ECOLOGY, BEHAVIOR AND BIONOMICS

Population Dynamics of the Invasive Species *Zaprionus indianus* (Gupta) (Diptera: Drosophilidae) in Communities of Drosophilids of Porto Alegre City, Southern of Brazil

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Dinâmica de Populações da Espécie Invasora *Zaprionus indianus* (Gupta) (Diptera: Drosophilidae) em Comunidades de Drosofilídeos da Cidade de Porto Alegre, RS

RESUMO - Estudos em populações de espécies invasoras permitem entender como os invasores reagem às novas condições bióticas e abióticas, e como espécies nativas reagem à invasão. Avaliou-se a eficiência de colonização da invasora *Zaprionus indianus* (Gupta), na área urbana da cidade de Porto Alegre, RS. Amostras de moscas foram tomadas de três parques urbanos, e índices ecológicos foram usados baseados na freqüência das espécies amostradas. Os índices foram calculados para sítios de oviposição e alimentação separadamente. A maior freqüência de *Z. indianus* comparada aos outros drosofilídeos foi registrada nas estações de temperaturas médias maiores, tanto para o componente sítio de alimentação como o de oviposição. Nessas mesmas estações, e para ambos os componentes, foram encontrados os maiores valores do índice de dominância (D) e os menores valores de diversidade (H'). Uma análise dos valores do índice de similaridade de Morisita mostrou que o Jardim Botânico e o Parque Farroupilha apresentam maior similaridade em termos de diversidade para o componente sítio de oviposição. Para o componente sítio de alimentação a maior similaridade foi entre Parque Farroupilha e Parque Gabriel Knijnik. Apesar de os três parques apresentarem algumas particularidades, a facilidade de estabelecimento de *Z. indianus* nesses locais parece ter sido a mesma. A chegada da invasora parece estar promovendo ajustes nas estratégias de sobrevivência das espécies residentes, pelo menos em certos períodos quando a freqüência das populações da invasora aumenta significantemente. Entretanto, pelo menos a maioria das espécies parece ter condições de coexistir com a invasora.

PALAVRAS-CHAVE: Invasão biológica, índice ecológico, parque urbano

ABSTRACT - Population studies of invasive species allow us to understand how invaders react to new biotic and abiotic conditions, and how native species react to invasion. We evaluated the colonisation efficiency of the invader *Zaprionus indianus* (Gupta), in the urban area of Porto Alegre city, southern of Brazil. Samples of flies were taken from three urban parks, and ecological indexes were used based on the frequency of the sampled species. The indexes were calculated for breeding and feeding sites separately. The highest frequencies of *Z. indianus* compared to the other drosophilids were registered during seasons of highest mean temperatures, both for the feeding and the breeding sites. The highest values for the dominance index (D) and the lowest values for diversity (*H*') were found at the same seasons and for both components. An analysis of the values for Morisita similarity index shows that the Botanical Garden and Farroupilha Park had higher similarity in terms of diversity of the breeding sites. For the feeding sites the highest similarity was between Farroupilha Park and Gabriel Knijnik Park. Despite the three parks have some particularities, the ease with which *Z. indianus* became established at these places seem to be the same. The arrival of this invader seems to be promoting adjustments in the survival strategies of the resident species, at least at certain periods when the frequency of the populations of the invader increases significantly. However, most of species seem to be able to coexist with the invader.

KEY WORDS: Biological invasion, ecological index, urban park

Recognition of the impact of biological invasions on the Earth's ecosystems has received ample attention from researchers to try to understand the factors that affect them (Vitousek *et al.* 1997). Recent reviews have considered invasions from a variety of viewpoints, including biological characteristics of invaders (Kolar & Lodge 2001), ecological characteristics of invaded communities (Lonsdale 1999, Tsutsui *et al*. 2000), interference of the invader in resources availability (Sher & Hyatt 1999, Davis *et al.* 2000) and presence of natural enemies and occupancy of space (Keane & Crawley 2002). Moreover, some studies "suggest that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity" (Lee 2002). Accordingly, these findings emphasize the utility of genomic approaches for determining invasion mechanisms, through analysis of gene expression, gene interactions, and genomic rearrangements that are associated with invasion events. As these issues are not independent, it is essential to find ways of considering them jointly (Shea & Chesson 2002). For D'Antonio & Kark (2002), the key challenge in invasion biology is to understand the interaction of species traits and ecosystem properties in determining which species will become invasive and where.

Species of drosophilids (and other animals) that are generalists in respect to trophic resource use and tolerance to variable climatic conditions are good candidates to be invasive on new territories, frequently far from their centres of origin (Brncic *et al*. 1985). The majority of the drosophilids feeds fundamentally on bacteria and yeasts participating in the fermentation of carbohydrate-rich substrates, specially decomposing fruits. Volatile substances originating in the fermentation of these substrates work as the main attractive for the flies (Carson 1971, Vilela *et al*. 2001). Some species are more restricted ecologically, using only one species as feeding and reproduction sites; others are more versatile, being able to exploit different kinds of resources (Throckmorton 1975). Moreover, there are many drosophilid species occurring along with or very close to human habitations, as gardens, orchards and waste deposits, ending up being spread with the creation of such habitats (Parsons 1987).

Zaprionus indianus (Gupta) is an afrotropical drosophilid that recently invaded South America (Vilela 1999) and quickly expanded its area of distribution, attaining the *status* of plague on fig crops in the Brazilian State of São Paulo. Since then, this fly invaded other Brazilian States (Castro & Valente 2001, De Toni *et al*. 2001, Tidon *et al*. 2003) and the Uruguayan territory (Goñi *et al*. 2001), in which it has been found, in the same period, as one of the most abundant members of local communities of Drosophilidae.

This work evaluates some possible colonisation strategies of this alien species and its impact in the local diversity of drosophilids. The urban area of the city of Porto Alegre, southern of Brazil, have been studied in terms of its drosophilid communities by researchers from our laboratory for the last twenty years, with regular field collections and research on the ecology, genetics and behaviour of the flies (Valente *et al*. 1989, Valiati & Valente 1996, 1997).

Material and Methods

Samples of flies were collected from three places in Porto Alegre city (30º02'S-51º14'W) with different urbanisation levels (Farroupilha Park (FP), high urbanisation level; Botanical Garden (BG), intermediate level; and Gabriel Knijnik Park (GKP), low urbanisation level) according to a classification by Ruszczyk (1986/1987). Sampling was done during seven seasons from February 2001 to September 2002, one sample per season for each place, in the period between 9 a.m. and 12 a.m.

Two sampling methods were employed: 1. adult flies were netted as they were flying over a variety of rotten fruits (both native and exotic), and during periods when fruits were not available, conventional banana baits were used; 2. pre-adult stages were collected from field collected fermenting fruits and kept in bottles containing vermiculite in the laboratory in chambers with controlled temperature and humidity (25 ± 1ºC, 60% R.H.). Adult specimens were identified (and counted) using keys of Freire-Maia & Pavan (1949) and Chassagnard & Tsacas (1993). The sibling cryptic species *Drosophila melanogaster* (J.W. Meigen) and *D. simulans* (A.H. Sturtevant), *D. willistoni* (A.H. Sturtevant) and *D. paulistorum* (T. Dobzhansky & C. Pavan) were joined together as subgroups (*melanogaster* and *willistoni*, respectively).

For the description of the communities, we used the following parameters: 1. relative abundance: the number of individuals of the species *i* divided by the total number of individuals in the sample; 2. species diversity index (*H'*), according to Shannon & Weaver (1949), modified by Hutcheson (1970): $H' = -(\Sigma p_i \ln p_i) - (S - 1)/2N$, were p_i = frequency of species *i*; *S* = number of species and N = sample size; 3. species richness (S): the number of different species found in the sample; 4. evenness index (J'), according to Pielou (1974): $J' = H'/H_{max}$, were *H'* = diversity index observed and H_{max} = maximum diversity of the sample, found when all species are equally abundant (= ln *S*), were *S* is the total number of species; 5. dominance index (*D*), according to Simpson (1949): $D = n_i (n_i - 1)/ N (N - 1)$; were, n_i is number of individuals of the species *i* and N is the total number of the samples; 6. Morisita-Horn (quantitative) similarity index, according to Morisita (1959), modified by Horn (1966): $C_{MH} = 2\Sigma(an_i \times bn_i)/(da+db)aN \times bN$, where aN is the number of individuals at place A; bN is the number of individuals at place B; an_i is the number of individuals of species *i* at place A; bn_i is the number of individuals of species *i* no place B; $da = \Sigma an_i^2/aN^2$; and $db = \Sigma bn_i^2/bN^2$.

The above indexes were calculated using the frequency of individuals flying over the fruits (feeding sites), and of imagoes emerging from fruits took to the laboratory (breeding sites), separately.

Temperature data were obtained from the Instituto Nacional de Metereologia of the Oitavo Distrito de Metereologia (INMET), in Porto Alegre, RS, Ministério da Agricultura, Pecuária e Abastecimento (MAPA).

Results and Discussion

We collected 48,609 drosophilids along the whole sample period in the three parks, with *Z. indianus* (19,146 individuals), subgroup willistoni (11,381 individuals) and subgroup melanogaster (9,495 individuals) the more abundant entities (Table 1). Together they represent 82.3% of the sample. Despite considering *D. melanogaster* and *D. simulans* as subgroup melanogaster and *D. willistoni* and *D. paulistorum* as subgroup willistoni, our previous experience (Valente *et al*. 1989; Santos & Valente 1990; Valiati & Valente 1996,1997) suggests that these subgroups correspond mostly to individual contributions from *D. simulans* and *D. willistoni*, respectively, the dominant species before the *Z. indianus* invasion.

The relative frequencies of *Z. indianus* compared to the other drosophilids collected across the seven seasons at the three sample places, both for adult feeding sites and breeding sites are showed in the Figs. 1 to 3. For some of the seasons and in some places, no drosophilids were found flying over fruits, or there were no fermenting fruits to be brought back to the laboratory. Independently of place, drosophilid community composition, or even substrate type (fruits) used as feeding and breeding sites, the highest frequencies of *Z. indianus* were obtained during seasons with higher mean temperatures (summer and spring) (Figs.1 to 4). Even though *Z. indianus* frequencies suffer a sharp drop during autumn and winter, they increase again in spring, especially for breeding sites, that demonstrates the invasive ability of this species (Figs. 1 and 2).

Da Cunha & Magalhães (1965) argued that the observed oscillations in species frequencies across the seasons would be reflecting differences in tolerance of the various species at a same local to the variable climatic conditions. Seasonal oscillations in the frequency of *Drosophila subobscura* (J.E. Colling), a colonizing species in Chile, were registered by Brncic *et al.* (1985). During three sampled years, this species had its highest frequencies between August and December. The authors suggest that changes in temperature and humidity affect vital parameters as: viability, crosses, fertility, development time from egg to adult, life span and other factors that influence survival of populations of species of genus *Drosophila*. The same could be happening with local populations of *Z. indianus* in Porto Alegre city.

The dominance affects species diversity significantly, both for the feeding sites component ($r = -0.9701$; $P < 0.0001$), and breeding sites ($r = -0.9294$; $P < 0.0001$). For example, the highest value of dominance (0.848), at Farroupilha Park, during summer of 2001, for the feeding sites component, was accompanied by the lowest value of H' (0.59) (Table 2). Similar results were seen for the breeding sites component, so that at Gabriel Knijnik Park, during the summer of 2001, the highest value of D (0.753) accompanied the lowest H'(0.77).

In general, the highest values of D were found during seasons with higher mean temperatures (summer and spring) (Table 2), when *Z. indianus* (at the three sample places, both flying over and emerging from fruits), had its highest frequencies, usually above 50%. At Farroupilha Park, for example, during the summer of 2001, the frequency of *Z. indianus* reached 92.0%, for feeding sites (Fig. 3a). However in autumn and winter, when mean temperatures fall, there is also a decrease in the frequency of *Z. indianus* and, consequently, an increase in the number and frequency of other species. Such fact is ratified by the negative correlation between dominance and richness, in terms of adult feeding sites ($r = -0.5518$; $P < 0.05$) as in breeding sites ($r = -0.6402$; $P < 0.01$).

The clear seasonal pattern in community structure is observed in an association between the higher values of evenness index and effective number of species ($r = 0.769$; $P < 0.01$), in seasons with lower mean temperatures (autumn and winter) whereas both indices are lower in summer and spring, periods of higher mean temperatures and highest frequencies of *Z. indianus*.

Saavedra *et al*. (1995), studying communities in Rio Grande do Sul State, southern of Brazil, showed that the lowest estimates for evenness index and effective number of species, were influenced by the strong dominance of *D. willistoni*, apparently similar to the effect of *Z. indianus* in the structure of communities of Drosophilidae in Porto Alegre.

We analysed the influence of some variables that may contribute to diversity and were able to explain only 19.9% of the diversity levels found (80.11% were not explained, see Table 3). This value is quite less than those obtained by Shorrocks (1975) and Brncic et al. (1985), for communities of *Drosophila* in England (82.4%) and Chile (63.3%), respectively. However, for both authors as well as for our work, the component contributing more to the explanation of diversity was the seasonal one (14.1%, see Table 3). Even thus, using similar components to the other authors, we could not explain much of the diversity in our drosophilid communities. That could stem from the methodology contemplating only one sample per season, differently from the monthly samples of the cited papers, so that for us a single sample represents a period of three months. Furthermore we would consider that the rest of the variation may be attributed to other variables not studied here, as microclimatic variations and fruit kinds available across the seasons.

The dendrograms presented in these work were generated from Morisita (1959) similarity indexes (Fig. 5). The latter represent the similarity between the places sampled during the seven seasons, both for breeding and feeding sites. The similarity index was calculated based on the number and frequency of sampled species at the three places. Botanical Garden and Farroupilha Park had a higher similarity among their diversities when the breeding sites component was considered (Fig.5a), while for feeding sites, similarity was higher between Farroupilha Park and Gabriel Knijnik Park (Fig.5b). All sites studied here are urban parks, though Gabriel Knijnik Park is located in what is considered a low urbanisation area. Even though the parks have different size, species number (S) and varied resources availability across the seasons, three parks had similarity above 83% (Fig. 5). Also, the places showed the mean of diversities (*H'*) closed, oscillating between 1.59 and 1.76 to breeding sites, and 1.95 and 2.18 to feeding sites (Table 2), as well as the absent of significant differences among

Table 1. Annual frequency of individuals sampled during 2001 and 2002 in Porto Alegre city.

Species	Author and year	Botanical Garden		Farroupilha Park		Gabriel Knijnik Park		Total
		2001	2002	2001	2002	2001	2002	
Z.indianus	Gupta, 1970	2604	4572	2681	4013	2640	2636	19146
sg. *melanogaster*		876	2704	1181	2887	738	1109	9495
sg. *willistoni*		1494	3143	1305	1697	1642	2100	11381
D. polymorpha	Dobzhansky & Pavan, 1943	30	144	90	39	118	359	780
D. mercatorum	Patterson & Wheeler, 1942	435	2479	275	159	209	177	3734
D. cardinoides	Dobzhansky & Pavan, 1943	21	10	120	24	144	7	326
D. nebulosa	Sturtevant, 1916	21	6	19	4	3	36	89
D. griseolineata	Duda, 1927	52	116	502	129	21	30	850
D. kikkawaii	Burla, 1954	26	97	238	323	7	9	700
D. mediopunctata	Dobzhansky & Pavan, 1943	18	61	10	29	63	30	211
D. mediostriata	Duda, 1925	12	368	6	79	17	72	554
D. mediopicta	Frota-Pessoa, 1954	2	4	4	0	11	19	40
D. mediosignata	Dobzhansky and Pavan, 1943	0	4	1	3	24	0	32
D. immigrans	Sturtevant, 1921	134	151	200	3	300	163	951
D. bandeirantorum	Dobzhansky & Pavan, 1943	5	0	3	0	0	2	10
D. maculifrons	Duda, 1927	6	15	53	29	31	6	140
D. busckii	Coquillett, 1901	6	0	0	0	5	0	11
D. zottii	Vilela, 1983	12	0	0	0	19	5	36
D. fumipennis	Duda, 1925	0	2	0	0	1	0	3
D. pulchella	Sturtevant, 1916	0	20	0	0	0	0	720
D. pallidipennis	Dobzhansky & Pavan, 1943	2	2	1	3	22	7	37
D. neocardini	Streisinger, 1946	0	2	0	0	0	29	31
D. angustibucca	Duda, 1925	0	3	0	3	0	15	21
Zygotricha sp.	Wiedemann, 1830	0	3	0	0	0	0	3
D. hydei	Sturtevant, 1921	0	0	0	0	2	0	2
D. prosaltans	Duda, 1927	0	0	0	0	2	0	2
D. bocainensis	Pavan & Cunha, 1947	0	0	0	0	0	4	4
Total		5756	13906	6689	9424	6019	6815	48609

sg = subgroup

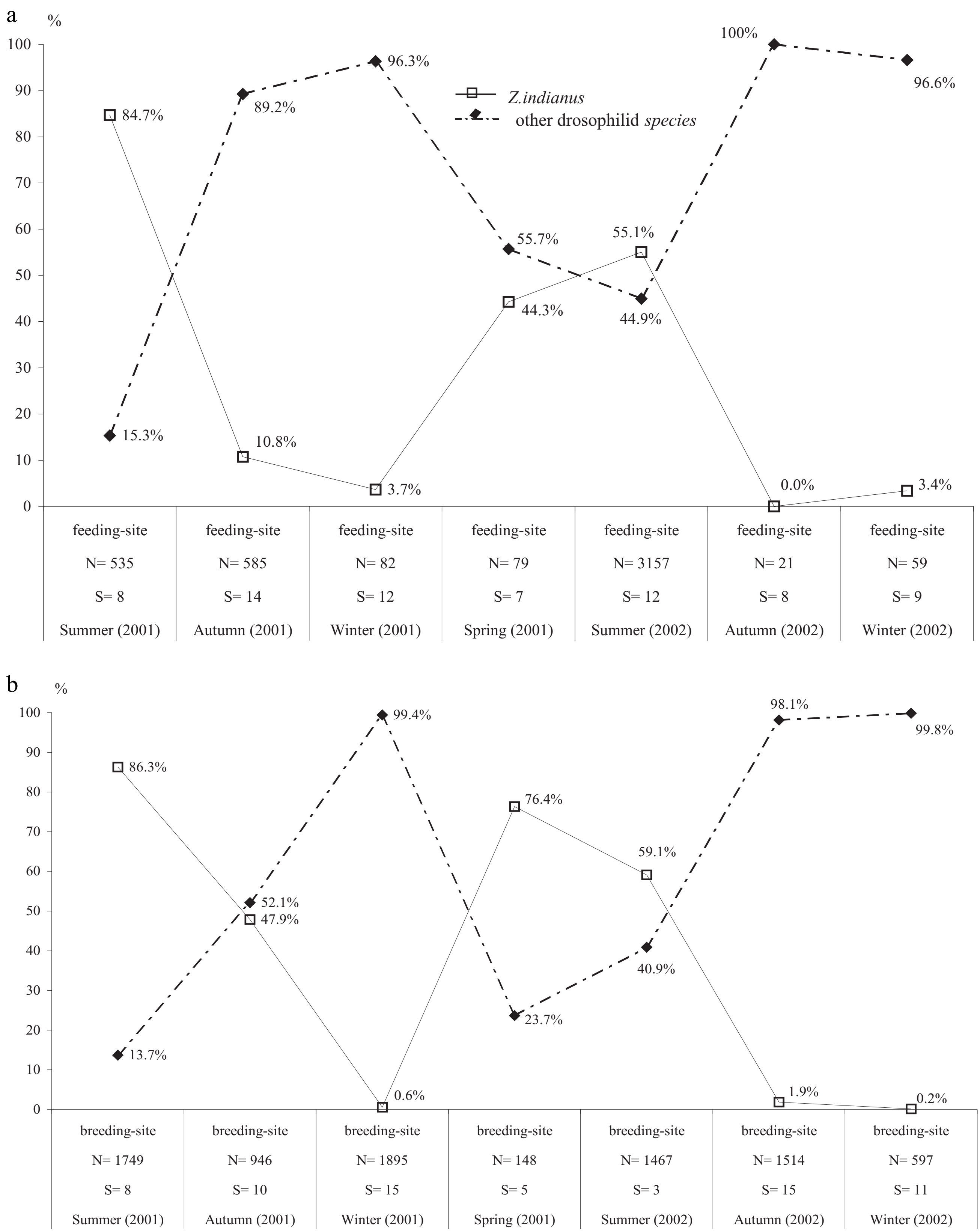

Figure 1. Frequency of *Z. indianus* and other drosophilid species in Gabriel Knijnik Park in Porto Alegre city collected during 2001 and 2002. The values presented in the graph correspond to the individuals attracted (a) and emerged (b), independently of trophic resource used by species. N = sample size; S = number of species.

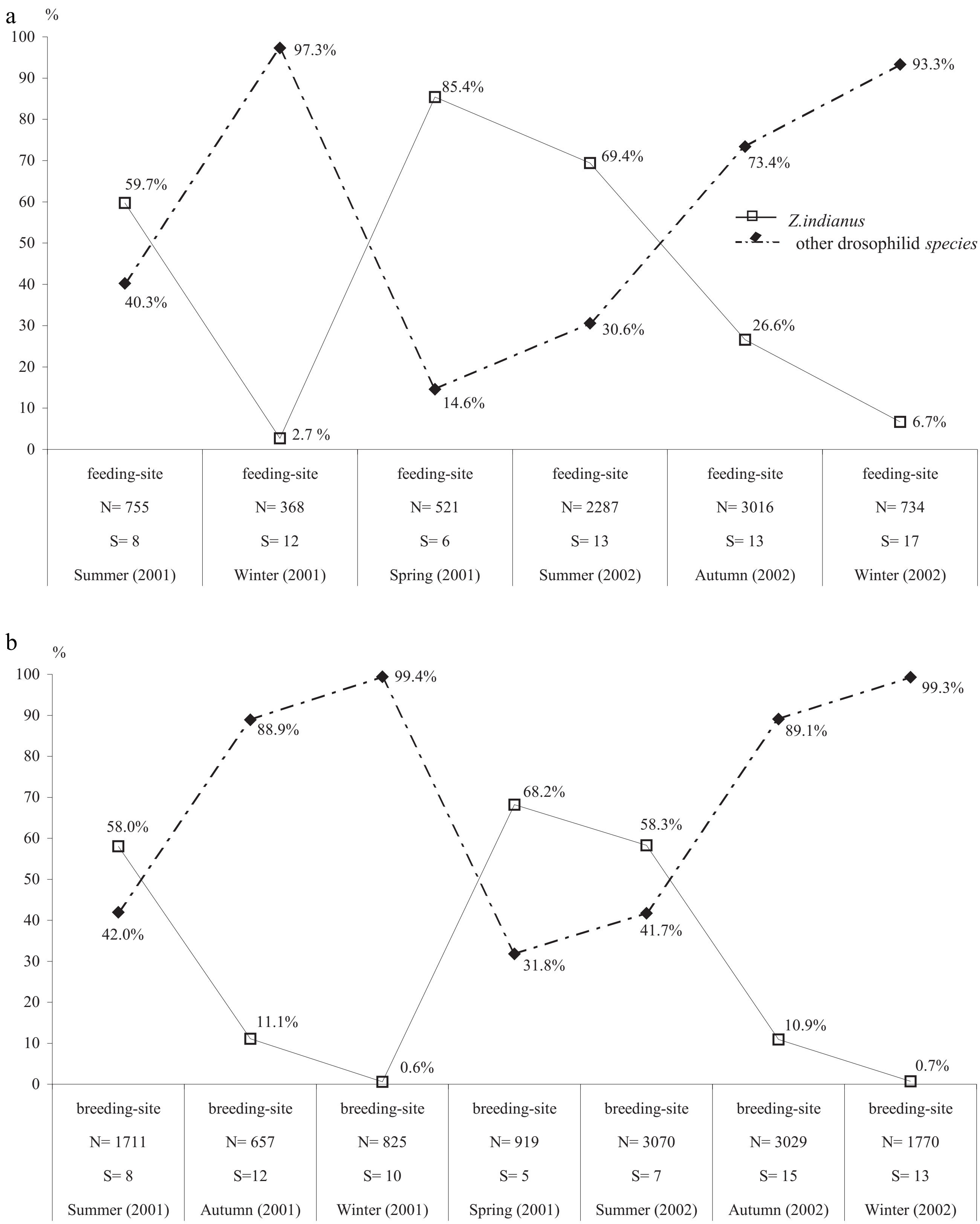

Figure 2. Frequency of *Z. indianus* and other drosophilid species in Botanical Garden in Porto Alegre city collected during 2001 and 2002. The values presented in the graph corresponded the individuals attracted (a) and emerged (b), independently trophic resource used by species. N = sample size; S = number of species.

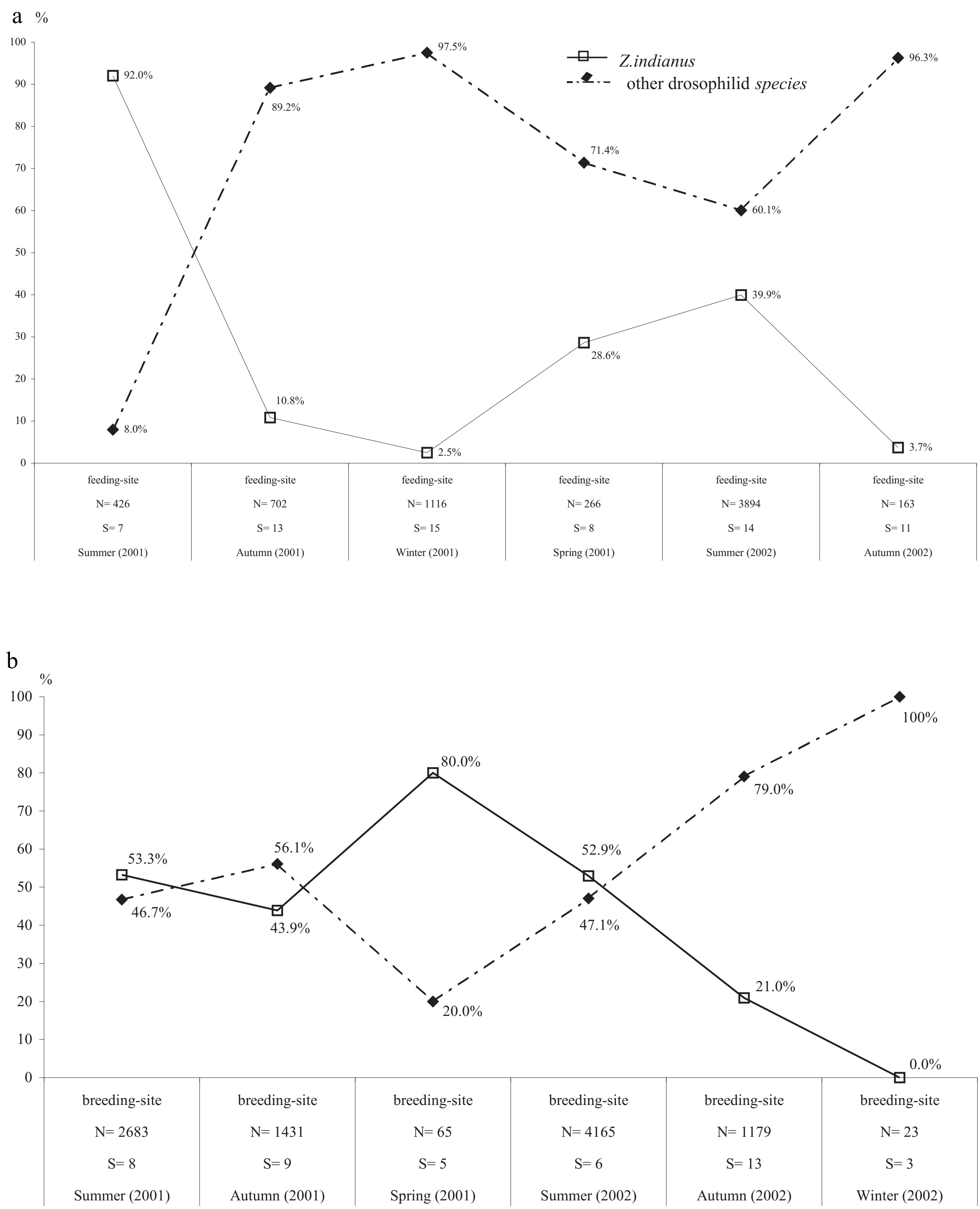

Figure 3. Frequency of *Z. indianus* and other drosophilid species in Farroupilha Park in Porto Alegre city collected during 2001 and 2002. The values presented in the graph corresponded the individuals attracted (a) and emerged (b), independently trophic resource used by species. N = sample size; S = number of species.

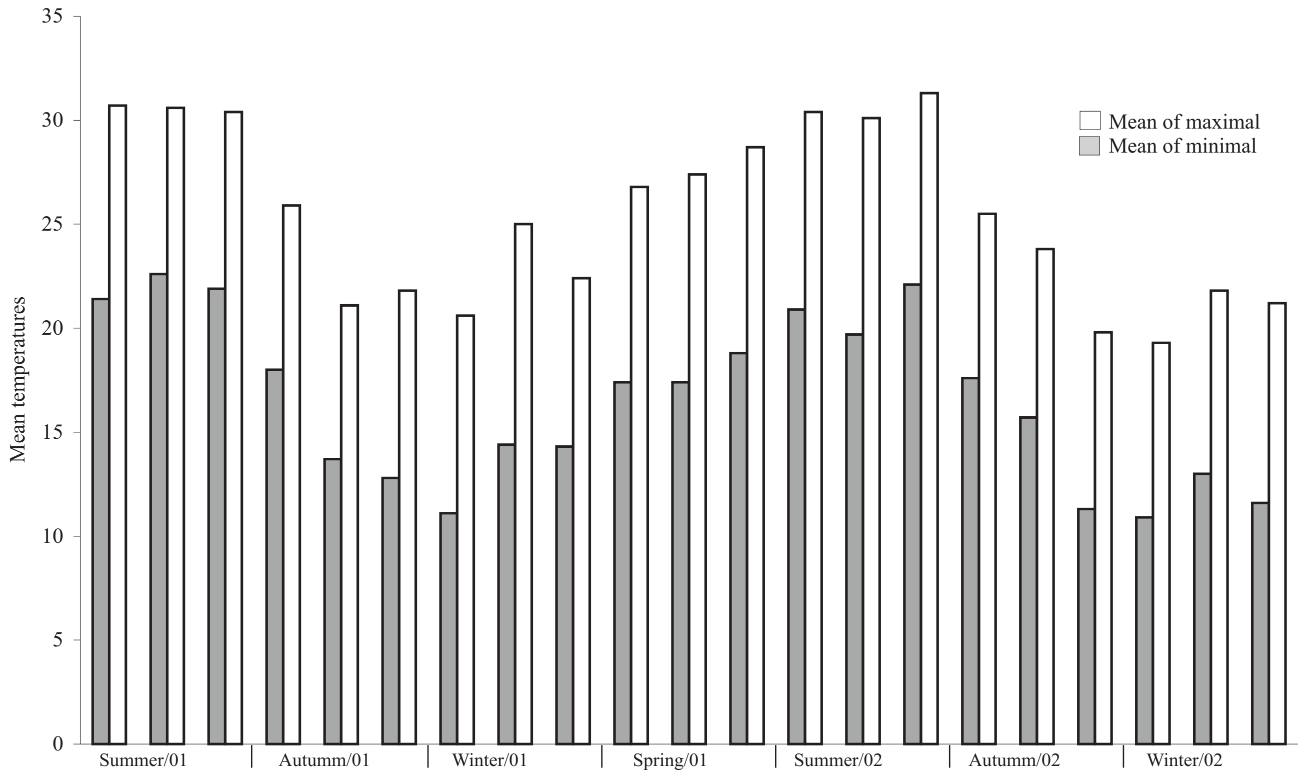

Figure 4. Graphic of mean monthly temperatures in Porto Alegre city, during seven seasons in 2001(01) and 2002(02).

the species richness (χ^2 = 9.672; P = 0.974).

There are many variables that could cause environments to differ, relative to the dynamics of drosophilid communities. Among these variables affecting species relationships in such communities we could have: (I) number and kind of resources available across seasons, correlated to the availability (or not) of different kinds of yeast and bacteria (participating in the process of fermentation of fruit substrates), to be used by different species; (II) differences in species composition across seasons, which is particularly true for regions with well defined seasons as in southern of Brazil; (III) environmental differences typical of each place, as the presence of forest patches; (IV) microclimatic conditions; (V) presence of predators; (VI) human action. Besides, the study of tropical communities is usually complex, since tropical environments have considerable ecological richness, with many species living in sympatry in very diverse habitats (Valente & Araújo 1991).

In spite of any differences among the three parks sampled (different dimensions, varied resources availability along the seasons and urbanisation level), the ease with which *Z. indianus* became established in each of those seem to be the same. This establishment seem to be responsible for promoting adjustments in the survival strategies of the resident species, at least for certain periods when the frequency of the populations of the invader increases significantly but, it is probable that many of the resident species are able to coexist ecologically with the invader.

Considering its possible colonisation strategies, our data suggest that, together with the ability to live in environments associated to humans, its capacity to recover high population levels, under favourable conditions, contribute to its competence for expansion and colonisation of new areas. However, we do not know how the species survives cold periods, whether there is diapause or the populations recuperate by reintroduction. Another hypothesis for further studies is the formation of heat islands in the Porto Alegre city, as a phenomenon associated to urbanisation (Danni 1980). These thermic islands could then be used as refuges for urban populations of insects during unfavorable periods.

Besides, the availability and diversity of substrates on the urban area opens up niches to explore and *Z. indianus* showed the ability to explore different substrates for feeding and breeding in the three parks. An important aspect to test is whether *Z. indianus* is good competitor in exploring the feeding substrates as a larva as it seems to be when in adult form.

The monitoring of Drosophilidae communities at these places, for longer time spans, will allow us to confirm or not these conclusions and will contribute to clarify the dynamics of the interactions between the populations of the invasive species with resident ones.

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Table 2. Estimates of species-diversity index (H’), species-effective number (ExpH’), evenness index (j’), species number (S) and dominance index (D) from communities of *Drosophila* and *Z.indianus* attracted to and emerged by different trophic resources in the Porto Alegre city.

Local	Season/Year		Feeding-site component						Breeding-site component				
			H’	ExpH’	J’	S	D		H’	ExpH’	J’	S	D
Botanical Garden	Summer/01		1.47	2.77	0.490	8	0.460		1.50	2.84	0.501	8	0.427
	Autumn/01		-	-	-	-	-		2.28	4.85	0.636	12	0.282
	Winter/01		2.48	5.59	0.693	12	0.242		2.16	4.46	0.650	10	0.277
	Spring/01		0.82	1.76	0.316	6	0.739		1.18	2.27	0.508	5	0.534
	Summer/02		1.43	2.70	0.387	13	0.518		1.21	2.31	0.429	7	0.485
	Autumn/02		2.44	5.43	0.660	13	0.220		2.14	4.40	0.547	15	0.278
	Winter/02		3.04	8.20	0.743	17	0.157		1.83	3.56	0.495	13	0.377
		Mean	1.95	4.41	0.548	11.5	0.389	Mean	1.76	3.53	0.538	10.0	0.380
		± SD	0.84	2.43	0.176	3.9	0.223	± SD	0.51	1.18	0.085	3.6	0.116
Farroupilha Park	Summer/01		0.59	1.50	0.209	7	0.848		1.74	3.35	0.581	8	0.370
	Autumn/01		2.97	7.85	0.803	13	0.144		1.96	3.90	0.619	9	0.321
	Winter/01		2.83	7.14	0.726	15	0.178		-	-	-	-	-
	Spring/01		1.86	3.63	0.620	8	0.358		1.11	2.15	0.476	5	0.646
	Summer/02		2.07	4.20	0.543	14	0.293		1.38	2.60	0.533	6	0.439
	Autumn/02		2.77	6.81	0.800	11	0.183		2.17	4.50	0.587	13	0.323
	Winter/02		-	-	-	-	-		1.15	2.22	0.725	3	0.518
		Mean	2.18	5.19	0.617	11.3	0.334	Mean	1.59	3.19	0.587	7.3	0.436
		± SD	0.90	2.47	0.224	3.3	0.264	± SD	0.43	0.95	0.056	3.1	0.135
Gabriel Knijnik Park	Summer/01		0.82	1.77	0.274	8	0.728		0.77	1.70	0.256	8	0.753
	Autumn/01		2.57	5.93	0.674	14	0.292		1.48	2.79	0.445	10	0.428
	Winter/01		2.83	7.11	0.789	12	0.199		2.47	5.53	0.632	15	0.248
	Spring/01		2.19	4.55	0.779	7	0.272		1.13	2.19	0.486	5	0.604
	Summer/02		1.59	3.01	0.443	12	0.395		1.33	2.52	0.842	3	0.446
	Autumn/02		2.70	6.50	0.900	8	0.138		1.99	3.97	0.509	15	0.434
	Winter/02		2.59	6.01	0.817	9	0.185		2.06	4.17	0.595	11	0.293
		Mean	2.18	4.98	0.668	10.0	0.316	Mean	1.60	3.27	0.538	9.6	0.458
		± SD	0.78	2.10	0.238	2.9	0.210	± SD	0.61	1.41	0.196	5.0	0.173

Table 3. Niche analysis for the Porto Alegre data.

Niche component	Contribution to diversity	
	H'	% total
Year to year	0.03	1.29
Seasonal	0.34	14.14
Total temporal variability	0.37	15.43
Spatial (Places)	0.08	3.42
Breeding and feeding site	0.02	1.04
H (not explained)	1.93	80.11
H total	2.41	100

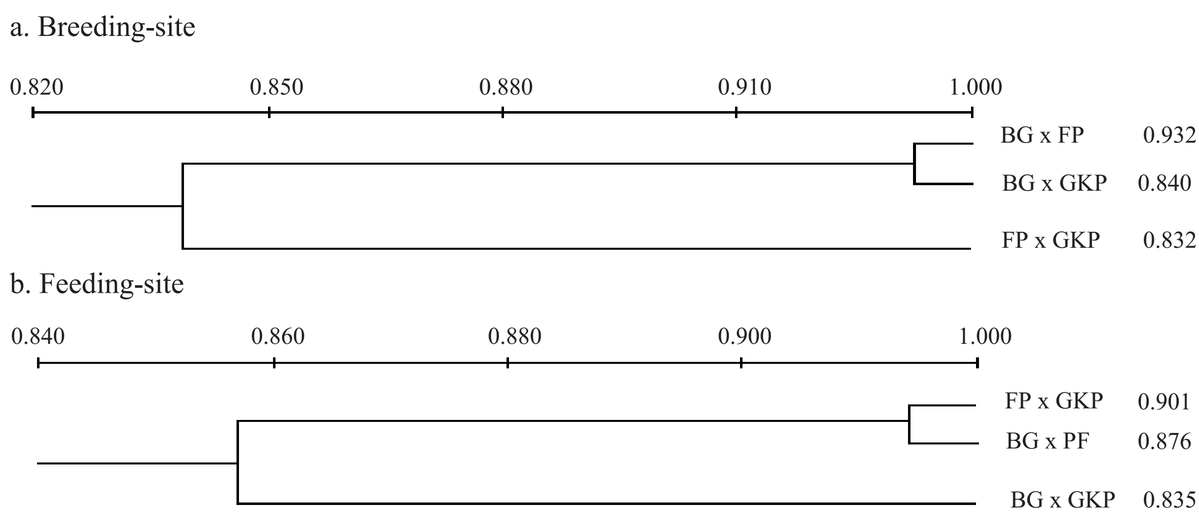

Figure 5. Dendrograms constructed using the UPGMA method (Sneath & Sokal 1973), based on similarity coefficients (Morisita 1959) from communities of drosophilids attracted to and emerged by different trophic resources in Porto Alegre city. BG (Botanical Garden); FP (Farroupilha Park); GKP (Gabriel Knijnik Park)

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