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Effects of seasonality on drosophilids (Insecta, Diptera) in the northern part of the Atlantic Forest, Brazil

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Abstract

Seasonality is an important aspect associated with population dynamic and structure of tropical insect assemblages. This study evaluated the effects of seasonality on abundance, richness, diversity and composition of an insect group, drosophilids, including species native to the Neotropical region and exotic ones. Three preserved fragments of the northern Atlantic Forest were surveyed, where temperatures are above 20 °C throughout the year and rainfall regimes define two seasons (dry and rainy). As opposed to other studies about arthropods in tropical regions, we observed that abundance of drosophilids was significantly higher in the dry season, possibly due to biological aspects and the colonization strategy adopted by the exotic species in these environments. Contrarily to abundance, we did not observe a seasonal pattern for richness. As for other parts of the Atlantic Forest, the most representative Neotropical species (*Drosophila willistoni*, *D. sturtevanti*, *D. paulistorum* and *D. prosaltans*) were significantly more abundant in the rainy season. Among the most abundant exotic species, *D. malerkotliana*, *Zaprionus indianus* and *Scaptodrosophila latifasciaeformis* were more importantly represented the dry season, while *D. simulans* was more abundant in the rainy period. The seasonality patterns exhibited by the most abundant species were compared to findings published in other studies. Our results indicate that exotic species were significantly more abundant in the dry season, while native ones exhibited an opposite pattern.

Keywords: abundance, exotic species, Neotropical species, richness

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Introduction

Arthropods represent approximately 80% of the species of the Animalia kingdom. Among these, insects have the highest richness and a considerable number of species live in rainforests (Zhang, 2011). Despite the deforestation, the Atlantic Forest is one of the largest rainforests in the Americas, with substantial species richness and endemism rates (Myers

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et al., 2000; Galindo-Leal & Câmara, 2003; Ribeiro *et al.*, 2009; Scarano & Ceotto, 2015). Its latitudinal range is around 29° extending along the Brazilian coast and adjacent regions in Argentina and Paraguay (Ribeiro *et al.*, 2009). This wide latitudinal extension of the Atlantic Forest and the significant oscillation in geographical relief result in different climate types and vegetation physiognomies across its domain area (Galindo-Leal & Câmara, 2003; Pinto & Brito, 2003; Tabarelli *et al.*, 2005).

Several studies have produced evidence of the seasonal changes in abundance, richness, composition and diversity of tropical insects (Janzen & Schoener, 1968; Pinheiro *et al.*, 2002; Basset *et al.*, 2003; Grimbacher & Stork, 2009; Neves *et al.*, 2010; Ferreira *et al.*, 2015). A specific group of insects, drosophilids, have become the object of considerable research addressing seasonal variations in the southern part of the Atlantic Forest in Brazil (Dobzhansky & Pavan, 1950; Saavedra *et al.*, 1995; De Toni *et al.*, 2007; Bizzo *et al.*, 2010; Garcia *et al.*, 2012), where marked temperature and rainfall changes are observed throughout the year, characterized by four distinct seasons. The seasonality of drosophilids inhabiting the northern part of the Brazilian Atlantic Forest has been little investigated, despite the influence of rainfall on the region's seasonal features, while the temperature range is less extensive. As opposed to the southern portion of the biome, only two seasons are observed, the rainy and the dry (Colombo & Joly, 2010).

Seasonality is an important factor in survival strategies adopted by numerous organisms, playing an essential role in the knowledge about populations and the structure of tropical insect communities in a given area (Wolda, 1978*a*, *b*; Spitzer *et al.*, 1993). Seasonal patterns may interfere in population size, reproductive activity and the availability of food resources, among other aspects (Wolda, 1988). Although several insect species may be living in similar seasonal situations, they do not exhibit the same response pattern to environmental changes permanently. In other words, each species exhibits particular adaptations that underline their seasonal cycles (Tauber & Tauber, 1981). From this perspective, understanding how seasonal changes impact ecological parameters of native as well as exotic insect species has fascinated researchers interested in evaluating the effects of biological invasions in natural environments (Sax *et al.*, 2007).

This study evaluated the influence of seasonality on abundance, richness, composition and diversity of the drosophilid assemblage focused on species native to the Neotropical region and exotic ones in Atlantic Forest fragments on the north region of its distribution range.

Material and methods

Study sites

Adult drosophilids were collected in three preserved fragments of the Atlantic Forest in the state of Pernambuco, northeast Brazil: Refúgio Ecológico Charles Darwin (Darwin, 07°48′S; 34°57′W), Estação Experimental de Itapirema (Itapirema, 07°38′S; 34°56′W) and Estação Ecológica do Tapacurá (Tapacurá, 08°03′S; 35°13′W) (fig. 1). The first two fragments cover an area of approximately 60 hectares (ha) (Costa-Lima, 1998; Mascarenhas *et al.*, 2005), while Tapacurá stretches across 382 ha (Coelho, 1979). The three areas studied have similar phytogeographic characteristics, and are classified as dense ombrophilous forests, all of which are located in the Pernambuco subregion (IBGE, 2012).

Fig. 1. Map of Brazil showing the Atlantic Forest domain in the country (grey area) and the three fragments where drosophilids were collected. Itapirema = Estação Experimental de Itapirema, Darwin = Refúgio Ecológico Charles Darwin and Tapacurá = Estação Ecológica do Tapacurá.

Climate in the region is type As according to the Köpen classification system, defined as tropical moist with dry summers and rainfall below 60 mm in the season of greater drought. The rainy season starts in April and ends in August, when almost 70% of all rain volume is recorded in a year. Annual rainfall exceeds 2000 mm. Mean temperature is approximately 25 °C, oscillating between 22 and 30 °C (INMET, 2016; LAMEPE, 2016).

Collection and identification of drosophilids

Two collections were carried out in the rainy (between June and August) and two in the dry (between January and March) seasons in each study fragment between March 2011 and June 2012. Ten traps baited with banana and constructed with plastic bottles according to Tidon & Sene (1988) were placed in each fragment for 3 days. Traps were hung 1.5 m above the ground and 30 m away from one another along a linear transect located 500 m away from the fragment edge.

The drosophilids captured were characterized using taxonomic keys (Freire-Maia & Pavan, 1949; Poppe *et al.*, 2014) and species descriptions (Val & Sene, 1980; Vilela & Bächli, 1990; Chassagnard & Tsacas, 1993; Bächli *et al.*, 2004; Culik & Ventura, 2009). Cryptic species were recognized after inspection of male genitalia. *Drosophila melanogaster* and *D. simulans* were identified based on the shape of the posterior salience of the genital arch (Salles, 1948). The males of the *willistoni* subgroup of *Drosophila* were named considering the shape of the hypandrium (Burla *et al.*, 1949; Malogolowkin 1952; Rohde *et al.*, 2010). Other cryptic species were documented after inspection male terminalia (Breuer & Pavan, 1950; Magalhães & Björnberg, 1957; Vilela, 1983; Vilela & Bächli, 1990; Vilela *et al.*, 2002). For the analysis of male terminalia, flies were prepared in potassium hydroxide (KOH) 10%, stained in acid fuchsin and dissected in glycerol (Bächli *et al.*, 2004). The

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number of females of cryptic species was estimated calculating each species' sex ratio.

Voucher specimens were deposited in the drosophilid collection of the Laboratório de Genetica, Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Brazil. The species were also categorized as native to the Neotropical region and exotic (Gottschalk *et al.*, 2008).

Ecological analyses

Richness and abundance of each species were recorded during each field excursion. These parameters were used to estimate the Shannon–Wiener diversity (H') and the Smith and Wilson's evenness (E_{var}) indices in the software Ecological Methodology (Kenney & Krebs, 2000).

Species accumulation curves were constructed for each fragment surveyed and compared using the jackknife 1 species estimator, calculated in the software Biodiversity Pro, version 2 (McAleece *et al.*, 1997).

Similarity trees were constructed using the Jaccard and Morisita indices in the software PAST, version 1.94b (Hammer *et al.*, 2001). The temporal and spatial distribution patterns of the Neotropical and exotic species were characterized based on the relative abundance of individuals. The Chi-square (χ^2) test was used to compare absolute richness and abundance considering the two seasons (dry and rainy), the three survey sites (Darwin, Itapirema and Tapacurá) and the species native to the Neotropical region and the exotic ones. The null hypothesis assumed was that these categories of comparison do not differ significantly.

Results

In total, 40,911 drosophilids of 36 species and 6 genera (*Drosophila*, *Neotanygastrella*, *Rhinoleucophenga*, *Scaptodrosophila*, *Zaprionus* and *Zygothrica*) were collected. *Drosophila* was the richest genus, with 29 species, followed by *Rhinoleucophenga*, with 3. The other genera included one species each (table 1). The Neotropical and exotic drosophilids captured were represented by 29 and 7 species, respectively. Exotic species accounted for 75.44% of total abundance recorded.

Spatial variation

The highest richness was recorded in Darwin (27 species), followed by Tapacurá (25 species) and Itapirema (22 species). The jackknife 1 estimator revealed that the richness values observed are similar to the values estimated for each fragment, when 35, 29 and 27 species were expected in Darwin, Tapacurá and Itapirema, respectively. Abundance followed an opposite pattern as that of richness, when Itapirema had the largest number of individuals, followed by Tapacurá and Darwin (table 1). The analysis of species composition estimated by the Jaccard index showed that species clustered for fragment surveyed (fig. 2a), indicating that the drosophilid assemblages living in the three sites were different.

Temporal variation

No significant difference was observed in richness between seasons: 34 species were recorded in the rainy season, 28 in the dry ($\chi^2 = 0.581$, df = 1, $P = 0.5250$). Species richness was higher in the rainy season in all localities (table 1), though with no significant difference ($\chi^2 = 0.286$, df = 2, $P = 0.8670$). Similarly, no differences were observed in richness of native ($\chi^2 = 0.750$, df = 1, $P = 0.3865$) and exotic ($\chi^2 = 0.070$, df = 1, $P = 0.7815$) species between seasons.

Abundance was five times as high during the dry season, with significant statistical difference ($\chi^2 = 18{,}368.472$, df = 1, $P < 0.0001$). In all localities, the number of individuals recorded was higher in this season (Itapirema: $\chi^2 = 15{,}231.761$, df = 1, $P < 0.0001$; Darwin: $\chi^2 = 3073.778$, df = 1, $P < 0.0001$; Tapacurá: $\chi^2 = 1488.783$, df = 1, $P < 0.0001$). In the dry season, exotic species were more abundant than Neotropical species, independently of fragment surveyed ($\chi^2 = 14{,}837.545$, df = 1, $P < 0.0001$). However, in the rainy season the species native to the Neotropical region were more abundant ($\chi^2 = 425.696$, df = 1, $P < 0.0001$) (fig. 3).

Rare species (with abundance values below 1%) represented 77.78% of the richness, but only 1.53% of the abundance. Eight species had relative abundance above 1%, four of which were exotic (*D. malerkotliana*, *Z. indianus*, *D. simulans* and *S. latifasciaeformis*) and four were Neotropical (*D. willistoni*, *D. sturtevanti*, *D. paulistorum* and *D. prosaltans*) (fig. 4). Together, these species accounted for 98.47% of the total abundance.

Concerning the most abundant exotic species, i.e. *D. malerkotliana*, *Z. indianus* and *S. latifasciaeformis* were more intensively captured in the dry season ($\chi^2 = 1527.360$, df = 1, $P < 0.0001$; $\chi^2 = 886.261$, df = 1, $P < 0.0001$; $\chi^2 = 232.865$, df = 1, $P < 0.0001$, respectively) (table 1). The three species were more representatively collected in this season, in all fragments studied. But the opposite behaviour was observed for *D. simulans*, which was more abundant during high rainfall periods ($\chi^2 = 1131.867$, df = 1, $P < 0.0001$) (fig. 5a).

Drosophila willistoni, *D. sturtevanti*, *D. paulistorum* and *D. prosaltans* were significantly more abundant in the rainy season ($\chi^2 = 275.179$, df = 1, $P < 0.0001$; $\chi^2 = 112.901$, df = 1, $P < 0.0001$; $\chi^2 = 111.284$, df = 1, $P < 0.0001$; $\chi^2 = 58.243$, df = 1, $P < 0.0001$, respectively) (table 1). The relative abundance of the four species was higher in this season, in all localities. The exception was *D. sturtevanti* in Tapacurá (fig. 5b).

Drosophila malerkotliana was the most abundant species recorded in this study, with more than 60% of the flies collected. It was the dominant species in the dry season, when it accounted for almost 70% of the individuals captured, against 21% in the rainy season. During this period *D. willistoni* was the main species, representing more than 40% of the total number of drosophilids observed, as opposed to <7% of the flies captured in the period of drought (table 1).

The similarity tree constructed using the Morisita index formed clusters for season (fig. 2b). The rainy season had higher diversity indices ($H' = 2.639$, $E_{var} = 0.119$), compared with the period of drought ($H' = 1.731$, $E_{var} = 0.076$). This was also observed for the fragment surveyed, when analysed separately (table 1).

Discussion

Seasonality in tropical regions is often marked by contrasting seasons concerning rainfall volumes, when temperature does not vary considerably (Peel *et al.*, 2007). In this study, we evaluated areas of similar characteristics in the northern Atlantic Forest, observing that drosophilids are significantly more abundant in the dry season. It was in this period that exotic species were more numerous, while native ones were more abundant in the rainy season. No significant differences were observed in richness between seasons and between the

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Table 1. List of drosophilid species native to the Neotropical region and exotic ones (*) in the rainy and dry seasons for the sampling excursions carried out in three fragments of the Atlantic Forest, north of their distribution.

				Rainy season			Dry season		
Genus	Subgenus	Group	Species	Itapirema	Darwin	Tapacurá	Itapirema	Darwin	Tapacurá
Drosophila	*Drosophila*	*Annulimana*	*D. ararama* Pavan & Cunha	0	5	10	0	16	1
			D. sp1	0	0	0	0	3	0
		Cardini	*D. cardinoides* Dobzhansky & Pavan	0	2	1	0	8	0
			D. neocardini Streisinger	15	11	4	16	18	3
			D. polymorpha Dobzhansky & Pavan	0	0	7	0	0	2
		Repleta	*D. ellisoni* Vilela	0	9	0	0	0	0
			D. mercatorum Patterson & Wheeler	0	4	92	13	4	87
			D. pictilis Wasserman	1	1	8	0	0	1
			D. zottii Vilela	0	0	4	0	0	0
		Tripunctata	*D.* sp2	0	1	0	0	4	0
			D. sp3	2	1	0	0	0	0
			D. sp4	0	0	1	0	0	0
			D. sp5	0	3	2	0	0	0
			D. sp6	8	0	0	0	0	0
			D. sp7	0	7	0	0	6	0
	Sophophora	*Melanogaster*	**D. ananassae* Doleschall	1	1	1	0	0	3
			**D. kikkawai* Burla	0	0	1	0	0	0
			**D. malerkotliana* Parshad & Paika	461	144	808	15,211	3796	4150
			**D. melanogaster* Meigan	1	0	1	36	4	10
			**D. simulans* Sturtevant	300	77	390	195	53	545
Drosophila	*Sophophora*	*Saltans*	*D. prosaltans* Duda	21	29	169	26	46	125
			D. sturtevanti Duda	259	142	193	1564	659	523
		Willistoni	*D. nebulosa* Sturtevant	7	7	20	25	12	37
			D. fumipennis Duda	16	16	0	3	5	0
			D. paulistorum Dobzhansky & Pavan	152	80	119	105	157	62
			D. willistoni Sturtevant	740	594	1442	727	632	913
	Not identified	–	*D.* sp8	0	0	0	0	1	0
			D. sp9	1	0	1	1	0	1
			D. sp10	1	0	0	0	3	0
Neotanygastrella	–	Not clustered	*N. tricoloripes* Duda	1	1	1	2	0	0
Rhinoleucophenga	–	Not clustered	*R. capixabensis* Culik & Ventura	0	1	0	0	0	0
			R. punctulata Duda	0	0	4	4	0	8
			R. sp1	1	0	0	1	0	0
Scaptodrosophila	–	*Latifasciaeformis*	**S. latifasciaeformis* Duda	22	17	18	613	154	123
Zaprionus	*Zaprionus*	*Armatus*	**Z. indianus* Gupta	184	0	100	2441	183	821
Zygothrica	–	*Orbitalis*	*Z. orbitalis* Sturtevant	0	0	5	0	0	0
			N	2194	1153	3402	20,983	5764	7415
			S	20	22	25	16	20	18
			H'	2.657	2.438	2.511	1.455	1.797	2.148
			E_{var}	0.113	0.175	0.118	0.080	0.133	0.091

N, number of individuals; S_{obs}, species richness observed; H', Shannon–Wiener heterogeneity index; E_{var}, Smith–Wilson evenness index.

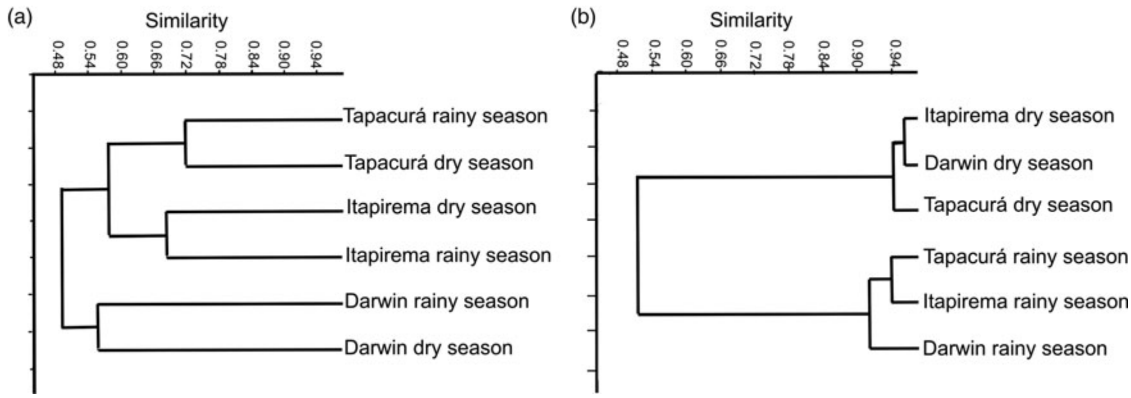

Fig. 2. Similarity tree based on the Jaccard (a) and Morisita (b) indices for the drosophilids collections carried out in the rainy and dry seasons in the Atlantic Forest domain, in Itapirema (Estação Experimental de Itapirema), Darwin (Refúgio Ecológico Charles Darwin) and Tapacurá (Estação Ecológica do Tapacurá).

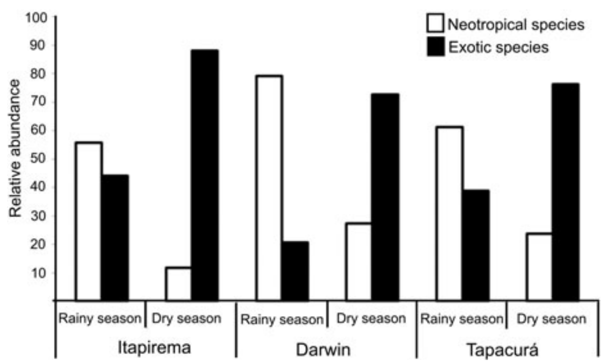

Fig. 3. Relative abundance of drosophilid species native to the Neotropical region and exotic ones in the rainy and dry seasons, in three Atlantic Forest fragments: Itapirema (Estação Experimental de Itapirema), Darwin (Refúgio Ecológico Charles Darwin) and Tapacurá (Estação Ecológica do Tapacurá).

fragments surveyed. Also, the highest diversity indices were recorded in the rainy period.

The average number of drosophilids captured per trap was similar to the values recorded in the northern Atlantic Forest (Garcia *et al.*, 2014; Monteiro *et al.*, 2016) and higher compared with studies carried out in the southern part of the biome (Gottschalk *et al.*, 2007; Döge *et al.*, 2008; Cavasini *et al.*, 2014). Richness values were near those observed in other parts of the Atlantic Forest (De Toni & Hofmann, 1995; Garcia *et al.*, 2008; Penariol & Madi-Ravazzi, 2013). These comparisons and the jackknife 1 values that were similar to the observed ones reveal that the sampling strategy adopted was efficient.

The similarity tree constructed using the Jaccard index clustered collections for study areas, indicating that drosophilid assemblages are different in the sites surveyed, even though these were geographically close. Differences in species composition in Atlantic Forest fragments in somewhat distant sites have been observed in other investigations about drosophilids (De Toni *et al.*, 2007; Gottschalk *et al.*, 2007; Döge *et al.*, 2008). The fact that the three fragments analysed in this study had heterogeneous assemblages and similar responses concerning the parameters investigated indicates that our results may reflect the patterns expected for these organisms in the northern Atlantic Forest.

Although a larger number of drosophilid species have been recorded in the rainy season, the seasonal differences in richness were not significant. In other areas of the northern Atlantic Forest (Monteiro *et al.*, 2016) as well as in the southern part of the biome (Torres & Madi-Ravazzi, 2006; Garcia *et al.*, 2012), higher richness values of these drosophilids were also observed in the rainy season. Concerning other arthropod groups, such as coleopterans, isopterans and arachnids, no significant differences were reported for richness in terms of seasonality in tropical forests (Vasconcellos, 2003; Dias *et al.*, 2006, Anu *et al.*, 2009).

In the Cerrado, a biome characterized by a dry season and a more intense water deficit compared with the northern Atlantic Forest, seasonal differences in richness have been observed for drosophilids, when the highest number of species was recorded in times of higher rainfall (Tidon, 2006; Mata *et al.*, 2008; Roque *et al.*, 2013). In the Atlantic Forest, humidity is more consistently preserved in periods of low rainfall (Por *et al.*, 2005). Therefore, reduced rain volumes do not seem to represent a limiting factor to drosophilid richness in this environment.

Contrasting with our results, several other studies about tropical insects have demonstrated the higher abundance of individuals in the rainy season (Owen & Chanter, 1970; Wolda, 1978*a*; Denlinger, 1980; Smythe, 1982; Frith & Frith, 1985, Hammond, 1990; Hill, 1993; Novotny & Basset, 1998; Devries & Walla, 2001). Although our findings did not reproduce this model when Neotropical and exotic species are considered together, the pattern is observed when only Neotropical species are included in the analysis. Probably, trophic resources are more readily available in the rainy season (Buril *et al.*, 2013), which is an advantage for native species (David *et al.*, 1983; Döge *et al.*, 2015). In turn, it may be supposed that exotic species were more successful when invading these natural areas, by using the resources available in the dry season.

There is no single pattern to describe the seasonal abundance of exotic and native drosophilids in different parts of the world. Our findings reflect the configuration observed by Srinath & Shivanna (2014), for instance, who investigated

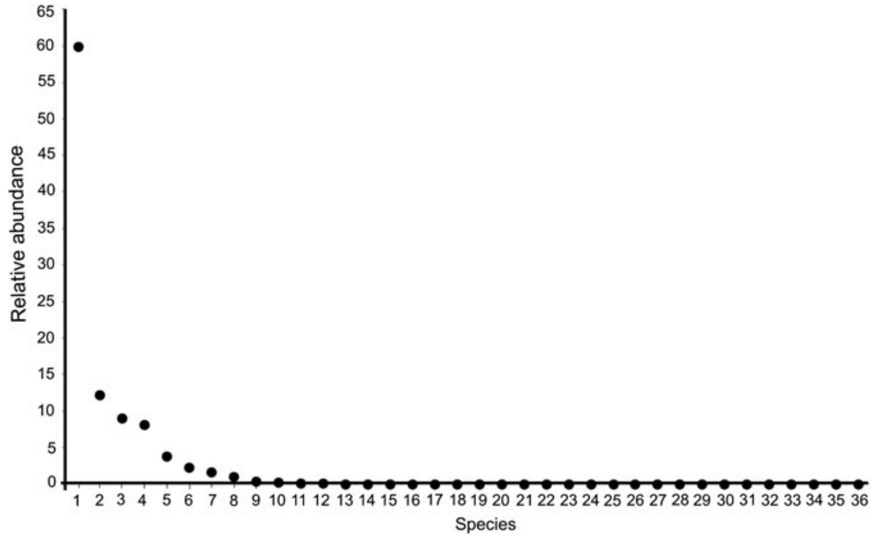

Fig. 4. Ranking based on abundance of 36 drosophilid species collected in three fragments of the Atlantic Forest. 1 = *Drosophila malerkotliana*, 2 = *D. willistoni*, 3 = *Zaprionus indianus*, 4 = *D. sturtevanti*, 5 = *D. simulans*, 6 = *Scaptodrosophila latifasciaeformis*, 7 = *D. paulistorum*, 8 = *D. prosaltans*, 9 = *D. mercatorum*, 10 = *D. nebulosa*, 11 = *D. neocardini*, 12 = *D. melanogaster*, 13 = *D. fumipennis*, 14 = *D. ararama*, 15 = *Rhinoleucophenga punctulata*, 16 = *D.* sp7, 17 = *D. cardinoides*, 18 = *D. pictilis*, 19 = *D. polymorpha*, 20 = *D. ellisoni*, 21 = *D.* sp6, 22 = *D. ananassae*, 23 = *D.* sp2, 24 = *D.* sp5, 25 = *Neotanygastrella tricoloripes*, 26 = *Zygothrica orbitalis*, 27 = *D. zottii*, 28 = *D.* sp9, 29 = *D.* sp10, 30 = *D.* sp1, 31 = *D.* sp3, 32 = *R.* sp1, 33 = *D.* sp4, 34 = *D.* sp8, 35 = *R. capixabensis*, 36 = *D. kikkawai*.

the drosophilid fauna in India, recording greater abundance of native species in the rainy season. This was also observed in Brazil, more specifically in the Cerrado (Mata *et al*., 2008) and in the southern part of the Atlantic Forest (Torres & Madi-Ravazzi, 2006). Concerning exotic species, Bombin & Reed (2016), confirm our results, noting that these flies are more abundant during drought periods in North America, similarly to what was reported by Mata *et al*. (2008) in Brazil.

The diversity indices (H' and E_{var}) were higher in the rainy season. In the southern Atlantic Forest, these indices have exhibited a trend towards increasing values during the dry period (De Toni & Hofmann, 1995; De Toni *et al*., 2007; Gottschalk *et al*., 2007). In this study, the high dominance of exotic species in the dry season justifies the lower E_{var} values recorded. The greater richness and evenness of abundance values when rainfall volumes are increased explain the higher H' values observed in this season.

Approximately 80% of the richness of the drosophilid assemblage analysed was formed by rare species, which are represented by those whose frequency is below 1%. This pattern is regularly observed for Neotropical arthropods (Novotny & Basset, 2000; Coddington *et al*., 2009), and it has been described in studies about drosophilids from the Atlantic Forest (Schmitz *et al*., 2010, Cavasini *et al*., 2014) and other biomes, such as the Amazon Forest (Acurio *et al*., 2010), the Cerrado (Roque *et al*., 2013) and the Caatinga (Oliveira *et al*., 2016). From the ecological and evolutionary standpoints, rare species are those that have become more specialized to a few environments (Dobzhansky & Pavan, 1950).

The occurrence of intraspecific variations in temporal abundance patterns of several insect groups has been well documented (Wolda & Broadhead, 1985; Wolda, 1989; Wolda *et al*., 1998; Noguera *et al*., 2002; Wiwatwitaya & Takeda, 2005; Kishimoto-Yamada *et al*., 2010). In this study, among the most abundant exotic drosophilids, *D. malerkotliana*, *Z. indianus* and *S. latifasciaeformis* were more considerably recorded in the dry season, while *D. simulans* was more abundant in the rainy period. Of these, low abundance of *S. latifasciaeformis* has been recorded in other areas of the Atlantic Forest (De Toni *et al*., 2007; Bizzo *et al*., 2010), making a comparison with our results more difficult.

The pattern observed for *D. simulans* has been recorded in the southern Atlantic Forest (Schmitz *et al*., 2007, Döge *et al*., 2008; Bizzo *et al*., 2010; Garcia *et al*., 2012). Ecological findings point to the higher sensitivity of this species to water deficit, compared with other drosophilids (David *et al*., 2004). Bombin & Reed (2016) also observed significant positive correlation of *D. simulans* with high rainfall periods in the USA. Studies have shown that this species is strongly influenced by the availability of trophic resources (Döge *et al*., 2015). It is possible that, in the fragments surveyed in this study, these resources are more plentiful during the rainy season (Buril *et al*., 2013), which may be favourable to this species.

Contrasting with the pattern observed, *D. malerkotliana* and *Z. indianus* have been recorded more abundantly during periods of more intense rains in their native sites, in Asia (Srinath & Shivanna, 2014) and Africa (Prigent *et al*., 2013), respectively. This pattern is also observed in the southern part of the Atlantic Forest (Tidon-Sklorz & Sene, 1992; De Toni *et al*., 2007; Bizzo *et al*., 2010). These data demonstrate that these species do not present a uniform seasonal fluctuation pattern concerning rainfall along their distribution range in the biome. It is possible that other abiotic factors such as temperature (which is comparatively low and varies more broadly in the southern Atlantic Forest) could explain these oscillations. Low temperatures may limit population sizes of *Z. indianus* in the southern Atlantic Forest (Garcia *et al*., 2008). At 18 °C, this species' biological cycle may extend for up to 1 month (Nava *et al*., 2007), which is too long for a colonizing drosophilid (Atkinson, 1979). Similarly, *D. malerkotliana* is also influenced by

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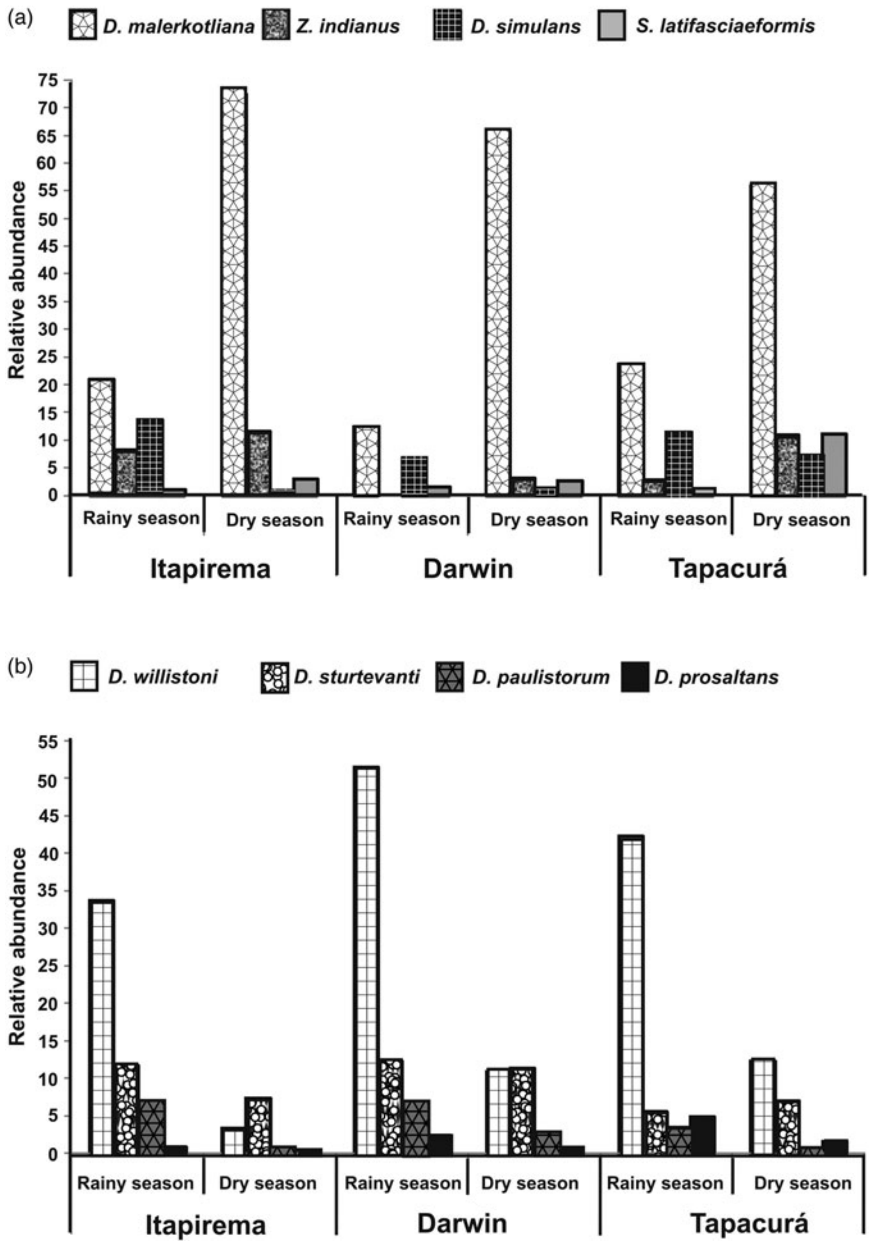

Fig. 5. Seasonal variation of exotic (a) and native drosophilid species to the Neotropical region (b) in three fragments of the Atlantic Forest: Itapirema (Estação Experimental de Itapirema), Darwin (Refúgio Ecológico Charles Darwin) and Tapacurá (Estação Ecológica do Tapacurá).

temperature, with reduced fertility below 20 °C and total interruption of its development at 15 °C (Medeiros *et al*., 2003).

Concerning *D. malerkotliana*, which was the most abundant species in this work, studies have shown its opportunistic character, taking over trophic resources at least 24 h before other drosophilids. This aspect, besides its short life cycle (Martins, 2001) and the likely occupation of sites that are inaccessible to other species are characteristics that may lend competitive advantages to *D. malerkotliana*, particularly in times when food resources are more limited.

The greater abundance of Neotropical species in the rainy season may be attributed mainly to species of the *willistoni* (*D. willistoni* and *D. paulistorum*) and of the *saltans* (*D. sturtevanti* and *D. prosaltans*) subgroups. In a study about the first subgroup, Garcia *et al*. (2014) had already observed the identical seasonal pattern in other fragments in the northern Atlantic Forest, which has also been reported for the southern part of the biome (Dobzhansky & Pavan 1950; Franck & Valente, 1985; Tidon-Sklorz & Sene, 1992; Saavedra *et al*., 1995; De Toni *et al*., 2007; Garcia *et al*., 2012). Dobzhansky (1957) and Spassky *et al*. (1971) highlight the fact that humidity is a limiting factor for these species, which may explain their higher abundance values in the rainy season.

Drosophila sturtevanti exhibited one single seasonal pattern along the whole extension of the Atlantic Forest, with greater abundance in the rainy season (Torres & Madi-Ravazzi 2006;

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De Toni *et al*., 2007). Torres & Madi-Ravazzi (2006) observed a positive correlation of this species with rainfall. Considering *D. prosaltans*, few individuals have been collected in the southern part of the Atlantic Forest, preventing any discussion about a seasonal pattern for this species along the biome.

In the dry season, when trophic resources (especially fruit) are less readily available in the northern Atlantic Forest (Buril *et al*., 2013), generalist species have greater survival success, which explains their dominance in this period. *Drosophila malerkotliana*, *Z. indianus*, *S. latifasciaeformis* and *D. simulans* are generalist species (Yassin *et al*., 2012), and the first three have larger populations during the dry period. These findings demonstrate that the seasonal pattern observed in this study is explained by differences in abundance between native and exotic species, indicating the adoption of adaptation strategies by these groups.

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