic features, as well as climate fluctuations during the Quaternary and human disturbance (Oliveira and Marquis, 2002). This system combines a set of ecological and historical contexts of special interest to those studying the complexities of tropical communities.

Data collection

During each collection event, two collectors searched for 30 minutes for fallen fruits on the ground in each area, for a sampling effort total of eight hours each month, and 128 hours throughout the study

for each collector. On these occasions, fruits of various species were collected, intact or partially degraded in different stages of decay. No more than 50 fruits from each plant species were collected in each area/day, but they rarely found more than this amount of fruit. As each fruit represents a portion of the entire resource (a species of fruit) and the larvae in each fruit is not able to disperse to other fruits, each fruit was considered a fragment of the resource. Fruits were identified using field guides (Silva-Júnior, 2005; Silva-Júnior and Pereira, 2009; Kuhlmann, 2012), and in some cases a specialist was consulted. In the laboratory, the fruits were weighed and stored individually in plastic containers with vermiculite moistened with a solution of Nipagin®, an inhibitor of filamentous fungi. These containers were covered with a thin, translucent piece of cloth to retain the adults that emerged from the fruit. All fruits were stored at a constant temperature (25 °C). The adults that emerged from the fruits were removed every other day and stored in microtubules with 70% alcohol. The identification of the flies was based on taxonomic keys (Burla and Pavan, 1953; Freire-Maia and Pavan, 1949), descriptions (Chassagnard and Tsacas, 1993), and on the male terminalia in the case of cryptic species (Vilela and Bächli, 1990). Voucher specimens were deposited in the drosophilid collection of the Laboratório de Biologia Evolutiva of the Instituto de Ciências Biológicas of the Universidade de Brasília. The authorship of drosophilid species can be found at TaxoDros (Bächli, 2014).

Analyses

Comparisons of abundance and richness between the two seasons were performed visually, using graphs and tables. Statistical analysis was not used at this stage because the sample sizes were extremely low in the dry season months. To quantify and test the associations between resource availability and fly community, Pearson's correlations were analysed in four contexts: (1) Log₁₀ of the fruit relative abundances x Log₁₀ of the drosophilid relative abundances; (2) Log₁₀ of the fruit relative abundances x Log₁₀ of the drosophilid species richness; (3) Log₁₀ of the fruit relative weights x Log₁₀ of the drosophilid relative abundances, and (4) Log₁₀ of the relative fruit weights x Log₁₀ of drosophilid richness. The variables evaluated were pooled for each month, standardized by the total (with the exception of Drosophilidae richness), and log₁₀ transformed to minimise the drastic differences between months and, consequently, maximize the detection of associations between variables.

To test for differences in fly richness between the two habitats, individual-based rarefaction curves were made for the forests and savannas, with individual fragments of fruit considered the sampling unit (EstimateS 9.0; Colwell, 2013). In addition, rank-abundance plots were obtained for forests and savanna species to investigate the species abundance distribution pattern in these environments.

Each month, the relative abundance of exotic and neotropical species in the two environments was compared with a chi-square test. The Bonferroni correction was used to prevent the spread of Type 1 error. To adjust the data to the test, these comparisons were made only for months when drosophilids were present in both habitats (total abundance = 1).

The drosophilid species (individually) were standardised and fourth-root transformed, in order to minimise the large differences in the number of drosophilid specimens among samples (fruit species) and to weight the rare species. Next, a similarity matrix between samples, based on the Bray-Curtis index, was calculated. Then, this matrix was submitted to the permutation multivariate analysis of variance (PERMANOVA) (Anderson, 2001; Anderson et al., 2008) to test for significant differences in the structure of drosophilid assemblages between forests and savannas.

The principal coordinates analysis (PCO) ordination was used to illustrate the dissimilarity relationships of the drosophilid assemblages of fruit species, classified according to the habitats where

Table 1. Abundance of the most common drosophilid species ($n > 20$) whose larvae develop in the most common Cerrado fruits ($n > 10$) in drosophilids and fruits, respectively, with less than 20 and 10 individuals pooled as “others”. The data were sampled between October 2010 and January 2012.

Fruit species	<i>D. nebulosa</i>	<i>Z. indianus</i>	<i>D. willistoni</i>	<i>D. malerkotiana</i>	<i>D. simulans</i>	<i>D. fumipennis</i>	<i>D. atrata</i>	<i>D. immigrans</i>	<i>Grip 01</i>	<i>D. mediopunctata</i>	<i>D. mediotriata</i>	<i>D. cardini</i>	<i>R. bivialis</i>	Others	Total abundance
Cerrado seuso stricto															
<i>Cariocar brasiliense</i>	1,109	403	475	46	20	39	0	16	0	0	3	9	0	11	2,131
<i>Pouteria ramiflora</i>	35	755	56	0	9	4	0	0	0	0	0	1	2	2	864
<i>Syagrus</i> sp.	30	43	0	0	8	0	0	0	0	0	0	0	2	1	84
<i>Syzygium jambos</i>	18	18	0	0	28	0	0	0	0	0	0	0	0	0	64
<i>Byrsonima</i> sp.	19	24	1	2	0	0	0	0	0	0	0	0	0	0	46
<i>Emmotum nitens</i>	5	23	0	0	1	0	0	0	0	0	0	0	0	0	29
<i>Eugenia dysenterica</i>	0	12	0	0	1	0	0	0	0	0	0	0	5	0	18
Other plant species	20	36	0	0	6	0	0	0	0	0	1	1	2	0	66
Drosophilid abundance in cerrados	1,236	1,314	532	48	73	43	0	16	0	0	4	11	11	14	3,302
Gallerly forest															
Fruit forest 01	31	9	92	240	2	11	8	1	1	12	0	0	0	2	409
<i>Alibertia edulis</i>	57	27	19	0	0	0	0	0	1	1	1	0	0	1	107
<i>Garcinia gardneriana</i>	5	0	73	14	0	0	0	0	0	0	0	0	0	6	98
<i>Diospyros hispida</i>	10	0	5	0	0	0	16	0	0	0	0	0	0	2	33
<i>Emmotum nitens</i>	6	7	4	0	0	0	0	0	0	0	0	0	0	0	17
Other plant species	13	0	13	0	2	0	0	0	14	2	8	0	0	4	56
Drosophilid abundance in forests	122	43	206	254	4	11	24	1	16	15	9	0	0	15	720
Total drosophilid abundance	1,358	1,357	738	302	77	54	24	17	16	15	13	11	11	29	4,022

they were found (savannas or forests). According to this analysis, fruit species that are similar to each other will be closer in multidimensional space, while those with different assemblages will be more distant. The Spearman correlation between drosophilid species and the first and second PCO axis pointed out which species were mainly responsible for grouping the fruits in the multidimensional space.

Results

In this study, 2,496 fruits from 57 plant taxa were sampled. Among these, only 548 fruits from 27 species were colonized by drosophilid larvae. From these substrates, 4,022 drosophilid adults emerged in the laboratory, representing 23 species, most (2,645 individuals) belonging to the genus *Drosophila*. We also found *Zaprius indianus*, *Scaptodrosophila latifasciaeformis*, *Rhinoleucophenga bivialis*, and four other morphospecies of *Drosophila*, one of which was classified in the *D. tripunctata* group (Grip01) (Table 1, Appendix 1).

Temporal variation

The richness and abundance of fruits and drosophilids were notably higher during the rainy season (Table 2). In the dry season, when the flies suffered a strong population bottleneck, there was a drastic reduction in the resource supply. The three drosophilid species found in the dry season (*D. nebulosa*, *D. simulans*, and *D. willistoni*) were among the five most abundant species of the rainy season.

The number of available fruits, both those colonised by flies and empty ones (those that did not register any emergence after an ob-

servation period of 30 days), fluctuated throughout time, as well as drosophilid abundance (Fig. 1) and richness (Fig. 2). During the core of the dry season (June to September), a strong population bottleneck was recorded (Fig. 1), even with available fruits (in the case of forests). Drosophilid species' richness also declined sharply during this season (Fig. 2). It is important to emphasise the large amount of empty fruits in both environments, except at the core of the dry season in the savanna vegetation (when we did not find any fruit) (Figs. 1 and 2).

The correlations (1) \log_{10} of the fruit relative abundances x \log_{10} of the drosophilid relative abundances and (2) \log_{10} of the fruit relative abundances x \log_{10} of the drosophilid species richness were strong ($r = 0.98$ and $r = 0.94$, respectively), as were the correlations (3) \log_{10} of the fruit relative weight x \log_{10} of the drosophilid relative abundances and (4) \log_{10} of the relative fruit weight x \log_{10} of drosophilid richness ($r = 0.91$ and $r = 0.84$, respectively). All correlations were significant ($p < 0.005$), confirming that the increased availability of fruits in terms of abundance and weight corresponds to a greater abundance and richness of flies.

Spatial variation

Rarefaction curves of drosophilid species showed that the forests were richer than the savannas, while the latter had more specimens (Fig. 3). The most abundant species in the savannas were *Zaprius indianus* (40%), *Drosophila nebulosa* (37%), and *D. willistoni* (16%), while the forests were dominated by *D. malerkotiana* (35%), *D. willistoni* (29%), and *D. nebulosa* (17%). Due to the extremely low sample size in the dry season months, these analyses were performed with combined data from both seasons.

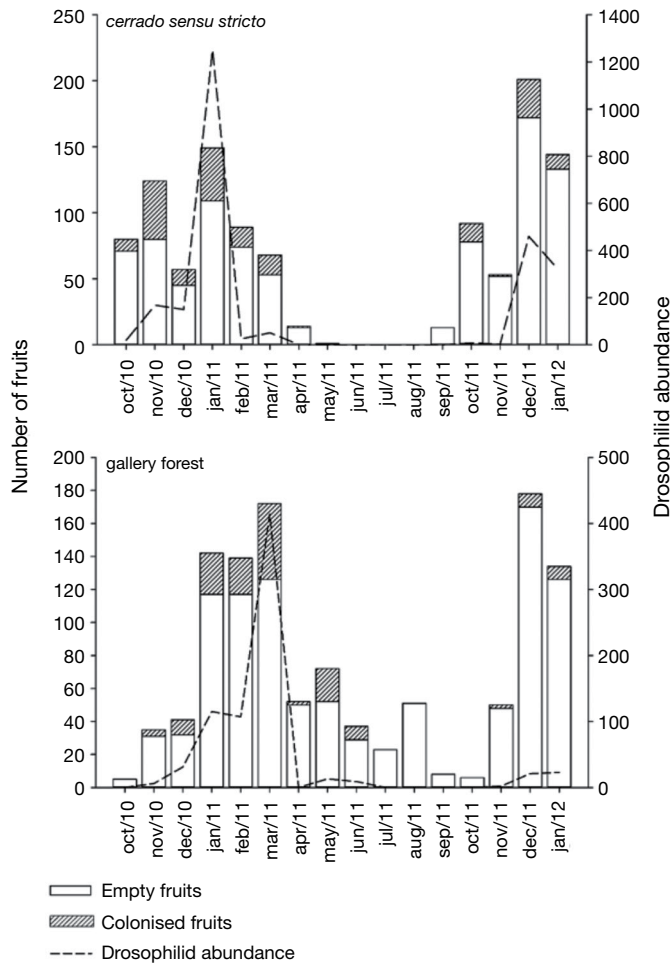


Figure 1. Availability of empty/colonised fruits, and drosophilid abundance between October 2010 and January 2012.

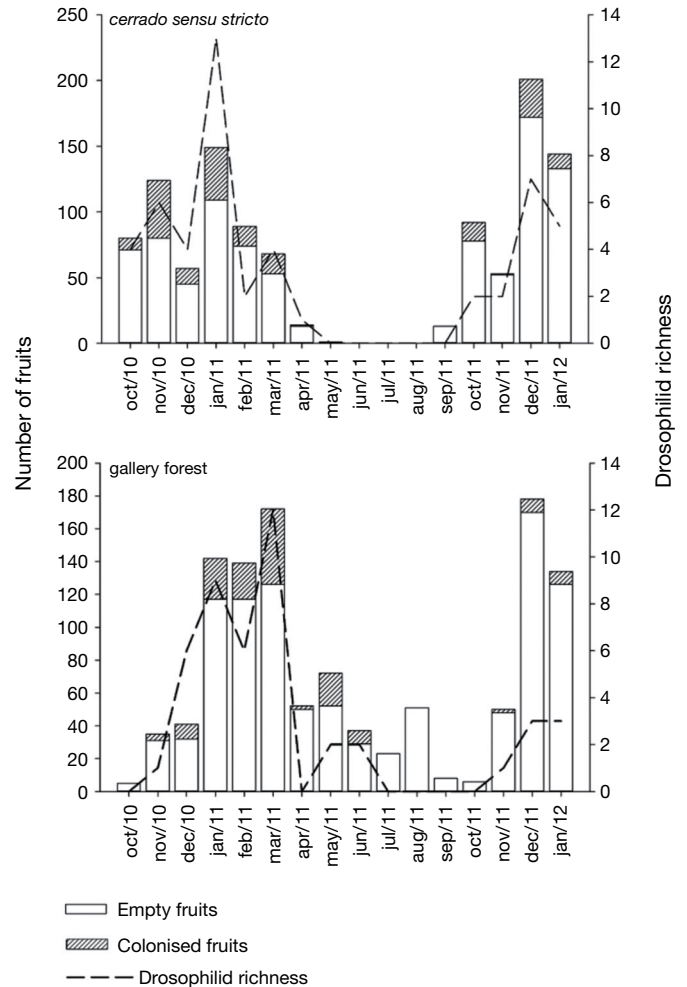


Figure 2. Availability of empty/colonised fruits, and drosophilid richness between October 2010 and January 2012.

The relative abundance of exotic and neotropical drosophilids also varied throughout months and between vegetations (Fig. 4). In the rainy season, the dominance of exotic species was higher in savannas than in forests, with the exception of March 2011 (Fig. 4A). The fruits of the forests were characterized by the predominance of neotropical drosophilids (between 75% and 100%), and only in March they reach a minimum of 53% (Fig. 4B).

The PERMANOVA results revealed significant differences in the structure of drosophilid assemblages between forests and savannas (Table 3). The PCO ordination of the fruit species, based on the structure of drosophilid assemblages, allocated forest fruits in the right side of the multidimensional space, while fruits from savannas tended to be located in the left lower side of this space. *Drosophila willistoni* ($r = 0.40$), *Rhinoleucophenga bivisualis* ($r = -0.46$), and *Zaprionus indianus* ($r = -0.54$) were more correlated to the first PCO axis. *Drosophila willistoni* ($r = 0.48$) was also correlated to the second PCO axis, together with some species of the *D. tripunctata* group: *Gtrip01* ($r = 0.38$), *D. mediotriata* ($r = 0.35$), and *D. mediopunctata* ($r = 0.35$) (Fig. 5).

Discussion

This is the first study investigating larval assemblages of drosophilids in the Neotropical Region, using a standardized sampling design at a considerable spatial and time scale and community multivariate

Table 2.

Richness and abundance of fruits and drosophilids in the two sampled seasons and vegetations.

Variables	Dry season		Rainy season	
	Cerrados	Forests	Cerrados	Forests
Fruit richness	1	2	15	12
Fruit abundance	1	13	359	176
Drosophilid richness	1	3	15	18
Drosophilid abundance	1	22	3,301	698

Table 3.

Results of a PERMANOVA showing differences in the structure of drosophilid assemblages (23 species) between cerrados and forests, as obtained using 9,999 permutations under a reduced model and based on Bray-Curtis similarity among fruit species (27 fruit species).

Source of variation	DF	SS	MS	Pseudo-F	P
Vegetation	1	16,114	16,114	7.4116	0.0001
Residual	26	56,527	2,174		
Total	27	72,641			

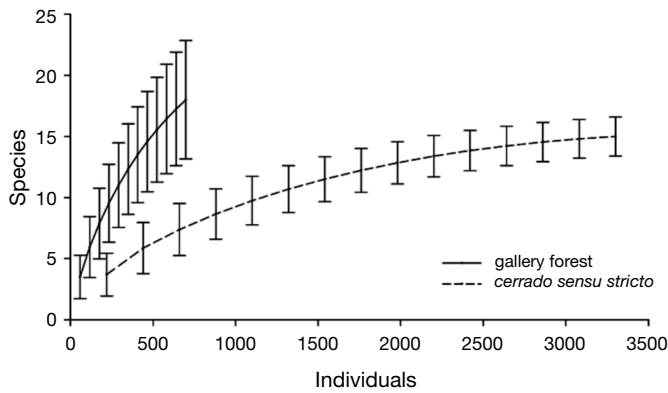


Figure 3. Rarefaction curves (Sobs randomised) of the drosophilid species in the fruits of the cerrados and forests. Vertical bars represent confidence intervals (95%).

analysis. It confirmed that the drosophilid larval assemblages associated with fruits varied within time and space, and reflected the same dynamics observed in adult communities (Mata and Tidon, 2013; Roque et al., 2013; Tidon et al., 2003; Tidon, 2006).

Temporal variation

Temporal fluctuations in insect populations have long been associated with fluctuations in environmental factors (Wolda, 1978, 1988). In fact, in temperate areas, many drosophilid species go through drastic bottlenecks during the winter, due to the intense cold (Patterson, 1943; Poppe et al., 2013). In the tropics, on the other hand, the temperature throughout the year varies less, and seasonal drosophilid population cycles are probably regulated by precipitation (Prakash and Reddy, 1979), the main climatic factor regulating the dry and rainy cycles. Nonetheless, previous studies in the Cerrado biome (Tidon, 2006) have not found consistent relationships between the abundance of drosophilid species and the climatic parameters (temperature, rainfall, relative humidity, and light intensity). Here, we showed that the biomass and the number of fruits available in the environment over time were closely associated with the temporal fluctuations of the fly assemblages. As such, this is the first study in the Brazilian savanna that shows strong and significant positive association between the flies and an environmental factor.

Spatial variation

The drosophilid larvae assemblages varied between forests and savannas. Forests, which are the richest habitats, were characterized by neotropical species such as those of the *Drosophila willistoni* subgroup and *D. tripunctata* group. The savannas, on the other hand, revealed higher drosophilid abundance but lower species richness, with great dominance of exotic species (*D. simulans* and *Z. indianus*). The differences in abiotic conditions between these two vegetations are probably affecting their respective drosophilid species subsets.

Savannas are probably stressful for most neotropical drosophilids due to their relatively harsh abiotic conditions (Eiten, 1972; Ribeiro and Walter, 1998). The strong dry season that characterizes this biome is far more pronounced in this open vegetation, imposing a great hydrological stress on the communities living under those conditions (Franco and Lüttge, 2002). In *Drosophila*, narrowly distributed tropical species have low means and low genetic variation for desiccation, as compared with those of widely distributed species (Kellermann et al., 2009). Thus, the conditions of environment in savanna may impose constraints or decrease the fitness of the species that do not present adaptive traits offering resistance to desiccation. Also, such seasonal fluctuations can act as a recurrent disturbance factor

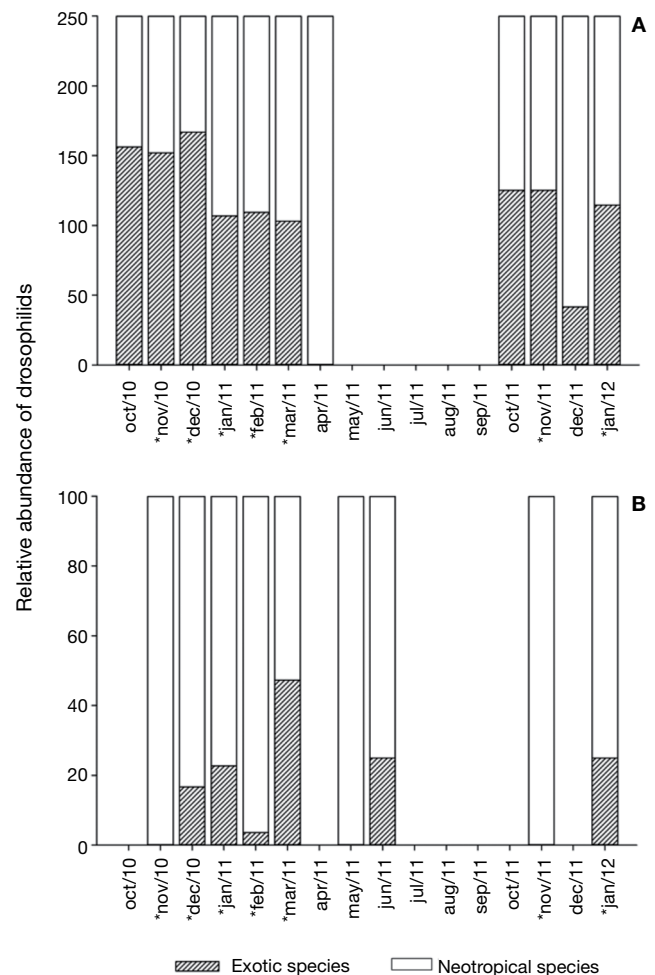


Figure 4. Relative abundance of exotic and neotropical species throughout the sampling months in cerrado (A) and forests (B). * indicates significant differences (#a = 0.007 after Bonferroni correction) in the proportions between habitats.

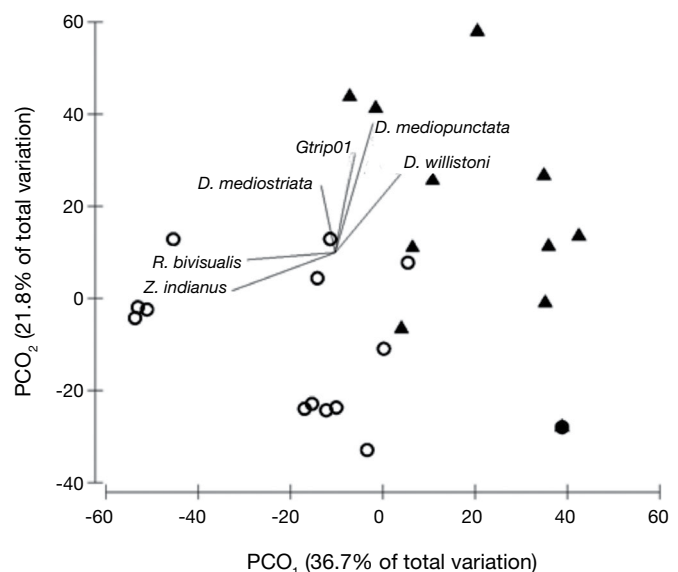


Figure 5. Principal Coordinate Analysis (PCO) showing the dissimilarity relationships, based on the drosophilid assemblage structure (23 species; Bray-Curtis similarity), among the fruit species (27 species), which were classified according to the habitats where they were sampled. Open circles are fruit species from cerrados, and closed triangles are fruit species from forests.

[illegible]

Season/ Habitat	Fruit species	<i>D. atrata</i>	<i>D. bocainenses</i>	<i>D. capricorni</i>	<i>D. cardini</i>	<i>D. fumipennis</i>	<i>D. hydei</i>	<i>D. immigrans</i>	<i>D. malerkotiana</i>	<i>D. mediopunctata</i>	<i>D. mediotriata</i>	<i>D. mercatorum</i>	<i>D. nebulosa</i>	<i>D. paulistorum</i>	<i>D. simulans</i>	<i>D. stutervanti</i>	<i>D. willistoni</i>	<i>Drosophila 01</i>	<i>Drosophila 02</i>	<i>Drosophila 03</i>	Ctrip 01	<i>R. bivittatus</i>	<i>S. latifasciaeformis</i>	<i>Z. indianus</i>	Total abundance
Forest	<i>Byrsonima</i> sp.							2					19				1							24	46
	<i>Emmotum nitens</i> (Benth.) Miers												5		1									23	29
	<i>Psidium salutare</i> (O.Berg) Landrum												14											6	20
	<i>Eugenia dysenterica</i> DC.														1							5		12	18
	Fruit cerrado 01												4		4									6	14
	<i>Salacia multiflora</i> (Lam.) DC.																							14	14
	<i>Brosimum gaudichaudii</i> Trécul																					2		4	6
	<i>Andira humilis</i> Mart. Ex Benth				1						1													2	4
	<i>Anacardium humile</i> A.St.-Hil.																							4	4
	<i>Campomanesia pubescens</i> (Mart. ex DC.) O.Berg.														2										2
	<i>Psidium</i> sp.												1												1
	Fruit forest 01	8				11		1	240	12			31		2		92	1		1	1			9	409
	<i>Alibertia edulis</i> (Rich.) A.Rich. ex DC.			1							1	1	57				19				1			27	107
	<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi								14				5				73						6		98
	<i>Diospyros hispida</i> A.DC.	16					1						3			1	4								25
	<i>Hymenaea martiana</i> Hayne										8								3		14				25
	<i>Emmotum nitens</i> (Benth.)												6				4							7	17
	Fruit forest 02												1				8								9
	Fruit forest 03												2												2
	<i>Cheiloclinium cognatum</i> (Miers) A.C.Sm.									2															2
	<i>Byrsonima basiloba</i> A.Juss.				1												1								2
	Fruit forest 04												1												1
	Fruit forest 05												1												1
Dry																									
Cerrado	<i>Psidium</i> sp.												1												1
Forest	<i>Mauritia flexuosa</i> L.f.												8		2		4								14
	<i>Diospyros hispida</i> A.DC.												7				1								8
Total abundance		24	1	2	11	54	1	17	302	15	13	4	1,358	1	77	6	738	1	3	1	16	11	9	1,357	4,022

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