ECOLOGY, BEHAVIOR AND BIONOMICS

Changes in Brazilian Drosophilidae (Diptera) Assemblages Across an Urbanisation Gradient

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Mudanças em Assembléias Brasileiras de Drosophilidae (Diptera) em um Gradiente de Urbanização

RESUMO - O presente estudo objetiva caracterizar as assembléias de Drosophilidae amostradas em quatro pontos sujeitos a diferentes níveis de urbanização, na cidade de Florianópolis, Sul do Brasil. Foram realizadas cinco amostragens entre agosto/2000 e agosto/2001 e cinco entre agosto/2002 e agosto/2003 em cada ponto. Uma mudança gradual nas espécies dominantes foi observada no gradiente de urbanização, com acréscimo na abundância relativa das espécies exóticas nas áreas urbanas. Entre as espécies nativas, houve um decréscimo expressivo na abundância relativa de *Drosophila capricorni* Dobzhansky & Pavan. Por outro lado, a riqueza no ponto de baixa urbanização aumentou, provavelmente devido à presença de áreas verdes na cidade. O índice de diversidade não variou significativamente entre os pontos, mas sua correlação com a equitabilidade e a riqueza se alterou.

PALAVRAS-CHAVE: Drosophila, Zaprionus, ecologia, diversidade, riqueza

ABSTRACT - The present study aims to characterise the assemblages of Drosophilidae sampled from four sites subject to different levels of urbanisation, in the city of Florianópolis, South Brazil. Five samples were collected between August 2000 and August 2001 and five between August 2002 and August 2003 in each site. A gradual change in the dominant species was observed in the urbanisation gradient, with an increase in relative abundance of exotic species in urban areas. Among the native species, the relative abundance of *Drosophila capricorni* Dobzhansky & Pavan had an expressive decrease. In the other hand the richness in the low urbanisation site increased, probably due to the presence of urban gardens. The diversity index did not vary significantly among sites, but its correlation with evenness and richness changed.

KEY WORDS: Drosophila, Zaprionus, ecology, diversity, richness

Cities and neighbouring areas can be considered as a particular ecosystem (Marcus & Detwyler 1972). Bryson & Ross (1972) suggested three main factors distinguishing cities from other environments: physical changes in soil surface, which promotes an increase in environmental aridity; air turbidity, which is the reduction in luminosity due to air pollution; and variation in heat production, which makes cities warmer than other environments. This variation in heat production is a consequence of the lower air circulation through buildings and of the paving of the soil, and is also influenced by air turbidity (Danni 1980).

Another important consequence of urbanisation is the biotic homogenisation, caused by the eradication of the wild fauna and flora by the introduction of exotic ones associated with the urbanisation process itself (Sukopp & Werner 1982, McKinney & Lockwood 1999, Pickett *et al.*

2001). For instance, several species of Drosophilidae are found in association with environments under anthropic influence (Parsons & Stanley 1981). These environmental changes usually define a gradient from wild to urbanised areas. Ruszczyk (1986/1987) identified this gradient in the city of Porto Alegre, southernmost Brazil, and suggested a classification for the different urbanisation levels based on the extent of plant covers and the kind and height of buildings.

Another sign of increased urbanisation is observed in the changed composition of associated animal communities (Blair 1996, Pickett *et al.* 2001, Crooks *et al.* 2004). This kind of change was detected in *Drosophila* assemblages studied by Valente and co-workers in Porto Alegre (Valente *et al.* 1989, Valiati & Valente 1996, Silva *et al.* 2005b). In these studies, besides the changes in the abundances of species at different sites in the city, several other alterations were also detected in the frequency of some genetic markers as chromosomal inversions, courtship patterns, and enzymatic polymorphisms in native species of *Drosophila*.

A number of other studies have recently investigated the urban fauna of Drosophilidae in the New World (Goñi *et al.* 1998, Avondet *et al.* 2003, Ferreira & Tidon 2005). All studies showed that the structures of these assemblages were similar, with a high predominance of the exotic species in detriment of the native species.

Considering that the urban ecosystem has not yet been sufficiently studied, despite its intrinsic importance, the present study aimed to characterise and compare the Drosophilidae assemblages inhabiting sites at different transitions points from wild to urbanised environments in southern Brazil.

Material and Methods

Study area. Collections were carried out in the Santa Catarina Island, city of Florianópolis, Santa Catarina State, southern Brazil. This island measures approximately 424

km² and is the location of the largest part of the city of Florianópolis, home to about 300,000 inhabitants. According to the Köeppen criteria, the climatic classification of the area is type Cfa, located in subtropical intermediate zone and belongs to the mesothermic humid group (Prefeitura Municipal de Florianópolis 2005). The variation of the monthly average of daily temperature and relative humidity, the total monthly rainfall measured in the collection period at the Meteorological Station of Instituto Nacional de Meteorologia (27°35'S; 48°34'W; altitude of 2m) are shown in Fig. 1.

Four collection sites were chosen and characterized for the urbanisation degree (Fig. 2A and B), in agreement with Ruszczyk's parameters (1986/1987): percentage of plant cover, and type and height of houses and buildings. As control, we sampled one site within a remaining area of the Atlantic Rain Forest at Morro da Lagoa da Conceição (27°35'268"S; 48°28'329"W), without urban influence (NU-not urbanised).

The low urbanisation site (LU) is in Morro da Cruz (27°35'040"S; 48°31'040"W) and is characterised by the occurrence of a degraded Atlantic Rain Forest surrounded

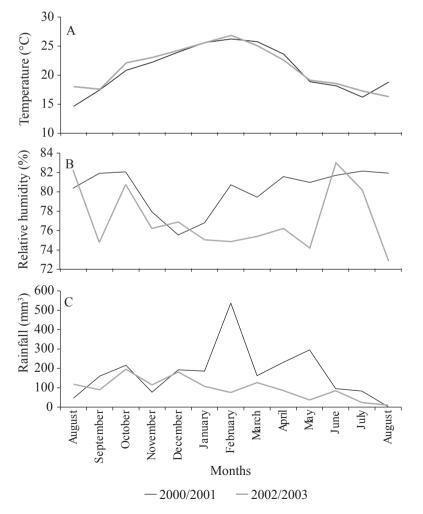


Fig. 1. Temperature and relative humidity averages and total rainfall in the months during collections in years 2000/2001 and 2002/2003.

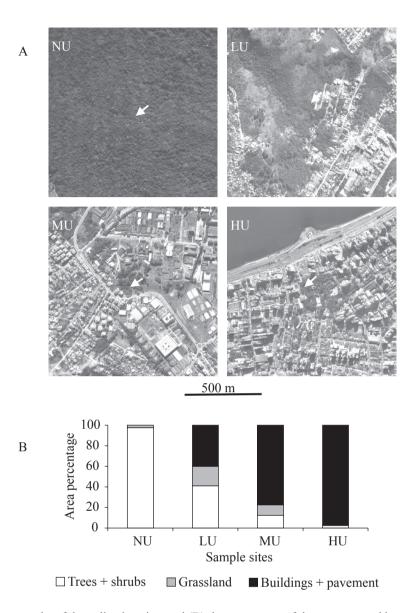


Fig. 2. (A) Aerial photographs of the collection sites and (B) the percentage of the area covered by trees+shrubs or grassland or buildings+pavement; radius = 1 km. The arrow shows where the traps were distributed. NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site.

by one-storey houses. The sampling site with a medium urbanisation level (MU) is in the Universidade Federal de Santa Catarina campus (27°36'129''S; 48°31'219''W), which is surrounded by several residential buildings up to four storeys high. The high urbanisation level site (HU) is in the 14^a Brigada Motorizada da Infantaria (27°35'273''S; 48°33'023''W). This area is circled by tall commercial and residential buildings over four storeys, although a small area covered by native species of trees survives in the zone.

Collection and identification of specimens. Ten samples were collected between August 2000 and August 2003. The samples were categorised as winter/2000 (collections between August 7th and September 1st), spring/2000 (October 25th to December 1st), summer/2001 (January 8th to February

7th), autumn/2001 (March 12th to April 21st), winter/2001 (July 9th to August 13th), winter/2002 (August 16th to September 7th), spring/2002 (November 7th to 22nd), summer/2003 (February 15th to 21st), autumn/2003 (April 9th to 16th) and winter/2003 (August 11th to 16th).

Flies were captured using 50 traps per sample, according to Tidon & Sene (1988), containing 5 kg of mashed bananas enriched with commercial yeast (Fleishmann®). Traps were hung 1.5 m high for three days.

The species identification was based on external morphology and on male genitalia (prepared according to Wheeler & Kambysellis 1966). When possible, a series of specimens of each species was deposited in the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul.

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Ecological and statistical analysis. The parameters used for diversity analysis were: number of individuals belonging to exotic species from the Neotropical area (N_{exot}) , number of native species individuals (N_{nat}) , number of exotic (S_{exot}) and native (S_{nat}) species, the Shannon-Wiener diversity index (H')(Magurran 1988, Krebs 1999), number of species estimated for 20 individuals with a rarefaction analysis (S_{rar}) (Magurran 1988, Krebs 1999), and the Smith-Wilson evenness index $(E_{\rm o})$ (Smith & Wilson 1996). Rarefaction curves were also built for each site (Magurran 1988, Krebs 1999). Comparisons between sites and seasons of the parameters available were accomplished by the MANOVA test, followed by a Tukey test (Krebs 1999, Zar 1999), and by Pearson correlations tests between H' and the other indices (Zar 1999). The Shapiro-Wilk test and Levene's test were used to verify normality and homogeneity of variances, respectively. For statistical analysis, we used natural logarithmic transformations in number of individuals (Ln N).

The importance of the spatial and temporal variables in the total heterogeneity index value was measured by niche analysis according Levins (1968), with the calculations of *H'between* = *H'total* – $(\sum Ni^*H'i)/N$; where *H'between* is the value of H' to a given component; H' total is the value of H'considering all the samples together; N is the total number of individuals in all samples, N_i is the number of individuals in component j and H'j is H' within component j. Two main components were available: spatial component (collection sites - NU, LU, MU and HU), and temporal component (years - 2000/2001 and 2002/2003, and seasons - winter, spring, summer, autumn). The interaction between spatial and temporal components (residual), which considered the variation between each collection individually, was also established. For comparisons between each collection we used the similarity Morisita's index (Krebs 1999), followed by the construction of an UPGMA dendrogram (Sneath & Sokal 1973).

The statistical analysis used the software Statistica '98 edition (Statsoft 1998). Diversity indices and dendrogram construction were carried out using the Past version 1.34 (Hammer *et al.* 2001) and the Ecological Methodology version 5.2 (Krebs 1999) softwares.

Results

A total of 253,374 specimens belonging to 105 Drosophilidae species were collected and analysed. The absolute abundances of the collected species in each site are shown in Table 1.

The relative abundance (*pi*) of the species that reached values above 5% of the total per sample in each site is shown in Fig. 3. In NU (Fig. 3A), *Drosophila capricorni* Dobzhansky & Pavan was the best-represented species in winter, followed by the *willistoni* subgroup (*D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky & Pavan). The predominance of *D. capricorni* also occurred in spring 2000. In the remaining samples, the *willistoni* subgroup was the most representative, followed by *D. polymorpha* Dobzhansky & Pavan or *D. capricorni*. In the LU site (Fig. 3B), the *willistoni* subgroup was the most predominant taxon in winter, and *Zaprionus*

indianus Gupta was the most representative species in summer and autumn 2001 and in spring 2002, followed either by the *willistoni* subgroup or by *D. simulans* Sturtevant. This latter species was predominant in spring 2000, and *D. malerkotliana* Parshad & Paika, followed by *D. simulans* prevailed in summer and autumn 2003.

In MU and HU (Fig. 3C and D), the assemblages showed the same dominant species, and in general, *D. simulans* was more abundant in the winter samples, followed by *Z. indianus*. An opposite tendency was observed in the spring and summer samples. In autumn, a great increase in the *pi* of *D. malerkotliana* was observed, becoming one of the dominant species, along with *Z. indianus*. *D. malerkotliana* was also the predominant species in summer 2003 in HU, followed by *D. simulans*, which was dominant in MU.

These patterns were also observed in the UPGMA dendrogram constructed with the Morisita's similarity index (Fig. 4). In the majority of MU and HU samples, there are at least two dominant species with pi > 0.20, and the samples collected in LU presented an intermediate situation: in winter the dominance is exerted by the *willistoni* subgroup, and in the other collections by one of the exotic species *D. simulans*, *Z. indianus* or *D. malerkotliana*.

The calculated ecological parameters are shown in Table 2. We observed a significant oscillation with the MANOVA test (between sites F = 7.70; P = 0.000 and between seasons F = 3.53; P = 0.0001). But, when we carried out the Tukey tests, only N_{evol} varied significantly between sites and seasons (Fig. 5), where NU was the lowest (P = 0.0002 for all the comparisons), and LU lower than HU (P = 0.002). As for seasons, winter values were lower than spring and the autumn values (P = 0.02 and 0.0002, respectively), and lower in summer than in autumn (P = 0.04). S_{nat} and S_{exot} variations were significant only in spatial terms, where S_{nat} was lower in NU than in LU (P = 0.007). Additionally, S was lower in NU than in LU, MU and HU (P = 0.03, 0.0003 and 0.0003, respectively) and in LU lower than in HU (P = 0.03). Although H' and S_m did not vary significantly, they presented higher values in LU and winters and lower values in NU and autumns. In terms of local variation, E_{var} values were higher in NU and lower in HU. Considering temporal variation, values observed were higher in winters and lower in autumns.

Rarefaction curves are shown in Fig. 6, together with the curve of De Toni *et al.* (2007). These authors carried out drosophilid collections in eight Atlantic forest sites of the Santa Catarina State during two consecutive years, and the observed total richness was used here as a measurement of regional richness. We observed that LU is the richest site, even when compared with NU, whose anthropic influence is much lower. Only the regional richness curve (De Toni *et al.* 2007) reached comparable values for LU.

Pearson correlation between the values of H' and of E_{var} , S_{rar} , N_{nat} , N_{exot} , S_{nat} and S_{exot} are shown in Table 3. In NU, H' correlated positively with E_{var} and negatively with $\ln N_{exot}$. On the contrary, in MU and HU, H' correlated positively with S_{rar} and S_{nat} . In like manner, in HU the H' also correlated positively with S_{exot} . In LU we found an intermediate situation, where H' is positively correlated with E_{var} and S_{rar} .

The analysis of niche contribution to the total value of diversity (H') is presented in Table 4. The contributions to

Collection sites Total Species NU MU HU LU Amiota sp. Diathoneura brasiliensis Duda Drosophila ananassae Doleschall Drosophila annulimana Duda Drosophila ararama Pavan & da Cunha Drosophila arassari da Cunha & Frota-Pessoa Drosophila atrata Burla & Pavan Drosophila bandeirantorum Dobzhansky & Pavan Drosophila bocainensis Pavan & da Cunha Drosophila bocainoides Carson Drosophila briegeri Pavan & Breuer Drosophila bromelioides Pavan & da Cunha Drosophila busckii Coquillett Drosophila caponei Pavan & da Cunha Drosophila capricorni Dobzhansky & Pavan 2,353 2,671 Drosophila cardini Sturtevant 1,292 1,208 2,611 Drosophila cardinoides Dobzhansky & Pavan Drosophila carolinae Vilela Drosophila drevfusi Dobzhansky & Pavan Drosophila fascioloides Dobzhansky & Pavan Drosophila flexa Loew Drosophila fumipennis Duda Drosophila fuscolineata Duda Drosophila gaucha Jaeger & Salzano Drosophila griseolineata Duda Drosophila guaraja King Drosophila hydei Sturtevant Drosophila immigrans Sturtevant 1,346 Drosophila kikkawai Burla Drosophila limensis Pavan & Patterson Drosophila maculifrons Duda * Drosophila malerkotliana Parshad & Paika 2,386 24,727 21,621 48,741 Drosophila mapiriensis Vilela & Bachli Drosophila mediopicta Frota-Pessoa Drosophila mediopunctata Dobzhansky & Pavan Drosophila mediostriata Duda 1,352 Drosophila melanogaster Meigen 1,235 Drosophila mercatorum Patterson & Wheeler 1,221 2,374 3,584 7,459

Table 1. Absolute abundance of the species collected in each site.

Table 1. Continuation.

Service	Collection sites					
Species	NU	LU	MU	HU	– Total	
Drosophila meridionalis Wasserman	0	2	1	0	3	
Drosophila nappae Vilela, Valente & Basso-da-Silva	2	50	1	24	77	
Drosophila nebulosa Sturtevant	0	5	16	1	22	
Drosophila neocardini Streisinger	65	1,053	410	943	2,471	
Drosophila neoelliptica Pavan & Magalhães	216	23	9	4	252	
Drosophila neoguaramunu Frydenberg	0	0	0	4	4	
Drosophila neosaltans Pavan & Magalhães	0	8	0	0	8	
Drosophila nigricruria Patterson & Mainland	0	2	0	1	3	
Drosophila onca Dobzhansky & Pavan	73	487	100	348	1,008	
Drosophila ornatifrons Duda	24	48	11	43	126	
Drosophila pallidipenis Dobzhansky & Pavan	9	28	46	87	170	
Drosophila papei Bächli & Vilela	0	0	0	1	1	
Drosophila paraguayensis Duda and Drosophila cuaso Bächli, Vilela & Ratcov	125	876	20	252	1,273	
Drosophila paramediostriata Townsend & Wheeler	0	11	1	23	35	
Drosophila polymorpha Dobzhansky & Pavan	2,662	1,850	711	2,271	7,494	
Drosophila quadrum (Wiedemann)	0	4	3	0	7	
Drosophila querubimae Vilela	1	4	3	237	245	
Drosophila repleta Wollaston	2	2	20	6	30	
Drosophila roehrae Pipkin & Heed	2	23	4	1	30	
Drosophila saltans Sturtevant and Drosophila prosaltans Duda	40	213	155	321	729	
Drosophila pauliceia Ratcov & Vilela	0	0	3	1	4	
Drosophila schineri Pereira & Vilela	0	32	7	0	39	
Drosophila serido Vilela & Sene	0	17	2	2	21	
Drosophila setula Heed & Wheeler	0	4	0	4	8	
Drosophila simulans Sturtevant	385	5,871	16,855	24,777	47,888	
Drosophila sturtevanti Duda	306	676	738	338	2,058	
Drosophila trifilum Frota-Pessoa	0	2	0	9	11	
Drosophila virilis Sturtevant	0	0	2	15	17	
Drosophila willistoni Sturtevant and Drosophila paulistorum Dobzhansky & Pavan	21,437	10,747	2,506	4,299	38,989	
Drosophila zottii Vilela	4	5	4	1	14	
Drosophila aff. elliptica Sturtevant	0	2	0	0	2	
Drosophila aff. senei Vilela	0	13	0	0	13	
Drosophila sp.1	0	1	2	0	3	
Drosophila sp.4	0	7	7	0	14	
Drosophila sp.A	1	1	0	1	3	
Drosophila sp.B	1	0	0	1	2	

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Spacing		Colle	ection sites	— Tota	
Species	NU	NU LU		HU	- 100
Drosophila sp.C	1	0	6	0	7
Drosophila sp.D	1	0	3	0	4
Drosophila sp.E	0	0	1	0	1
Drosophila sp.G	0	7	0	0	7
Drosophila sp.G12	0	1	0	2	3
Drosophila sp.G13	0	7	0	0	7
Drosophila sp.G14	0	3	0	0	3
Drosophila sp.G16	1	0	1	0	2
Drosophila sp.GORD	0	1	0	0	1
Drosophila sp.H	0	1	0	0	1
Drosophila sp.M4	0	1	0	0	1
Drosophila sp.Q2	2	3	0	0	5
Drosophila sp.R2	0	0	3	0	3
Drosophila sp.R3	0	1	0	0	1
Drosophila sp.T3	0	1	0	1	2
Hirtodrosophila sp.1	0	1	0	0	1
Hirtodrosophila sp.Z2	3	72	1	0	76
Hirtodrosophila sp.Z3	0	3	0	0	3
Hirtodrosophila sp.Z4	0	5	0	0	5
Rhinoleucophenga obesa (Loew)	0	1	0	0	1
Scaptodrosophila latifasciaeformis (Duda)	2	1,127	875	70	2,074
Zaprionus indianus Gupta	248	10,451	35,417	34,069	80,185
Zygothrica bilineata (Williston)	0	1	0	0	1
Zygothrica dispar (Wiedemann)	0	29	0	0	29
Zygothrica orbitalis (Sturtevant)	16	8	10	3	37
Zygothrica prodispar Duda	0	8	0	0	8
Zygothrica vittimaculosa Burla	0	8	1	8	17
Zygothrica sp. C	0	1	0	0	1
Total	28,762	39,241	87,457	97,914	253,374

Table 1. Continuation.

NU - not urbanized site, LU - low urbanisation site, MU - medium urbanisation site, HU - high urbanisation site, *exotic species.

the diversity of spatial and temporal variation were small, of approximately 14% and 7%, respectively. The residual contribution (spatial *vs.* temporal contribution) explains only 29% of the total value of H'.

Discussion

The present study sheds new light on the role of Drosophilidae as indicators of alterations in urban, transitional and wild environments in the Neotropical region.

The Drosophilidae fauna of urban areas and Atlantic Forest was characterized by their dominant species. The exotic species were quite dominant in the studied urban environments. The association of the *melanogaster* group with anthropic environments is a consensus among the drosophilists. The species of this group are associated with altered or open environments in Brazil, as cities, cerrados, strand forests and dunes (Sene *et al.* 1980, Ferreira & Tidon 2005, Tidon 2006).

The great dominance of the recently introduced African fly Z. *indianus* in the assemblages of MU and HU and the

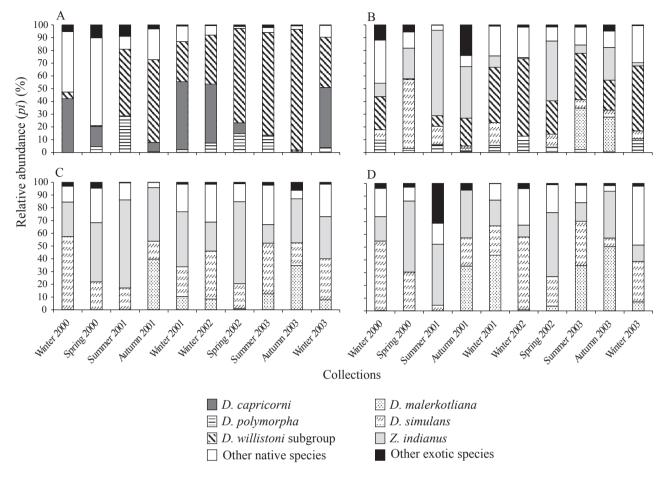


Fig. 3. Relative abundance of the main species sampled in each sampling site ($p_i > 0.05$). A) NU – not urbanized site. B) LU – low urbanisation site. C) MU – medium urbanisation site. D) HU – high urbanisation site.

almost absence in the forest also deserves attention. Tidon *et al.* (2003), in collections made in wild environments of Central Brazil, observed that *Z. indianus* is more abundant in open areas of the cerrado, but not in gallery forest environments. Silva *et al.* (2005a, b) also verified the high abundance of this fly in the urban areas of the city of Porto Alegre, in the southernmost state of Brazil.

In general, the exotic species are being appointed as indicators of disturbed environments (Ferreira & Tidon 2005; Silva *et al.* 2005a,b), except *D. simulans* that, in some studies, was cited as naturalised in the Brazilian environments (Dobzhansky & Pavan 1950, Pavan 1959). Yet, this naturalisation cannot be generalized, since its populations collected in places covered with Atlantic forest vegetation are scarce, in comparison with those sampled in other wild environments like mangroves and strand forests (H.J. Schmitz and L.E.M. Bizzo, personal communication). *D. simulans* distribution in the urban gradient suggests that perhaps the species cannot so easily establish in wild Atlantic forest.

The *willistoni* subgroup, typical of forests (Martins 1987, 2001; Saavedra *et al.* 1995), was very abundant in our collections, including those carried out in urbanized areas. The presence of these species in urban areas was previously related by Valente *et al.* (1993), by Valiati & Valente (1996),

and recently by Silva *et al.* (2005a,b), who sampled it at high abundance in Porto Alegre, southernmost Brazil. Moreover, due to the high abundance of the exotic species in the city, the expressiveness of *willistoni* subgroup is low in areas of medium and high urbanisation.

However, *D. capricorni*, another member of the *willistoni* group, had a very pronounced decrease in the city, behaving as a typical urban-sensitive species. Similarly low abundances have been observed in open environments (Sene *et al.* 1980, Tidon 2006). Due to this high susceptibility to environmental changes, this species appears to be a suitable indicator of preserved areas covered by Atlantic Forest vegetation.

The influence of urbanisation over Drosophilidae assemblages apparently attained its maximum effect in the medium urbanisation site. This observation is in accordance with Ferreira & Tidon (2005), who verified the same effect in Brasília. Apparently, it can be said that the assemblages belonging to the low urbanisation site were characterized as transitory between those belonging to wild and disturbed areas.

The values of H', E_{var} and S_{rar} were very close to what was observed in other studies carried out in other environments in the south of Brazil (Saavedra *et al.* 1995, Silva *et al.* 2005b, De Toni *et al.* 2007) and the peak in abundance of *Drosophila*

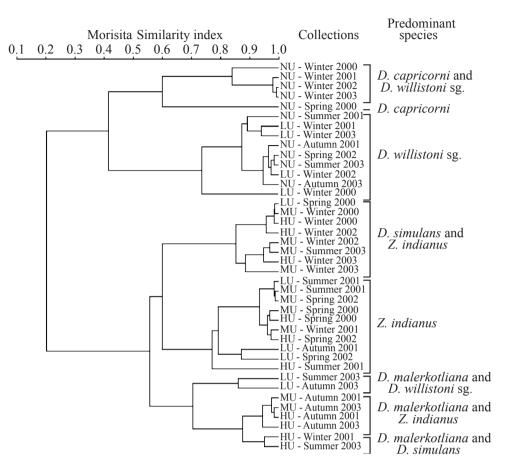


Fig. 4. UPGMA dendrogram constructed with Morisita's similarity index and the predominant species in each sample. NU - not urbanized site, LU - low urbanisation site, MU - medium urbanisation site, HU - high urbanisation site.

Sites	Year	Seasons	H'	E_{var}	S_{rar}	S_{nat}	S_{exot}	N _{nat}	N_{exot}
	2000	Winter	1.93	0.73	10	8	2	16	4
	2000	Spring	2.46	0.489	10	19	3	106	12
		Summer	1.37	0.111	4.8	16	3	4346	423
	2001	Autumn	1.19	0.196	4.4	15	3	919	29
NILI		Winter	1.34	0.224	4.6	20	1	688	6
NU	2002	Winter	1.3	0.156	4.2	16	2	1980	11
	2002	Spring	0.87	0.115	3.3	15	3	4650	53
		Summer	0.73	0.147	3	13	2	2454	51
	2003	Autumn	0.33	0.135	2	16	4	12097	87
		Winter	1.25	0.174	4.2	14	1	817	3
LU	2000	Winter	2.46	0.505	9.8	13	5	150	67
	2000	Spring	1.44	0.112	5	24	5	975	4934
		Summer	1.15	0.129	4.3	19	4	960	4195
	2001	Autumn	1.71	0.169	5.5	26	6	1127	2393
		Winter	2.05	0.154	7.6	29	6	2055	768
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Table 2. Ecological indices calculated for each collection.

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Sites	Year	Seasons	H'	E_{var}	S_{rar}	Snat	Sexot	N _{nat}	N _{exot}
	2002	Winter	1.7	0.179	6.6	31	4	2550	164
	2002	Spring	1.63	0.127	5.6	25	5	1571	2236
		Summer	1.77	0.177	6.3	15	4	453	405
	2003	Autumn	1.92	0.125	6.4	40	6	2631	4523
		Winter	1.91	0.126	7.2	42	5	6346	734
	2000	Winter	1.29	0.185	4.4	14	7	167	1092
	2000	Spring	1.58	0.145	5.3	20	5	608	1642
		Summer	1.09	0.183	4.1	10	3	116	752
	2001	Autumn	1.2	0.074	3.7	12	4	1721	39962
MU		Winter	1.82	0.173	6.4	20	8	398	1436
MU	2002	Winter	1.9	0.158	6.6	27	8	744	1761
	2002	Spring	1.23	0.117	4.5	20	6	1088	6601
		Summer	1.87	0.13	6.6	19	7	617	1407
	2003	Autumn	1.54	0.081	5	27	7	1300	18434
		Winter	1.84	0.126	6.3	31	9	1973	5638
	2000	Winter	1.69	0.206	6.2	21	7	353	1260
	2000	Spring	1.27	0.117	4.3	21	8	936	7162
		Summer	1.38	0.12	4.6	14	4	640	3260
	2001	Autumn	1.28	0.074	3.8	18	5	1337	24552
HU		Winter	1.55	0.121	5.1	19	5	495	3306
	2002	Winter	1.75	0.141	6.6	31	10	3102	7686
	2002	Spring	1.6	0.101	5.7	26	7	3667	13077
		Summer	1.62	0.12	5.4	18	7	548	3463
	2003	Autumn	1.18	0.079	3.8	12	6	741	15638
		Winter	2.14	0.128	7.6	27	8	3093	3598

Table 2. Continuation.

H' – Shannon-Wiener index, E_{var} – Smith-Wilson index, S_{rar} – Number of rarefact species, S_{nat} – Number of native species, S_{exot} – Number of exotic species, N_{nat} – Absolute abundance of native species, N_{exot} – Absolute abundance of exotic species, NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site.

species in autumn and spring has been recorded by Basden (1953) and Martins (1987), respectively. Avondet *et al.* (2003) and Ferreira & Tidon (2005) also observed the increasing abundance of exotic species in cities, and we propose that this increase could act as an indicative of disturbance in wild forest environments.

On the other hand, there was a surprisingly low influence of urbanisation over some native species, as *D. polymorpha* and the *willistoni* subgroup. Also, not only did richness apparently remain unaltered in urbanized areas, but also increased in LU. Such observation is particularly interesting, since several species collected in city are clearly non-generalists, such as those of the *annulimana*, *repleta* and *tripunctata* groups.

McIntyre (2000) lists several factors, including pollution and the fragmentation of natural habitats with the ultimate isolation of natural populations as the main causes of the loss of richness in urban environments. However, in studies with birds and butterflies, a high richness in moderate disturbed environments was observed, like in LU (Blair 1996, Blair & Launer 1997, Crooks et al. 2004). This can be explained by the association of the native species with small areas covered by vegetation close to the sampling sites. Zapparoli (1997), investigating insects in Rome, also observed that when the sampling sites were close to gardens, the richness and the diversity of species were high. Besides this, areas with vegetation in the city promote more favourable environmental conditions also for the surrounding ones (Danni 1980). In the two more urbanized sites investigated in the present study, there is at least one small area with native vegetation in the neighbourhoods. Conversely, the low urbanisation site is located in a partially urbanised hill, which can act as a safe haven for native species in the city. It is possible to assume that these green areas are supporting the survival of Drosophila native species in urban areas.

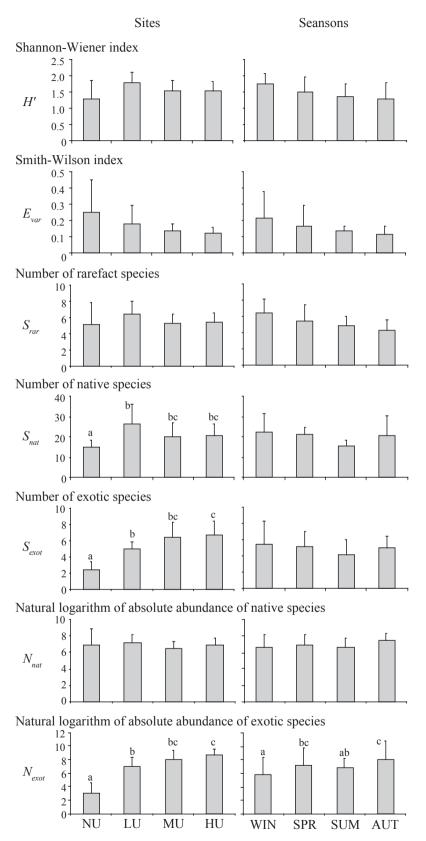


Fig. 5. Average of indices per site and per season, and significant differences. NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site, WIN – winter, SPR – spring, SUM – summer, AUT – autumn. Different letters represent significant differences in the ANOVA test at $\alpha = 0.05$, and the absence of letters means no significant differences.

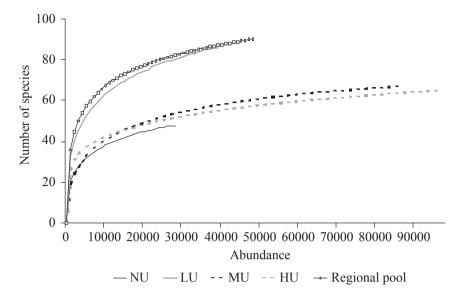


Fig. 6. Curves with rarefaction data of the collection sites and the data from regional pool (De Toni *et al.* 2007). NU - not urbanized site, LU - low urbanisation site, MU - medium urbanisation site, HU - high urbanisation site.

Table 3. Pearson correlations between the Shannon-Wiener diversity index (H') and the other ecological parameters observed.

	NU	LU	MU	HU
H' vs. E_{var}	r = +0.74	r = +0.71	r = +0.52	r = +0.06
	P = 0.01*	P = 0.02*	P = 0.13	P = 0.87
H' vs. S _{rar}	r = +0.51	r = +0.87	r = +0.85	r = +0.85
	P = 0.13	P = 0.001*	P = 0.002*	P = 0.002*
H' vs. S _{nat}	r = +0.27	r = +0.15	r = +0.73	r = +0.66
	P = 0.45	P = 0.68	P = 0.02*	P = 0.04*
H' vs. S _{exot}	r = -0.24	r = +0.49	r = +0.54	r = +0.80
	P = 0.50	P = 0.15	P = 0.11	P = 0.01*
H' vs. N _{nat}	r = -0.41	r = +0.13	r = +0.14	r = +0.19
	P = 0.24	P = 0.73	P = 0.70	P = 0.60
H' vs. N _{exot}	r = -0.75	r = -0.49	r = -0.38	r = -0.04
	P = 0.01*	P = 0.15	P = 0.28	P = 0.91

 $\overline{E_{var}}$ – Smith-Wilson index, S_{rar} – number of rarefact species, S_{nat} – number of native species, S_{exot} – number of exotic species, N_{nat} – natural logarithm of absolute abundance of native species, N_{exot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – natural logarithm of absolute abundance of exotic species, N_{uxot} – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site. * Significant values at α = 0.05.

This attribute of urban gardens was also observed for other insects, as butterflies (Blair & Launer 1997, Wood & Pullin 2002, Shapiro 2002) and mosquitoes (Barbosa *et al.* 2003, Navarro-Silva *et al.* 2004). Nevertheless, Levy & Connor (2004) point that the populations found in these gardens could not be maintained due to a lack of local resources, and that these areas probably act as sink environments for these populations. Could the populations of native species of Drosophilidae survive in urban environments? This question can only be answered with further investigation of the substrata used as breeding site by these species in urban areas. Another possibility to explain the highest richness of native species in urban areas, especially in low urbanisation sites, is the increased attractiveness of the baits in the city. It can happen by an increase in the stressing factors and a lack of natural resources in the city. Like this, the loss of richness becomes apparent when compared with the regional values. Crooks *et al.* (2004) observed that local bird diversity increases in moderately disturbed environments, but decreases in the overall regional diversity. These authors attribute this loss of richness to the biotic homogenisation of urban environments (McKinney & Lockwood 1999). It is very unlikely that the urban areas are as rich as, or even Table 4. Niche analysis of diversity for temporal and spatial components.

Niche component	Contribution to diversity			
-	H'	% total		
Spatial variability				
between sites	0.277	14.03		
Temporal variability				
between years	0.002	0.08		
between seasons	0.141	7.14		
Spatial x temporal variability (residual)				
between collections	0.576	29.19		
Not explained	0.978	49.57		
Total	1.972	100.00		

richer than native areas as the Atlantic Forest. The rarefaction analysis show that LU exhibits the same richness as detected by De Toni *et al.* (2007), who collected samples in eight points of the Atlantic Forest for two consecutive years. The data obtained by De Toni *et al.* (2007) could be used as a regional pool, in spite of the difference in the number of sampling sites. We also observed that our urban assemblages are not as rich as the regional pool.

Sevenster & van Alphen (1996) could explained the coexistence of local species of *Drosophila* in a forest of Panama with the aggregation model (see Sevenster 1996), which presupposes that, if the resources are discrete and ephemeral, they could support the coexistence of competitor species when these distribute gregariously. However, Krijger & Sevenster (2001) found that, in disturbed environments, the aggregation of species is lower than in wild environments. The species coexistence mechanism in cities has not yet been elucidated. Yet, evidence says that the competitive exclusion of native species by exotic species is not very probable, since we found all of them in sympatry and with abundances sustained along time.

The seasonal variation observed in the forest environment was already reported in studies of drosophilids (Martins 1987, De Toni et al. 2007). But the patterns of seasonal variation observed in the urbanized regions of the Neotropics have not so far been recorded. Tidon et al. (2003) verified that Z. indianus inhabiting the Brazilian cerrado is more common in summer and scarcer in winter. These authors mention that this pattern is similar to that found in its place of origin, in Africa, and that this species is well acclimatised in the open Brazilian environments. Franck & Valente (1985) and Martins (1987) did not associate seasonal fluctuation of melanogaster group species in disturbed environments to defined climatic factors. In our study, however, an apparently regular fluctuation was detected for these species, with D. malerkotliana, D. simulans and Z. indianus showing higher relative abundances in autumn, winter, and in spring, respectively.

In the Atlantic forest, diversity increased concomitantly to an increase in evenness and to a decrease in abundance of exotic species. The presence of the exotic species could influence the wild assemblages by decreasing evenness in hot periods. In the urban environments, H' was related with an increase in richness. The exotic species were most dominant in the city, what could be responsible for the decreased evenness of the assemblages and for the oscillation in diversity, as compared to richness. In the low urbanization site, diversity correlates both with evenness and richness. These differences in the manner these indices relate to one another probably reflect the individual characteristics of each environment studied and, again, LU shows a transitory character between forest and urban sites.

Even with these variations in the structure of local diversity, the difference between collection sites contributes but discretely to the total diversity observed, and therefore to the seasonal and annual variation. The residual value was the largest contribution to the total diversity. This variation carries but little informational worth, because it shows the contribution of the variation among each collection and could thus be considered as a casual effect. Irrespective of these observations, the contributions of all these factors do not surpass 50% of all the observed diversity. This lower value related to these factors was not expected, since we compared different environments that could explain a large portion of the total diversity observed, which nevertheless was not the case. Both Shorrocks (1974) and Brncic et al. (1985), when collecting in sites with temperate climate, found higher values for temporal factors with this analysis (35.69% and 46.23%, respectively). In temperate climates, the assemblages were simpler than in hotter places and seasonality could answer for most of the diversity observed.

In this way, it becomes difficult to anticipate which is the principal factor influencing the observed diversity. It is probable that a combination of many factors, not considered in this work, such as the richness and abundance of breeding sites, could contribute with the maintenance of diversity.

We observed a gradual modification in the dominant species in the assemblages related to the increased urbanisation. We also depicted a seasonal pattern of dominance in the assemblages collected in wild and urban environments. In the wild assemblages from Atlantic forest, *D. capricorni* and the *willistoni* subgroup were the dominant species, while in the city the dominance is exerted by *D. simulans*, *D. malerkotliana*, and *Z. indianus*.

Some parameters are proposed as indicators of the growth of urban impact in Brazilian Atlantic Rain Forest: 1) the high relative abundance and number of exotic species, as *D. simulans*, *D. malerkotliana* and *Z. indianus*; 2) the low relative abundance of the *willistoni* subgroup and, mainly, *D. capricorni*, which is proposed as an important sensitive species. However, the number of native species is not an advisable measure, since we observed a high richness in the disturbed environments. Probably, the richness in the urban sites could be supported by the occurrence of gardens in Florianópolis, but they could be acting as sink environments. In this sense, the richness observed in the highly urbanized sites is lower than the regional richness.

Finally, we observed that the assemblage structures in each environment were different. In the wild environment studied, diversity was related with evenness and, in the urban environment, with the number of species collected. The total diversity observed was neither explained by these differences, nor by the differences in the environments.

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