ECOLOGY, BEHAVIOR AND BIONOMICS

Study of the Drosophilidae (Diptera) Communities on Atlantic Forest Islands of Santa Catarina State, Brazil

Daniela C. de Toni[1], Marco S. Gottschalk[2], Juliana Cordeiro[3], Paulo P.R. Hofmann[1] and Vera L.S. Valente[2,3,4]

[1]*Depto. Biologia Celular, Embriologia e Genética, sala 304, Univ.Federal de Santa Catarina - UFSC 88010970, Florianópolis, SC, detoni@ccb.ufsc.br*
[2]*Programa de Pós-Graduação em Biologia Animal;* [3]*Programa de Pós Graduação em Genética e Biologia Molecular*
[4]*Depto. Genética. Univ. Federal do Rio Grande do Sul -UFRGS, Av. Bento Gonçalves, 9500 Campus do Vale, 91501970, Porto Alegre, RS*

Neotropical Entomology 36(3):356-375 (2007)

Estudo das Assembléias de Drosofilídeos (Diptera) de Ilhas com Mata Atlântica de Santa Catarina

RESUMO - Foi realizado um estudo de dinâmica de assembléias de drosofilídeos em seis comunidades insulares e duas continentais em visitas estacionais ao longo de dois anos, em Santa Catarina. Os índices de diversidade foram elevados se comparados com os de assembléias de clima temperado. Com relação ao índice de heterogeneidade de espécies de Shannon-Wiener (*H'*), os pontos localizados no continente (Serra do Tabuleiro) foram os mais elevados. Esses sítios apresentam Mata Atlântica primária e, teoricamente, deteriam a maior variabilidade de nichos ecológicos. Um dendograma mostrando a similaridade entre as assembléias (medida pelo índice de Morisita), apontou para 60% de similaridade. Nele os pontos continentais e insulares foram os que mais se diferenciaram. Os seis pontos insulares se separam em dois grupos: um que inclui os pontos da Ilha de Santa Catarina, e outro compreendendo as demais ilhas adjacentes a essa ilha maior. Os agrupamentos mostram a importância do componente espacial na previsão da estrutura das comunidades. Esse fato levanta a discussão a respeito da grande complexidade do ecossistema de Mata Atlântica e, conseqüentemente, sua imprevisibilidade, em termos de composição faunística, evidenciando a necessidade de sua conservação.

PALAVRAS-CHAVE: *Drosophila*, diversidade, Brasil, ecologia

ABSTRACT - A study of the community dynamics of Drosophilidae was carried out in six insular communities and two others on the mainland. Seasonal collections were carried out throughout two years in Santa Catarina State, southern of Brazil. The diversity index calculations show high values when compared with temperate climate communities. The sites on the mainland (Serra do Tabuleiro) presented the highest diversity, which was measured by the Diversity Index (*H'*). These sites are covered by primary Atlantic Forest and theoretically should have a higher variation of ecological niches. A dendogram showing the similarity between the communities, calculated by Morisita Index, points to a level of similarity equal to 60% for all communities. In this diagram, we can see two clades: one on the mainland and the other on the islands. The six island sites are grouped into one clade and separated into two subclades, one including the sites on Santa Catarina Island and the other consisting of the islands adjacent to this last and very much larger one. These groupings show the very important role of the spatial component on the prediction of the structure of the communities. This fact raises the discussion about the high complexity of the Atlantic Forest ecosystem and consequently the unpredictability of its fauna, highlighting the need of its conservation.

KEY WORDS: *Drosophila*, biodiversity, ecology

The biological diversity of the Atlantic Forest is, doubtless, one of the highest of the planet, being one of the 25 worldwide ecological hotspots of conservation (Myers *et al.* 2000). Even though its area has been drastically reduced in relation to the original size (less than 5% of the earlier 1,000,000 km^2), it is still capable of supporting an incredible variety of life forms. According to the 1992 Action Plan of the Biosphere Reserve of the Atlantic Forest, it is characterized by being a full forest with other associated ecosystems such as coastal fens and mangroves, rivers estuaries and lagoons (environments that can, in some extension, receive influence from the tides), forests of strand vegetation, pines forests and altitude fields.

The flies of the *Drosophila* genus became the preferred insects for the study of genetics from the time of the classic works of Thomas Morgan in 1910, when crucial aspects of the chromosome theory and the inheritance were elucidated. The importance of this organism grew throughout the rest of 20th century, and nowadays the organism still has an important role in genomic study (Schmitz *et al.* submitted).

However, Remsen & O'Grady (2002) remark that, although this insect is frequently utilized in biological research, the knowledge about Drosophilidae is still sparse. It contains 3,800 species distributed in 65 genera (Bächli 2006), but even with this significant number, and its importance to the geneticists, models of *Drosophila* have been only rarely used to illustrate the mechanisms underlying the dynamics of the tropical assemblies.

In Santa Catarina State, some remnants of the Atlantic Forest are still found, many located on coastal islands, but mostly of small extension. In these places, we carried out monthly collections in previous years, and we were able to visualize a general panorama of the wealth of the Drosophilidae assemblies of the region (Döge *et al*. 2004, Gottschalk *et al*. 2006).

Few studies approaching the population dynamics, estimating parameters of diversity and similarity, have been carried out on the assemblies of *Drosophila* of the insular Atlantic Forest in Santa Catarina. Furthermore, little has been done in terms of evolutionary studies with these insects. Nothing has been elucidated yet in relation to their degree of ecological diversity or patterns and possible relations of coexistence among the species. The present work represents an initial attempt to fill this gap.

Methodology

Samples were taken as adults, flying over fermented banana bait and natural trophic resources (fermented fruits), at eight different sites (Fig. 1). Two of these sites were located on Santa Catarina Island: Morro da Lagoa da Conceição (27º35'27'S; 48º28'33'W – site A), a collecting point with *sensu strictu* secondary Atlantic Forest, in advanced process of regeneration and without recent human influence; and the Municipal Park of Lagoa do Peri (27º45'23'S; 48º32'58'W

Fig. 1. Map of South America, showing Brazil and Santa Catarina State with the collection sites of Drosophilidae: A) Canto da Lagoa, Ilha de Santa Catarina ; B) Ilha Ratones Grande; C) Ilha Ratones Pequeno; D) Sertão do Peri, Ilha de Santa Catarina; E) Serra do Tabuleiro I; F) Parque Serra do Tabuleiro II, (E and F are on the mainland), G) Ilha Arvoredo; H) Ilha Campeche.

- site D), classified as *sensu latu* Atlantic Forest, being one of the few regions with remnants of Primary Forest on Santa Catarina Island, suffering only from small spots of deforested area and some abandoned agricultural zones.

Four sites are located on small islands near the mainland: Ratones Grande Island (27º28’58’S; 48º33’71’W - site B), located to the north of Santa Catarina Bay, approximately 0.8 km from the west coast of Santa Catarina Island; Ratones Pequeno Island (27º29’69’S; 48º33’97’W - site C), positioned a few hundred meters from Ratones Grande Island; Campeche Island (27º41’81’S; 48º28’88’W - Site H), to the east of the Island of Santa Catarina, approximately 1.5 km from the coast, being the most extreme easterly located collection site of this research; and Arvoredo Island (27º17’57’S; 48º21’23’W - Site G), situated 8 km from the north of Santa Catarina Island, being the northernmost sampling site studied in this research.

Two other collecting sites were located on the mainland in the Serra do Tabuleiro State Park (27º44’48’S; 48º48’44’W - Site E; 27º44’55’S; 48º48’72’W - Site F). This park is the biggest conservation unit of Santa Catarina, with an area of 87,405 ha, showing varied vegetation and congregating five of the six botanical compositions of the State of Santa Catarina.

Three to six days were spent at each site for collecting. These collection phases were seasonal and lasted two years beginning in March 1999. Concomitant with the accomplishment of the sampling stage, the identification of the flies by external morphology observation was effected (Freire-Maia & Pavan 1949). In cases of sibling species, dissection of the male terminalia was also done. A representative number of individuals were conserved and kept in the Drosofilid Laboratory of the UFSC collection.

The description of the assemblies in terms of absolute (*ni*) and relative (*pi*) abundance of the species (Brower & Zar 1984) was made for each sample and site. The heterogeneity estimators of Shannon-Wiener - *H’*, the estimation of evenness (Smith & Wilson 1996) - E_{VAR}, and the species richness (*S*) were calculated. The species number was used in the calculations of the rarefaction analyses - S_{RAR}, for each collection. To compare the results with those of other ecology studies of Drosophilidae in Brazil, the values of the dominance index of Simpsom (*D*), the effective number of species that had contributed to the diversity (*Exp H’*) and the Pielou’s evenness (*J’*) were calculated.

Even if all these ecological parameters were only for application at the species level, the use of the subgroup was adopted in the case of the two *willistoni* subgroup species (*D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky and Pavan) because they were the most abundant species in our collections they were very similar in morphology, and the identification of the females would have been impossible without checking their male progenies. This procedure led to a small bias towards underestimating the diversity and evenness indices, and also an overestimation of the dominance indices.

The software Ecological Methodology 5.2 (Krebs 1999) was used to calculate the species rarefaction. In order to compare different samples, the minimum sampling number for a collection (51 individuals) was used, as suggested by Begon *et al.* (1996).

Variance analysis was carried out by ANOVA - Turkey’s HSD test to verify whether the calculated diversity indices had differentiated between the places and seasons, using Statistica Software 5.1’ 98 edition (StatSoft 1998). Rarefaction curves for each point of collection were plotted.

The decomposition of the diversity values was conducted, trying to establish the reasons for the different patterns obtained. This decomposition was achieved using the divergences found between the index of heterogeneity *H’* of each assembly, considering the factors space, time and season.

The similarity between the subsamples was calculated by the index of Morisita (*IM*). To facilitate the visualization of this similarity, dendograms were constructed using the analysis of groupings *UPGMA* – unweighted pair-group method using arithmetic averages (Sneath & Sokal 1973).

Results and Discussion

A total of 49,368 Drosophilidae were collected during the entire sampling period. In the Annex (Tables 1 to 8) we present the data of the absolute (*ni*) and relative (*pi*) abundance of the different identified species of Drosophilidae at the eight studied sites during the different seasons of the year. Is noticeable that some species present a higher abundance in the community to which they belong, consequently influencing the diversity of this association (Table 1).

Generally, the sites D, E, F and H tend to have higher values for the heterogeneity index of Shannon-Wiener (*H’*), but the only significant difference found was between points F and A. The first one presented the highest values (ANOVA: F = 3.25, df = 7, P = 0.01; Turkey: P =.032). Despite the seasonal variations of *H*’, which was not significant, it turned out to be higher in the winter and spring.

When the values of the evenness index of Smith-Wilson (E_{VAR}) were compared, there were no significant differences among the sampled sites. However, this index showed seasonal differences: the values for winter are higher than those for the autumn and summer (ANOVA: F = 5.42, df = 3, P = 0.004; Turkey: P = 0.005 and 0.039 for the respective comparisons).

The number of species observed (*S*) in each collection presented only seasonal variation (ANOVA: F = 5.42, df = 3, P = 0.004). The differences between the sampled points were small, but E and F, the most preserved sites, tended to be the richest areas. Comparing the number of species for the different seasons, the autumn presented the highest *S*, followed by spring. These two seasons have significantly more species than the winter (Turkey: P = 0.002 and 0.027, respectively). The numbers of species measured with the rarefaction technique (S_{RAR}) also showed significant differences, but only in the seasonal comparisons, where the values for the spring were higher than those for the winter (ANOVA stops: F = 3.36, df = 3, P = 0.031; Turkey: P = 0.039).

Tidon (2006) compared Drosophilidae populations of the Cerrado biome and the Gallery Forest, pointing to a more elevated diversity in the dry season (winter) in both ecosystems, despite the higher specific richness in the humid periods. The author attributes this fact to the population reduction of almost all species, due to the environmental stress in the dry season

Table 1. Average and standard error of the observed indices values in each collection site, with the respective P. For the abbreviations of the indices see text.

Indices/collecting sites	*H'*	E_{VAR}	S	S_{RAR}	*D*	*J'*	*Exp H'*
A – Morro da Lagoa	1.61 (0.98)	0.22 (0.10)	17.0 (3.6)	6.41 (3.97)	0.53 (0.25)	0.39 (0.22)	8.32 (11.43)
B - Ilha de Ratones Grande	1.70 (0.33)	0.21 (0.02)	18.0 (6.6)	6.48 (1.32)	0.49 (0.09)	0.43 (0.10)	5.72 (2.06)
C - Ilha de Ratones Pequena	1.87 (0.28)	0.18 (0.05)	15.6 (5.5)	6.58 (1.24)	0.42 (0.10)	0.49 (0.10)	6.69 (1.79)
D – Sertão do Peri	2.31 (0.98)	0.26 (0.16)	16.5 (6.3)	7.64 (4.24)	0.35 (0.27)	0.59 (0.23)	13.79 (8.91)
E - Serra do Tabuleiro I	2.27 (0.65)	0.29 (0.08)	14.8 (5.2)	8.45 (1.80)	0.32 (0.18)	0.60 (0.16)	11.31 (5.83)
F - Serra do Tabuleiro II	2.52 (0.57)	0.29 (0.09)	14.9 (3.7)	9.13 (2.08)	0.27 (0.11)	0.65 (0.13)	14.27 (8.25)
G - Ilha do Arvoredo	1.74 (0.52)	0.25 (0.16)	14.8 (6.6)	5.90 (1.61)	0.46 (0.15)	0.48 (0.18)	6.45 (3.54)
H - Ilha do Campeche	2.17 (0.52)	0.24 (0.05)	16.1 (4.2)	7.71 (1.86)	0.35 (0.13)	0.54 (0.10)	9.82 (4.79)

and the migration of these species to the adjacent ecosystems. In this case, the diversity is increased by the evenness of the contribution of each individual species.

In the autumn months, an increase of the richness of species was observed in the studied assemblies. But in the winter, in a more elevated environmental stress situation, the populations were reduced, causing an increment of the diversity related to the increase of the evenness as observed by Tidon (2006).

The rarefaction curves, based on the accumulated data of each sampling site (Fig. 2), show a very similar richness of species among the collection points as well. The most diverse was the point F, corroborating the results of the ANOVA tests. In Fig. 2, it is also possible to observe in the number of collected species a trend towards stabilization.

Despite the fact that the ANOVA analysis did not point to a significant difference between the found diversity values *H'*, its decomposition (Table 2) indicates the spatial

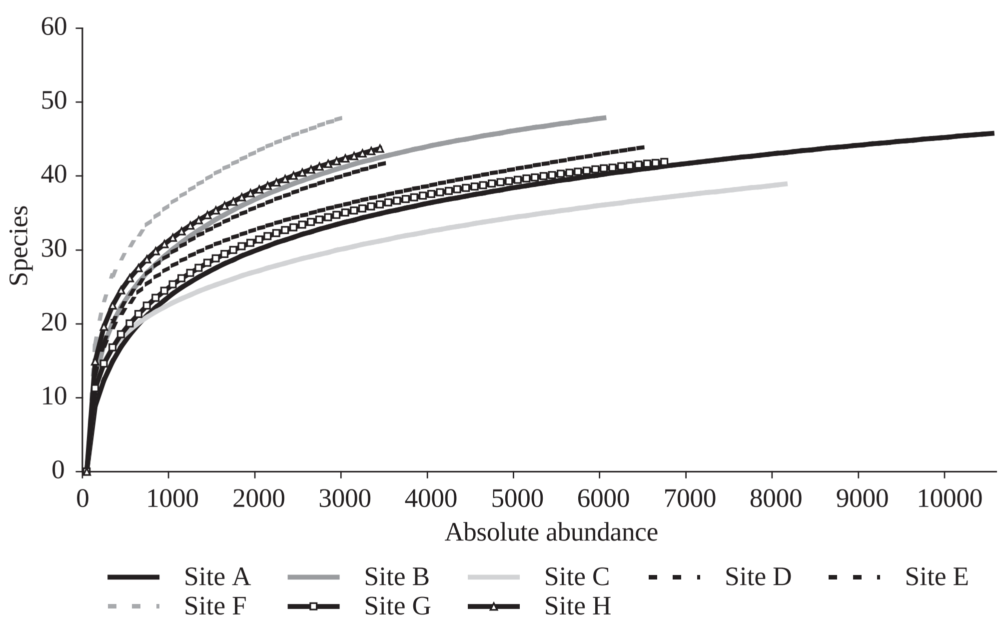

Fig. 2. Total rarefaction of species number per site.

component as the most important for its determination (36.0%), followed by the seasons (26.6%). These results reflect the great complexity and environmental heterogeneity of the Atlantic Forest, and consequently its unpredictable fauna composition.

Benado & Brncic (1994) studied the decomposition of the diversity components of the Drosophilidae community during eight years in La Florida, Chile. They showed that the variation throughout the years had an importance of only 5.15% in the explanation of the total variation. The seasonal component had a participation of 23.53%, the monthly value obtained was 39.70% and 31.62% of the variation was considered to be inexplicable. In other words, among the temporal variations in this Chilean assembly, the monthly accumulated variation added to the seasonal variation totaled 62.6%, pointing to the seasonal component as being one of the main factors responsible for maintaining the values of *H'*. However, the studied Chilean community is located in a region of temperate climate, which might possibly have maximized the importance of the seasonal factor.

Bearing in mind the huge diversity of insects, Fager (1968) suggested that one could determine a dominant species in a guild of invertebrates. However, in a temperate zone, this same species can lose its dominance, a fact that would be entirely unpredictable. In the assemblies of *Drosophila* analyzed in this study though, it was often possible to forecast which species would be dominant in a specified period.

In the studied communities, almost all sampling points (with the exception of C and F) had high levels of *S*, and the values found for the diversity were low due to the elevated dominance of the *willistoni* subgroup (Table 1).

Brncic *et al.* (1985), in their three-year-long analysis of another Drosophilid assembly, stated that the seasonal patterns of occurrence of each species is the product of a long and continuous process of adaptation to the environmental conditions in which the species live.

Thus, the different climatic conditions throughout the year are critical to the population fluctuation. It is well known that temperature and humidity affect the majority of the vital *Drosophila* parameters such as viability, mating behavior, fertility, development time, offspring, and other factors that are directly related to the growth of a population. Also, the temperature affects the agility and therefore the number of flies moving towards the bait.

Temperature, humidity and light intensity are considered factors that, even independently of density, regulate the population growth. Besides that these elements also have influence over the alimentary resources and the action of parasites and predators (density dependent factors). The plant phenology explored by the *Drosophila* species depends, in turn, directly on the climatic factors, strengthening the importance of the seasons for the composition of the assemblies.

Table 2. Differences observed in the *H'* between sites, between seasons and between years plotted for each collecting site and the respective percentage on the total variation observed.

Differences observed	*H'*	%
Between sites	0.68	36.0
Between seasons	0.50	26.6
Between years	0.00	0.0
Not explained	0.70	37.4
Total	1.88	100.0

Concerning the *willistoni* group, several studies regarding the frequency of seasonal fluctuations of this group have already been done, due precisely to the importance of these species in the Brazilian assemblies. *D. willistoni*, the most representative species of the subgroup, exerted dominance in almost all of our collections (Table 1). According to diverse authors, the *willistoni* subgroup species have a clear preference for the summer and autumn, seasons with warmer and more humid months (Patterson 1943, Dobzhansky & Pavan 1950, Franck & Valente 1985). Curiously, Borba & Napp (1985) did not find these species in abundance in Rio Grande Do Sul during the summer. However, they observed that the occurrence of some warm and humid days in the winter is sufficient to modify the phenological patterns of the fruit trees and thus to trigger the availability of feeding and breeding sites for the species of this subgroup throughout the year. Burla *et al.* (1950) affirm that *D. willistoni* is common on the Angra dos Reis islands even in the absence of fruits. Valiati & Valente (1996) point out that the species of this subgroup have great ecological versatility.

Our data corresponded to these results and seem to strengthen the idea of the *willistoni* subgroup's appearance following the phenology of the palm trees in the Atlantic Forest (Borba & Napp 1985, Valente & Araújo 1986, Saavedra *et al.* 1995). Our collections with the highest abundance of these species were those executed during September and May, on Ratones Grande Island, where its preferred resource, the palm fruits (*S. romanzoffiana* Glassman), were abundant in these months. In these months, we had the highest peak of occurrence of these species.

Drosophila capricorni was collected by Dobzhansky & Pavan (1950) in he Vila Atlântica, SP, in the months of August until November and, again, from May through July. The trend of preference for mild temperature months shown by this species was also observed at almost all of our collection points. Because of its intense presence in the colder months at the F site, it was considered to be the dominant species there.

Dobzhansky & Pavan (1950) also state that, from January to March, there is an observable increment in the population of *D. fumipennis*. This was confirmed by our records, since the most representative collection of samples of this species occurred in exactly the same period. *D. nebulosa*, in turn, is known for being more frequently collected in open vegetal formations (Val *et al.* 1981, Martins 1987). This species is always rare in forest environments, and in fact its frequencies were very low in our collections, coinciding with the sampled driest periods. These data agree with the results obtained by Petersen (1960), who took samples in Rio Grande do Sul State.

The species of the *cardini* group have, according to Rohde & Valente (1996), divergent preferences regarding the environment that they colonize. In the period covered by this study, *D. polymorpha* was found more abundantly in cold and dry months and *D. cardinoides* was found more abundantly in the warm and humid months. The Spearman correlations obtained were positive concerning the high humidity for the former species and negative for the latter. On the other hand, Petersen (1960) collected *D. polymorpha* in December, with high temperatures, in some forest localities of Rio Grande do Sul.

In our study, the flies of this group, especially *D. polymorpha*, showed a preference for the warmer months, in contrast with what was observed in the study of Rohde & Valente (1996), carried out in the city of Porto Alegre. This species was present in almost all of our collections, with its occurrence apparently more tied to the relative humidity than to the temperature.

De Toni & Hofmann (1995) have found more elevated amounts of *D. griseolineata* in the mild temperature months. According to Sene *et al.* (1980) this species and *D. maculifrons* have been collected together in many forests of Brazil, but this coincidence was not observed in the present investigation and we believe that *D. maculifrons* tends to have a westernmost distribution in Santa Catarina State, as observed by Val *et al.* (1981) for a São Paulo State population. De Toni & Hofmann (1995) have collected *D. sturtevanti* and *D. neoelliptica* predominantly in the warmer periods. In the collections of the present research, besides these two species, we also found *D. saltans, D. prosaltans* and *D. parasaltans* (*cf.*), all of which are very rare and, like the other species of the group, they appeared principally in the warmer months.

Other genera of Drosophilidae such as *Zaprionus, Zygothrica*, *Rhinoleucophenga*, Cladochaeta, *Diathoneura, Mycodrosophila, Leucophenga, Scaptodrosophila* and *Amiota* have also been collected. *Zaprionus indianus*, an invader species, initially appeared in lower frequencies that increased gradually in the subsequent collections. This type of invasion was also registered by Sevenster (1992), who found the emergence of *D. malerkotliana* in natural resources of Panama, a place where this species is an invader, surpassing the native species in frequency, and confirming the generalist and polyphagic character of these invaders. Concerning the seasonal fluctuations of these other genera, with the exception of *Zaprionus* that has a clear preference for the warmer months, (corroborated by Silva *et al.* 2005), no seasonal trend was registered.

Brncic & Valente (1978) suggested that perhaps the gregarious habit in *Drosophila* occurs even without sufficient density to allow competition, since as Dobzhansky & Pavan (1950) observed, many species of the genus are found in the same regions and seasons, apparently without mutual influence. Da Cunha *et al.* (1951) supposed that the coexistence could take place due to the different alimentary source utilized by each species. Later, this idea was confirmed by Dobzhansky & Da Cunha (1955), Da Cunha *et al.*(1957) and Klaczko *et al.* (1983, 1986). However, Brncic & Valente (1978) stated that the niche interference in a physical space shared by the larvae would probably affect the survival of the individuals. The occurrence, in our samples, of fermented fruits not containing preadults of *Drosophila* seems to indicate that the amount of food does not represent a key factor in the coexistence of these species. In contrast, the interference would be the most decisive factor. These last authors remember that in the laboratory, the larvae of *D. pavani* Brncic inhibit the growth of other species, particularly of *D. willistoni*, and that facilitates the development of its own larvae (Budnik & Brncic 1974). Therefore, this kind of interspecific relationship could explain why some species like *D. willistoni, D. simulans, D. mercatorum*, *D. pallidipennis* and *D. bandeirantorum* have an aggregate distribution that is independent of the available resources, tending to facilitate themselves.

This fact illustrates the difficulty of understanding the complex patterns found in the assemblies of Neotropical insects, and it is a sign of the stability of species in the mature assemblies. As Tidon-Sklorz & Sene (1992) affirm, the complexity of the dynamics of the tropical assemblies is a result of the interventions in the populations by factors such as ambient variation, natural selection, genetic derivation and inbreeding at different times and in different spaces. The interaction of all these factors, in alternating periods, can lead to an instability that could help to clarify the tropical diversity through the constant adaptation and differentiation of the populations.

Comparing the diversity of the analyzed assemblies with the values calculated by Saavedra *et al.* (1995) for the assemblies of Rio Grande do Sul State, it is perceivable that the values obtained in this study are closer to the ones found for the Guaíba localities (sites covered by a kind of forest known as "capões", where the climatic conditions are unstable, and the resources are scarce and unpredictable) and Bento Gonçalves (a forest of low altitude and temperature). In these places, the *H'* was 1.69 for Guaíba, very close to 1.74, the value found for Arvoredo Island (Point G). However, these three assemblies presented different richnesses of species (S). On Arvoredo Island 42 species were captured, while at Guaíba and Bento Gonçalves, only 13 were captured. This fact reinforces the importance of the dominance that the species of the *willistoni* subgroup exert in the studied communities. It is especially clear in Morro da Lagoa (site A), a place where an elevated quantity of species (46) was found and its diversity was similar to those of the Rio Grande do Sul sites mentioned above, which revealed only 13 different species each. The values of *J'* were higher in Guaíba (0.66) and Bento Gonçalves (0.60), indicating that the well-distributed though small number of species found at these points contribute more regularly to the perpetuation of the local diversity than those of higher quantity from Santa Catarina involved in this study.

It is shown in Table 2 that the Morro da Lagoa site presented the least diversity of all points analyzed in the present study (*H'* = 1.61). However, a higher number of species were found, suggesting that the environmental stability leads to a constancy in the species richness and a better possibility of adaptation for native species, as exemplified by *D. willistoni*.

Comparing the values of *H'* for all the assemblies studied in Santa Catarina with those of Rio Grande do Sul, we realize that they are not discriminating, despite the fact that the numbers of species shown in the assemblies of Santa Catarina were higher than those of Rio Grande do Sul. Brncic *et al.* (1985) also carried out diversity index calculations for the Chilean assemblies of La Florida, where their data were acquired monthly, over a collection period of three years. They found differences in two periods of sampling: January to May, with lower *H'* and *J';* and June to December, with higher *H'* and *J'*. The highest diversity verified by the authors was in December (*Exp H'* = 5.29 and *J'* = 0.70) and the lowest was in March (*Exp H'* = 1.17 and *J'* = 0.25). The values of *S* were 6 and 13 species for the respective months, and a total of 17 different species collected for the whole period. Again, the low values of *S* when compared with the ones of the Atlantic Forest assemblies are evident. Although some dominant species occurred in the Chilean communities such as the cosmopolitan *D. simulans* and the invader *D. subobscura Collin* these species do not represent as large a portion of the community as the *willistoni* subgroup does in the Santa Catarina State. A similar situation arises when we compare the Santa Catarina State assemblies to the ones studied by Benado & Brncic (1994). These authors also analyzed the diversity of the assemblies of La Florida, in Chile. They found that the values of *H'* varied from 1.78 in winter to 0.53 in the autumn, with *S* values ranging from 12 species collected in the winter to three in the autumn, totaling 16 species. *D. simulans* and *D. subobscura* had exerted some dominance, but it was incomparable to the supremacy imposed by the *willistoni* subgroup in assemblies studied in this research, since the values of *H'* were considerably higher even with a small value of *S*.

A contrasting fact in our results was the greater diversity found in the winter due to the decrease in the dominance of some species. De Toni & Hofmann´s (1995) one year analysis for a Drosophilid community of Morro da Lagoa da Conceição found higher values of *H'* for October (0.94), August (0.91) and June (0.77), and lower values for the autumn and summer months. The number of species by collection (*S*) ranged from seven in January to 20 in November. In these collections, a number for *S* was close to the values we obtained in this present study. However, the dominance of *D. willistoni* led to a decrease in the indices of diversity in the present work.

In the drosophilid community that emerged from *Parahancornia amapa* Ducke, studied by Martins (1996) during a period of three years in the Amazon, the values of *H'* were 1.78 in 1990, 1.50 in 1991 and 1.37 in 1992; *J'* index values were 0.38 in 1990, 0.53 in 1991 and 0.34 in 1992, and S resulted in 25 species in 1990, 7 species in 1991 and 17 species in 1992. This tendency towards reduction in the diversity is interpreted by the author as the result of invasion by the exotic *D. malerkotliana*, which dislocated the native species and thus reduced the diversity level. However, although the values for diversity were elevated, there was no constancy of the relative contribution of the species to the increment of this index (*J'*). This demonstrates that, in this Amazonian assembly, the dominance is also an important factor in its structure, as well as in the Santa Catarina assemblies (*D* = 0.58, 0.62 and 0.57 for the years 1990, 1991 and 1992 respectively). The values of *D* were low in almost all of the assemblies of the present study (Table 1), with the exception of the community of Morro da Lagoa (D = 0.61).

D. schineri and *D. fuscolineata* were collected for the first time in the south of Brazil, widening, therefore, the southern limit of distribution of these species.

Our results revealed a high level of biological richness for the communities of the Atlantic Forest when compared with the same index of other ecosystems. This fact demonstrates that efforts towards the conservation of this ecosystem are extremely necessary because, even though it is highly devastated, approximately 7% of the remainder of this forest still lodges a diversity which is vastly superior to that of the ecosystems of temperate climate.

The degree of similarity between the different assemblies was compared in relation to the different sites and seasons through the Morisita index (*MI*), in which the data were transformed (log (n+1)) as suggested by Wolda (1992), represented in Figs. 3 and 4 in the form of UPGMA phylogenies.

In Fig. 3, the relationship of similarity for the sampling sites is represented at each collection point. The set of assemblies presents a similarity of approximately 60%. The primary separation is in two clades: the first of which is continental (with about 90% of similarity) and the second of which is insular (with 81% of similarity), showing the importance of the spatial component in the forecast of the community structure. The six insular grouped sites are separated into two other clades (with 82% of similarity): one including the sites on Santa Catarina Island and the other, with two subclades, comprising the adjacent islands and subdividing itself into 2 others, joining the Ratones Grande Island with Campeche Island (B and H) and Ratones Pequeno Island with Arvoredo Island (C and G). In this in case, the grouping is due to the similarity of environments found on each island. The most greatly modified environments were found in the C and G clades, in which an increase was found in the abundance of "exotic" species, such as *D. simulans*.

In Fig. 4, the similarities of each collection are represented individually. We can observe that some collections at points like E and F are separated from the rest. They include the best-preserved Atlantic Forest region of all the collecting points. Site F is the only one with primary Atlantic Forest. The remaining sites are grouped in function

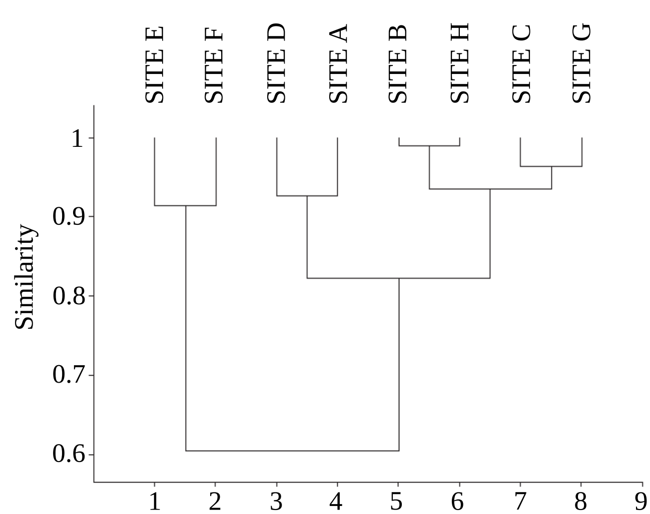

Fig. 3. Dendogram showing the similarity relationships between the studied assemblies.

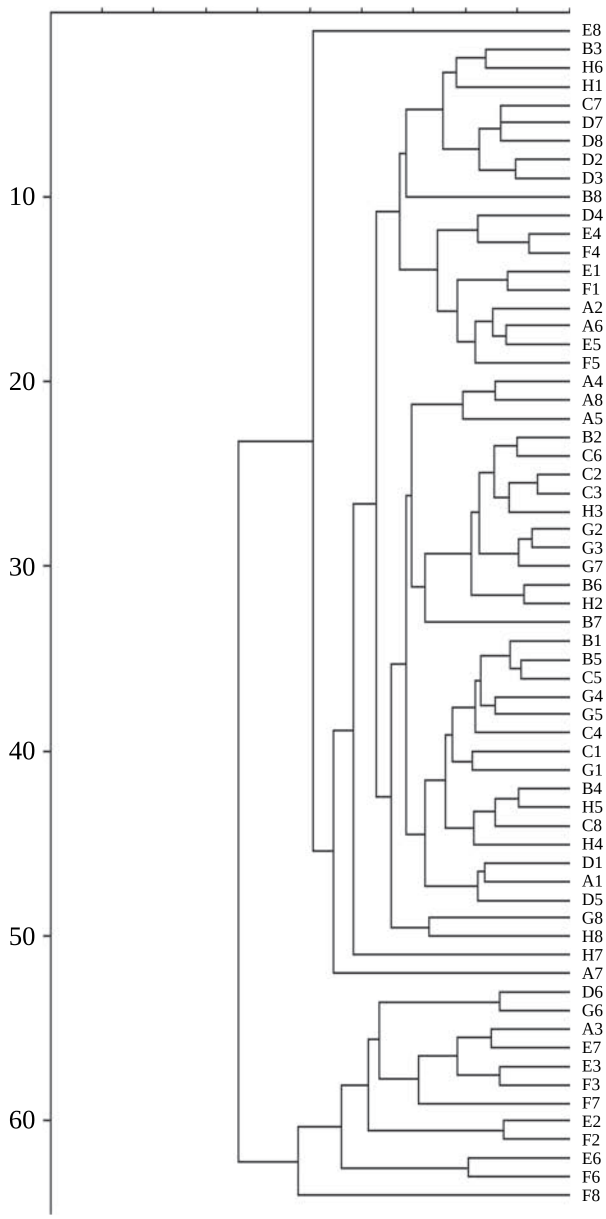

Fig. 4. Dendogram showing the similarity relationships between the studied assemblies at the different seasons. Numbers after the letter indicate the collecting site are corresponding with the months of the year.

of the influence of seasonal variation over the composition of the assemblies, since they are all covered by Atlantic Forest that is in the process of regeneration.

The species of the *melanogaster* group and *Z. indianus* are more representative in the most altered sites. The presence of these Atlantic Forest cosmopolitan and invader species causes the higher similarity in the communities of these localities. This information is corroborated by Döge *et al.* (2004), Ferreira & Tidon (2005) and Silva *et al.* (2005).

Acknowledgements

The authors are extremely grateful to the entire team of the *Drosophila* laboratories of UFSC and UFRGS for their assistance in collection and analysis; to the Polícia Ambiental de Florianópolis for transportation to the biological reserve of Ilha do Arvoredo; to the Associação Couto de Magalhães for transportation to the Ilha Campeche; to DAEX of the Universidade Federal de Santa Catarina for the transportation to the Ilha Ratones; to the Hotel Plaza Caldas da Imperatriz, particularly to the biologist Fernando Brügemann, for the facilities in the Serra do Tabuleiro collection. This research was financed by CNPq, FAPERGS, FINEP, and PROPESQ-UFRGS.

References

Bächli, G. 2006. Taxodros: The database on taxonomy of Drosophilidae. Consulted May 2006. URL: http://www.taxodros.unizh.ch/.

Begon, M., J.L. Harper & C.R. Townsend. 1996. Ecology: Individuals, populations and communities. Oxford, Blackwell, 885p.

Benado, M. & D. Brncic. 1994. An eight year phenological study of a local drosophilid community in Central Chile. Z. Zool. Syst. Evolut.-forsch 32: 51-63.

Borba, C.M.B. & M. Napp. 1985. Contribuição ao estudo das populações naturais de *Drosophila willistoni* do Estado do Rio Grande do Sul. Cienc. Natur. 7: 181-195.

Brncic, D., M. Budnik & R. Guiñez. 1985. An analysis of a *Drosophila* community in Central Chile during a three-year period. Z. Zool. Syst. Evolut-forsch 23: 90-100.

Brncic, D. & V.L.S. Valente. 1978. Dinâmica de comunidades de *Drosophila* que se estabelecem em frutos silvestres no Rio Grande do Sul. Cienc. Cult. 30: 1104-1111.

Brower, E.J. & H.J. Zar. 1984. Field and laboratory methods for general ecology. 2ª ed. Iowa, Wm. C. Brown (Publishers), 226p.

Budnik, M. & D. Brncic. 1974. Preadult competition between *Drosophila pavani* and *D. melanogaster* Meigen, *D. simulans* and *D. willistoni*. Ecology 55: 657-661.

Burla, H., A.B. Da Cunha, A.G.L. Cavalcanti, T. Dobzhansky & C. Pavan. 1950. Population density and dispersal rates in Brazilian *Drosophila willistoni*. Ecology 31: 393-404.

Cunha, A.B. Da, T. Dobzhansky & A. Sokoloff. 1951. On food preferences of sympatric species of *Drosophila*. Evolution 5: 97-101.

Cunha, A.B. Da, A.M. Shehata & W. Oliveira. 1957. A study of the diets and nutritional preferences of tropical species of *Drosophila*. Ecology 38: 98-106.

Dobzhansky, T. & A.B. Da Cunha. 1955. Differentiation of nutritional preferences in Brazilian species of *Drosophila*. J. Anim. Ecol. 19: 1-14.

Dobzhansky, T. & C. Pavan. 1950. Local and seasonal variations in relative frequencies of species of *Drosophila* in Brazil. J. Anim. Ecol. 19: 1-14.

Döge, J.S., M.S. Gottschalk, D.C. De Toni, L.E. Bizzo, S.C.F. Oliveira, V.L.S. Valente & P.R.P. Hofmann. 2004. New records of six species of subgenus *Sophophora* (*Drosophila*, Drosophilidae) collected in Brazil. Zootaxa 675:1-6.

Fager, E.W. 1968. The community of invertebrates in decaying oak wood. J. Anim. Ecol. 7: 121-42.

Ferreira, L.B. & R. Tidon. 2005. Colonizing potential of Drosophilidae (Insecta, Diptera) in environments with different grades of urbanization. Biodiv. Conserv. 14: 1809-1821.

Franck, G. & V.L.S. Valente. 1985. Study on the flutuation in *Drosophila* populations of Bento Gonçalves, RS, Brasil. Rev. Bras. Biol. 45: 133-141.

Freire-Maia, N. & C. Pavan. 1949. Introdução ao estudo da drosófila. Cultus 1: 1-171.

Gottschalk, M.S., J.S. Döge, S.C.F. Oliveira, D.C. De Toni, V.L.S. Valente & P.R.P. Hofmann. 2006. On the geographic distribution of the *Drosophila* subgenus in southern Brazil (Drosophilidae, Diptera). The *Drosophila repleta* species group Sturtevant 1942. Trop. Zool. 19: 129-139.

Klaczko, L.B., J.R. Powell & C.E. Taylor. 1983. *Drosophila* baits: Species attracted. Oecologia 59: 411-413.

Klaczko, L.B., C.E. Taylor & J.R. Powell. 1986. Genetic variation for dispersal by *Drosophila pseudoobscura* and *Drosophila persimilis*. Genetica 112: 229-235.

Krebs, C.J. 1999. Ecological metodology. New York, ED., 620p.

Martins, M. 1987. Variação espacial e temporal de algumas espécies e grupos de *Drosophila* (Diptera) em duas reservas de matas isoladas, nas vizinhanças de Manaus (Amazonas, Brasil). Bol. Mus. Para. Emilio Goeldi Ser. Zool. 3: 195-217.

Martins, M.N. 1996. Drosófilas e outros insetos associados a frutos de *Parahanchornia amapa* dispersos sobre o solo da floresta. Tese de Doutoramento em Ecologia, Universidade Estadual de Campinas, Campinas, 203p.

Myers, N., R.A. Mittermeyer, C.G. Mittermeyer, G.A.B. Fonseca & J. Kent. 2000. Biodiversity spots for conservation priorities. Nature 403: 853-858.

Patterson, J. T. 1943. The Drosophilidae of the soutwest. Univ. Texas Publ. 4313: 7-216.

Petersen, J. A. 1960. Studies on the ecology of the genus *Drosophila*. I. Collection in two different life zones and seasonal variations in Rio Grande do Sul, Brazil. Rev. Bras. Biol. 20: 3-16.

Remsen, J. & P. O'Grady. 2002. Phylogeny of Drosophilinae (Diptera: Drosophilidae), with comments on combined analysis and character support. Mol. Phyl. Evol. 24: 249-264.

Rohde, C. & V.L.S. Valente. 1996. Ecological characteristics of urban populations of *Drosophila polymorpha* Dobzhansky & Pavan and *Drosophila cardinoides* Dobzhansky & Pavan (Diptera, Drosophilidae). Rev. Bras. Entomol. 40: 75-79.

Saavedra, C.C.R., S.M. Callegari-Jacques, M. Napp & V.L.S Valente. 1995. A descriptive and analytical study of four neotropical Drosophilid communities. J. Zool. Syst. Evol. Res. 33: 62-74.

Schmitz, H.J., P.R.P. Hofmann & V.L.S. Valente. Ecology of communities of drosophilids (Diptera, Drosophilidae) in mangrove forests. Biotropica (submitted).

Sene, F.M., F.C. Val, C.R. Vilela & M.A.Q.R. Pereira. 1980. Preliminary data of geographical distribution of *Drosophila* species within morphoclimatic domains of Brazil. Pap. Avulsos Zool. 33: 315-326.

Sevenster, J.G. 1992. The community ecology of frugivorous *Drosophila* in a neotropical forest. Univ. Leiden, The Netherlands, 167p.

Silva N.M., C.C. Fantinel, V.L.S. Valente & V.H. Valiati. 2005. Ecology of colonizing populations of the figfly *Zaprionus indianus* (Diptera, Drosophilidae) in Porto Alegre, Southern Brazil. Iheringia Ser. Zool. 95: 233-240.

Smith, B. & B. Wilson. 1996. A consumer's guide to evenness indices. OIKOS 76: 70-82.

Sneath, P.H. & R.R. Sokal. 1973. Numerical taxonomy. San Francisco, Freeman & Co., 573p.

StatSoft, Inc. 1998. STATISTICA for Windows [Computer program manual]. Tulsa, OK: URL: http://www.statsoft.com.

Tidon, R. 2006. Relationships between drosophilids (Diptera, Drosophilidae) and the environment in two contrasting tropical vegetations. Zool. J. Linn. Soc. 87: 233-247.

Tidon-Sklorz, R. & F.M. Sene. 1992. Vertical and temporal distribution of *Drosophila* (Diptera, Drosophilidae) species in a wooden area in the state of São Paulo, Brazil. Rev. Bras. Biol. 52: 311-317.

Toni, D.C. De & P.R.P. Hofmann. 1995. Preliminary taxonomic survey of the genus *Drosophila* (Diptera, Drosophilidae) at Morro Lagoa da Conceição, Santa Catarina Island, Brazil. Rev. Bras. Biol. 55: 347-35.

Val, F.C., C.R. Vilela & M.D. Marques. 1981. Drosophilidae of the Neotropical region, p.2-168a. In M. Ashburner, H.L. Carson & I.N. Thompson Jr. (eds.), The genetics and biology of Drosophila. Academic Press, New York, 168p.

Valente, V.L.S. & A.M. Araújo. 1986. Comments on breeding sites of *Drosophila willistoni* Sturtevant (Diptera, Drosophilidae). Rev. Bras. Entomol. 30: 281-286.

Valiati, V.H. & V.L.S. Valente. 1996. Observations on ecological parameters of urban populations of *Drosophila paulistorum* Dobzhansky & Pavan (Diptera, Drosophilidae). Rev. Bras. Entomol. 40: 225-231.

Wolda, H. 1992. Trends in abundance of tropical insects. Oecologia 89: 47-52.

Received 25/V/06. Accepted 18/IX/06.

Annex

Table 1. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Morro da Lagoa da Conceição (site A) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	A1	A2	A3	A4	A5	A6	A7	A8	*ni*	*pi*
*Amiota sp.*1				1					1	0.0001
D. alagitans Patterson & Mainland		7							7	0.0007
D. angustibucca Duda						2			2	0.0002
D. annulimana Duda					1		2		3	0.0003
D. atrata Burla & Pavan	1								1	0.0001
D. bandeirantorum Dobzhansky & Pavan			6			6	1		13	0.0012
D. bocainensis Pavan & Cunha						2			2	0.0002
D. bocainoides Carson						2			2	0.0002
D. sp. (*cf.*) *bodemannae* Pipkin & Heed					1				1	0.0001
D. buskii Coquillett							3		3	0.0003
D. capricorni Dobzhansky & Pavan	3	266	96	25	47	576	85	9	1107	0.1030
D. dreyfusi Dobzhansky & Pavan			4			1	12		17	0.0016
D. fascioloides Dobzhansky & Pavan				1					1	0.0001
D. fumipennis Duda	18	5		2	155	65		1	246	0.0229
D. griseolineata Duda	70	6	4	4	2	3	3	1	93	0.0087
D. hydei Sturtevant							23		23	0.0021
D. immigrans Sturtevant							10	1	11	0.0010
D. maculifrons Duda								2	2	0.0002
D. malerkotliana Parshad & Paika	59					1	1		61	0.0057
D. mediopicta Frota-Pessoa	1	2	47	2	3	8	2		65	0.0060
D. mediopunctata Dobzhansky & Pavan	2	8	8		3	30	13	1	65	0.0060
D. mediostriata Duda	1			2	1			1	5	0.0005
D. melanogaster Meigen							17		17	0.0016
D. mercatorum Patterson & Wheeler	0		1		1		6	10	18	0.0017
D. nebulosa Sturtevant	2								2	0.0002
D. neocardini Streisinger	1		2	2	3			1	9	0.0008
D. neoelliptica Pavan & Magalhaes	3	1		5		2	7		18	0.0017
D. neosaltans Pavan & Magalhaes				1					1	0.0001
D. onca Dobzhansky & Pavan		1					10	1	12	0.0011
D. ornatifrons Duda							5		5	0.0005
D. paraguayensis Duda	4	3	7		1	5	2		22	0.0020
D. platitarsus Frota-Pessoa		1							1	0.0001
D. polymorpha Dobzhansky & Pavan	6	19	4	258	52	19	10	75	443	0.0412
D. prosaltans Duda					5	1			6	0.0006
D. replete Wollaston							7		7	0.0007
D. roehrae Pipkin & Heed		1			1	3			5	0.0005

Continue

Table 1. Continuation.

Species	A1	A2	A3	A4	A5	A6	A7	A8	*ni*	*pi*
D. sellata Sturtevant								1	1	0.0001
D. simulans Sturtevant	12				7	33	3	3	58	0.0054
D. sturtevanti Duda	3	3	2	11	2	2	27		50	0.0047
D. sp.1	1								1	0.0001
Rhinoleucophenga obesa Loew	2			2					4	0.0004
Mycodrosophila sp.1		1							1	0.0001
S. latifasciaeformis Duda					1				1	0.0001
D. willistoni sp. subgroup Pavan	902	116	2	1268	811	1085	32	4095	8311	0.7732
Zaprionus indianus Gupta					18		1	3	22	0.0020
Zygothrica orbitalis Sturtevant	3								3	0.0003
Total	1094	440	183	1584	1115	1846	282	4205	10749	1.0000

Table 2. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Ratones Grande Island (site B) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	B1	B2	B3	B4	B5	B6	B7	B8	*ni*	*pi*
D. angustibucca Duda		1							1	0.0002
D. annulimana Duda					1				1	0.0002
D. atrata Burla & Pavan	13	1	3		28				45	0.0074
D. bandeirantorum Dobzhansky & Pavan			4	1	1			6	12	0.0020
D. bocainoides Carson		1					1		2	0.0003
D. briegeri Pavan & Breurer			1						1	0.0002
D. capricorni Dobzhansky & Pavan		6	49	4	1	1	49	7	117	0.0192
D. cardinoides Dobzhansky & Pavan	2					1			3	0.0005
D. dreyfusi Dobzhansky & Pavan			3						3	0.0005
D. sp. (*cf.*) *freilejoni* Hunter			1						1	0.0002
D. fumipennis Duda	7	3	3	1	20		1		35	0.0057
D. griseolineata Sturtevant	9	1	6	2	64		15	1	98	0.0161
D. hydei Sturtevant				1			1		2	0.0003
D. immigrans Sturtevant			1				3	1	5	0.0008
D. malerkotliana Parshad & Paika	119			1	17				137	0.0225
D. mediopicta Frota-Pessoa		2	13				2	3	20	0.0033
D. mediopunctata Dobzhansky & Pavan	18	7	2		5			5	37	0.0061
D. mediostriata Duda	4			2	1				7	0.0011
D. melanogaster Meigen		1	6	2					9	0.0015
D. mercatorum Patterson & Wheeler	7	1	10	5	6		14		43	0.0071
D. meridionalis Wasserman								4	4	0.0007
D. moju Pavan		1							1	0.0002
D. nebulosa Sturtevant					3				3	0.0005

Continue

Table 2. Continuation.

Species	B1	B2	B3	B4	B5	B6	B7	B8	ni	pi
D. neocardini Streisinger	2	3	9	9				5	28	0.0046
D. neosaltans Pavan & Magalhaes							1		1	0.0002
D. neoelliptica Pavan & Magalhaes							1	1	2	0.0003
D. sp. (*cf.*) *obscura* Fallen								1	1	0.0002
D. onca Dobzhansky & Pavan		1	2		2		6	5	16	0.0026
D. ornatifrons Duda			1					4	5	0.0008
D. pallidipennis Dobzhansky & Pavan	2				1			1	4	0.0007
D. paraguayensis Duda	5	3	4	1	14			2	29	0.0047
D. polymorpha Dobzhansky & Pavan	21	15	196	64	112	4	41	97	550	0.0903
D. prosaltans Duda			3	4					7	0.0011
D. repleta Wollaston			2						2	0.0003
D. sellata Sturtevant	1		1	1				47	50	0.0082
D. senei Vilela			1						1	0.0002
D. serido Vilela & Sene								5	5	0.0008
D. simulans Sturtevant	61	74	861	45	148	40	135	30	1394	0.2289
D. sturtevanti Duda	50	3			42			1	96	0.0158
D. sp. (*cf.*) *triangula* Wheeler					1				1	0.0002
D. zottii Vilela			5						5	0.0008
D. sp. *1*								1	1	0.0002
D. sp. *2*								6	6	0.0010
D. sp. *3*								12	12	0.0020
Rhinoleucophenga obesa Loew				1	2				3	0.0005
D. willistoni sp. subgroup Pavan	725	388	23	400	917	66	4	701	3224	0.5294
S. latifasciaeformis Duda	2				2				4	0.0007
Zaprionus indianus Gupta				9	32			13	54	0.0089
Zygothrica dispar Duda			2						2	0.0003
Total	1048	512	1212	553	1420	112	274	959	6090	1.0000

Table 3. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Ratones Pequeno Island (site C) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	C1	C2	C3	C4	C5	C6	C7	C8	*ni*	*pi*
D. atrata Burla & Pavan	1	2		1	10		6		20	0.0024
D. bandeirantorum Dobzhansky & Pavan			1	3		1	12	5	22	0.0027
D. bocainensis Pavan & Cunha							1		1	0.0001
D. capricorni Dobzhansky & Pavan		10	14	2		13	79		118	0.0144
D. fumipennis Duda	1	1			3				5	0.0006
D. griseolineata Sturtevant	5	15	19	112	9		34		194	0.0237
D. guaru Dobzhansky & Pavan				1					1	0.0001
D. hydei Sturtevant							1	1	2	0.0002

Continue

Table 3. Continuation.

Species	C1	C2	C3	C4	C5	C6	C7	C8	ni	pi
D. immigrans Sturtevant							20	1	21	0.0026
D. malerkotliana Parshad & Paika	26			9	53	4			92	0.0112
D. mediopicta Frota-Pessoa							15	2	17	0.0021
D. mediopunctata Dobzhansky & Pavan		2	3	35	2	6	112	11	171	0.0209
D. mediosignata Dobzhansky & Pavan	2			14		3	30	1	50	0.0061
D. mediostriata Duda	1			4	1				6	0.0007
D. melanogaster Meigen						3			3	0.0004
D. mercatorum Patterson & Wheeler	28	3		7	2		96	17	153	0.0187
D. moju Pavan		1							1	0.0001
D. nebulosa Sturtevant	2							1	3	0.0004
D. neocardini Streisinger	2	15	2	2			9	8	38	0.0046
D. neoelliptica Pavan & Magalhaes							2	1	3	0.0004
D. onca Dobzhansky & Pavan				2			2		4	0.0005
D. ornatifrons Duda	68						1		69	0.0084
D. pallidipennis Dobzhansky & Pavan								3	3	0.0004
D. platitarsus Frota-Pessoa						1			1	0.0001
D. polymorpha Dobzhansky & Pavan	20	56	83	109	208	10	85	188	759	0.0927
D. sp. (*cf.*) *pseudoobscura* Frolova							1		1	0.0001
D. repleta Wollaston							1		1	0.0001
D. nappae Vilela, Valente & Basso							3		3	0.0004
D. sellata Sturtevant			1	13					14	0.0017
D. serido Vilela & Sene				2				5	7	0.0009
D. simulans Sturtevant	21	160	608	5	245	72	1939	58	3108	0.3796
D. sturtevanti Duda	25	3	1	10	33	3	1	15	91	0.0111
D. sp. (*cf.*) *tarsata* Schiner				1					1	0.0001
D. sp. (*cf.*) *triangula* Wheeler					1				1	0.0001
D. sp. (*cf.*) *tripunctata* Loew							1		1	0.0001
D. zottii Vilela							1		1	0.0001
Rhinoleucophenga obesa Loew							1		1	0.0001
S. latifasciaeformis Duda	1			1					2	0.0002
D. willistoni sp. subgroup Pavan	331	95	251	488	861	97	37	901	3061	0.3739
Zaprionus indianus Gupta				4	33	1	8	91	137	0.0167
Total	534	363	983	825	1461	214	2498	1309	8187	1.0000

Table 4. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Sertão do Peri (site D) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	D1	D2	D3	D4	D5	D6	D7	D8	*ni*	*Pi*
D. angustibucca Duda		4	2						6	0.0009
D. annulimana Duda			1						1	0.0002
D. atrata Burla & Pavan	8	2					1		11	0.0017
D. bandeirantorum Dobzhansky & Pavan	3	8	8	2			4	5	30	0.0046
D. bocainensis Pavan & Cunha		10	4						14	0.0021
D. sp. (*cf.*) *caponei* Pavan & Cunha				7					7	0.0011
D. capricorni Dobzhansky & Pavan		36	149	65	13	5	10	10	288	0.0441
D. sp. (*cf.*) *divisa* Duda			1						1	0.0002
D. fascioloides Dobzhansky & Pavan	1								1	0.0002
D. fumipennis Duda	8		3		14				25	0.0038
D. griseolineata Sturtevant	4	72	51	59	14	2	297	160	659	0.1010
D. immigrans Sturtevant							16		16	0.0025
D. kikkawai Burla				1					1	0.0002
D. malerkotliana Parshad & Paika	8			2					10	0.0015
D. sp. (*cf.*) *medioimpressa* Frota-Pessoa			3						3	0.0005
D. mediopicta Frota-Pessoa	2	8	18	1		1	23	4	57	0.0087
D. mediopunctata Dobzhansky & Pavan	26	18	16	6	1	12	168	29	276	0.0423
D. mediosignata Dobzhansky & Pavan	54	48	16	20	14	4	186	40	382	0.0585
D. melanogaster Meigen	1			18					19	0.0029
D. mercatorum Patterson & Wheeler	0	6	7	4			12	16	45	0.0069
D. sp. (*cf.*) *mesostigma* Frota-Pessoa			5	33			1		39	0.0060
D. neocardini Streissinger	1		1	50			16	20	88	0.0135
D. neoelliptica Pavan & Magalhaes					1		4		5	0.0008
D. onca Dobzhansky & Pavan	0	1	7				8		16	0.0025
D. ornatifrons Duda	0		3				7	2	12	0.0018
D. pallidipennis Dobzhansky & Pavan								1	1	0.0002
D. paraguayensis Duda								19	19	0.0029
D. neosaltans Pavan & Magalhaes					1				1	0.0002
D. mediopictoides Heed & Wheeler							34		34	0.0052
D. platitarsus Frota-Pessoa						2			2	0.0003
D. sp. (*cf.*) *platitarsus* Frota-Pessoa		1	1						2	0.0003
D. polymorpha Dobzhansky & Pavan	6	87	29	109	3		90	153	477	0.0731
D. prosaltans Duda			2						2	0.0003
D. nappae Vilela, Valente & Basso							2	2	4	0.0006
D. sellata Sturtevant			1				10	1	12	0.0018
D. schilde Malloch	1								1	0.0002
D. simulans Sturtevant	9	6	32		16		101	118	282	0.0432
D. sturtevanti Duda	9	3	1	19	33		8		73	0.0112

Continue

Table 4. Continuation.

Species	D1	D2	D3	D4	D5	D6	D7	D8	ni	Pi
D. unipunctata Patterson & Mainland							1		1	0.0002
D. willistoni sp. subgroup Pavan	2097	121	54	279	482	2	127	434	3596	0.5510
Rhinoleucophenga obesa Loew							1		1	0.0002
Micodrosophila sp. 1							1		1	0.0002
D. tripunctata sp. group Sturtevant	1								1	0.0002
D. sp. *1*				1					1	0.0002
Zaprionus indianus Gupta							1	1	2	0.0003
Zygothrica orbitalis Sturtevant								1	1	0.0002
Total	2239	431	415	676	592	28	1129	1016	6526	1.0000

Table 5. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Serra do Tabuleiro - I (site E) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	E1	E2	E3	E4	E5	E6	E7	E8	*ni*	*pi*
Cladochaeta bomplandi Coquillett		6							6	0.0017
D. angustibucca Duda	27		11						38	0.0107
D. atrata Burla & Pavan		2							2	0.0006
D. bandeirantorum Dobzhansky & Pavan			20	2	4		6	4	36	0.0101
D. bocainensis Pavan & Cunha	8		3			1	1		13	0.0037
D. bocainoides Carson							2		2	0.0006
D. sp. (*cf.*) *bodemannae* Pipkin & Heed		1							1	0.0003
D. calloptera Schiner	1				1				2	0.0006
D. capricorni Dobzhansky & Pavan	701	39	59	45	207	7	58		1116	0.3135
D. dreyfusi Dobzhansky & Pavan	1				12	3			16	0.0045
D. fascioloides Dobzhansky & Pavan	1								1	0.0003
D. fumipennis Duda	1				10				11	0.0031
D. fuscolineata Duda					1				1	0.0003
D. griseolineata Sturtevant	5	4	4	5	17	1	13	1	50	0.0140
D. guarani Dobzhansky & Pavan	1								1	0.0003
D. immigrans Sturtevant	0						2		2	0.0006
D. maculifrons Duda				1					1	0.0003
D. medioimpressa Frota-Pessoa			2	1					3	0.0008
D. mediopicta Frota-Pessoa	17	2	68	24	8	2	39	6	166	0.0466
D. mediopunctata Dobzhansky & Pavan	20	2	24	6	8	4	21	7	92	0.0258
D. melanogaster Meigen					2			4	6	0.0017
D. mercatorum Patterson & Wheeler	0			1	9				10	0.0028
D. mesostigma Frota-Pessoa			4	8					12	0.0033
D. neocardini Streisinger				1					1	0.0003
D. neoelliptica Pavan & Magalhaes	4				3				7	0.0020

Continue

Table 5. Continuation.

Species	E1	E2	E3	E4	E5	E6	E7	E8	*ni*	*pi*
D. ornatifrons Duda			3				1	1	5	0.0014
D. paraguayensis Duda	93	17	32	23	20	45	15		245	0.0688
D. platitarsus Frota-Pessoa		26	5	5	2	2	3		43	0.0121
D. polymorpha Dobzhansky & Pavan	13		1	62	24		2		102	0.0287
D. prosaltans Duda	4		2						6	0.0017
D. repleta Wollaston	2								2	0.0006
D. nappae Vilela, Valente & Basso						14	9		23	0.0065
D. roehrae Pipkin & Heed	1								1	0.0003
D. schineri Pereira & Vilela	3				2				5	0.0014
D. simulans Sturtevant	1			2	10				13	0.0037
D. sturtevanti Duda	35				25			1	61	0.0171
D. tristriata Heed & Wheeler		1							1	0.0003
D. willistoni sp. subgroup Pavan	819	2	3	112	380		5	130	1451	0.4076
D. zottii Vilela	1								1	0.0003
Diathoneura brasiliensis Duda			1						1	0.0003
D. sp. 1	1								1	0.0003
Rhinoleucophenga obesa Loew	1						1		2	0.0006
Zygothrica orbitalis Sturtevant		1							1	0.0003
Total	1761	103	242	298	745	79	178	154	3560	1.0000

Table 6. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Serra do Tabuleiro - II (site F) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	1	F2	F3	F4	F5	F6	F7	F8	*ni*	*pi*
Cladochaeta bomplandi Coquillett		9					1		10	0.0033
D. angustibucca Duda	16		2						18	0.0060
D. sp. *arapuan* Cunha & Pavan or *araçai* Cunha & Frota-Pessoa						1			1	0.0003
D. atrata Burla & Pavan		2				1			3	0.0010
D. bandeirantorum Dobzhansky & Pavan	2		13	8			5		28	0.0093
D. bocainensis Pavan & Cunha	21	1				2	15		39	0.0130
D. bodemannae Pipkin & Heed		1							1	0.0003
D. briegeri Pavan & Breurer	1		9		14				24	0.0080
D. sp. (*cf.*) *caponei* Pavan & Cunha				3					3	0.0010
D. capricorni Dobzhansky & Pavan	630	15	23	85	96	10	108	27	994	0.3307
D. sp. (*cf.*) *colmenares* Hunter					1				1	0.0003
D. dreyfusi Dobzhansky & Pavan	6		2	4	22	19			53	0.0176
D. sp. (*cf.*) *fairchildi* Pipkin & Heed					1				1	0.0003
D. fascioloides Dobzhansky & Pavan	1								1	0.0003
D. fumipennis Duda			2		22	1			25	0.0083

Continue

Table 6. Continuation.

Species	1	F2	F3	F4	F5	F6	F7	F8	*ni*	*pi*
D. griseolineata Sturtevant		4	1	2	17		8	1	33	0.0110
D. immigrans Sturtevant				1			9		10	0.0033
D. maculifrons Duda								2	2	0.0007
D. medioimpressa Frota-Pessoa			4		10	7			21	0.0070
D. mediopicta Frota-Pessoa	13	6	39	43	25		31	21	178	0.0592
D. mediopunctata Dobzhansky & Pavan	7	3	14	3	40	10	135		212	0.0705
D. mediostriata Duda	2								2	0.0007
D. melanogaster Meigen				5					5	0.0017
D. mercatorum Patterson & Wheeler					1				1	0.0003
D. sp. (*cf.*) *mesophragmatica* Duda	1								1	0.0003
D. sp. (*cf.*) *mesostigma* Frota-Pessoa			12	17				2	31	0.0103
D. neocardini Streisinger				1			1	1	3	0.0010
D. neoelliptica Pavan & Magalhaes					2				2	0.0007
D. onca Dobzhansky & Pavan						1			1	0.0003
D. ornatifrons Duda							8	4	12	0.0040
D. paraguayensis Duda	110	129	17	18	55	44			373	0.1241
D. sp. (*cf.*) *mediopictoides* Heed & Wheeler						19			19	0.0063
D. platitarsus Frota-Pessoa		25	27	2	3	2			59	0.0197
D. polymorpha Dobzhansky & Pavan	3			44	8		5	2	62	0.0206
D. sp. (*cf.*) *nappae* Vilela, Valente & Basso						18			18	0.0060
D. roehrae Pipkin & Heed	2				12				14	0.0047
D. senei Vilela		1							1	0.0003
D. setula Heed & Wheeler		8							8	0.0027
D. simulans Sturtevant		1			17		1		19	0.0063
D. sturtevanti Duda	1			3	19		1		24	0.0080
D. sp. (*cf.*) *tristriata* Heed & Wheeler					2				2	0.0007
D. unipunctata Patterson & Mainland							1		1	0.0003
Diathoneura brasiliensis Duda		2							2	0.0007
Rhinoleucophenga obesa Loew			2						2	0.0007
Leucophenga sp.1							2		2	0.0007
D. willistoni sp. subgroup Pavan	280		5	204	186				675	0.2246
D. sp. 2	8								8	0.0027
Zygothrica orbitalis Sturtevant					1				1	0.0003
Total	1104	207	172	443	554	135	331	60	3006	1.0000

Table 7. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Arvoredo Island (site G) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	G1	G2	G3	G4	G5	G6	G7	G8	*ni*	*pi*
D. angustibucca Duda			1		1				2	0.0003
D. atrata Burla & Pavan				3	1				4	0.0006
D. sp. (*cf.*) *bodemannae* Pipkin & Heed					3				3	0.0004
D. capricorni Dobzhansky & Pavan	3	5	1			20			29	0.0043
D. cardinoides Dobzhansky & Pavan								1	1	0.0001
D. sp. (*cf.*) *fragilis* Wheeler					1				1	0.0001
D. fumipennis Duda	3			5					8	0.0012
D. griseolineata Sturtevant	2		1	20	180	12		2	217	0.0319
D. guaru Dobzhansky & Pavan					1				1	0.0001
D. hydei Sturtevant	2								2	0.0003
D. immigrans Sturtevant		2	1						3	0.0004
D. kikkawai Burla	5								5	0.0007
D. maculifrons Duda								12	12	0.0018
D. malerkotliana Parshad & Paika	694				23				717	0.1055
D. mediopicta Frota-Pessoa	8								8	0.0012
D. mediopunctata Dobzhansky & Pavan	5	3			15	32	1		56	0.0082
D. mediostriata Duda	3								3	0.0004
D. melanogaster Meigen	1				1			6	8	0.0012
D. mercatorum Patterson & Wheeler	7	5	4	12	5		3	115	151	0.0222
D. mesostigma Frota-Pessoa					4				4	0.0006
D. nebulosa Sturtevant	13		1					3	17	0.0025
D. neocardini Streisinger	16	5	3	11	5		3		43	0.0063
D. onca Dobzhansky & Pavan		5		3	2		2		12	0.0018
D. pallidipennis Dobzhansky & Pavan					1				1	0.0001
D. paraguayensis Duda	2			21	37	10			70	0.0103
D. platitarsus Frota-Pessoa					1				1	0.0001
D. polymorpha Dobzhansky & Pavan	53	81	48	32	23		12		249	0.0366
D. prosaltans Duda	1			1	1		4		7	0.0010
D. sellata Sturtevant	1	1	1		2		1		6	0.0009
D. serido Vilela & Sene	7	1		2					10	0.0015
D. simulans Sturtevant	184	449	411	93	690	5	164	41	2037	0.2998
D. sturtevanti Duda	31			18	11	3			63	0.0093
D. zottii Vilela			1						1	0.0001
Diathoneura brasiliensis Duda					2				2	0.0003
D. willistoni sp. subgroup Pavan	1817	83	63	221	155		23	560	2922	0.4301
S. latifasciaeformis Duda	3	1		1	1			4	10	0.0015
D. tripunctata sp. group Sturtevant				2					2	0.0003
D. sp.1				1			3		4	0.0006

Continue

Table 7. Continuation.

Species	G1	G2	G3	G4	G5	G6	G7	G8	*ni*	*pi*
D. sp. 2							1		1	0.0001
D. sp. 3							1		1	0.0001
Zaprionus indianus Gupta				17	75			6	98	0.0144
Zygothrica dispar Duda		1			1				2	0.0003
Total	2861	642	536	463	1242	82	218	750	6794	1.0000

Table 8. Absolute abundance (*ni*) and relative abundance (*pi*) of the collected species from Campeche Island (site H) at different seasons. The numbers after the site letter mean: 1 = autumn 1, 2 = winter 1, 3 = spring 1, 4 = summer 1, 5 = autumn 2, 6 = winter 2, 7 = spring 2 and 8 = summer 2.

Species	H1	H2	H3	H4	H5	H6	H7	H8	*ni*	*pi*
D. angustibucca Duda	2								2	0.0006
D. atrata Burla & Pavan	14	1		1	1	3		1	21	0.0060
D. bandeirantorum Dobzhansky & Pavan						9	1		10	0.0029
D. bocainensis Pavan & Cunha	1								1	0.0003
D. sp. (*cf.*) *bodemannae*Pipkin & Heed					1				1	0.0003
D. bromelioides Pavan & Cunha				8				1	9	0.0026
D. capricorni Dobzhansky & Pavan		3	9	1		19		3	35	0.0100
D. cardinoides Dobzhansky & Pavan	2		2						4	0.0011
D. fascioloides Dobzhansky & Pavan			1						1	0.0003
D. sp. (*cf.*) *fragilis* Wheeler							3		3	0.0009
D. griseolineata Sturtevant	1		18	12	2	1	37	5	76	0.0218
D. guaraja King						1	3		4	0.0012
D. guaru Dobzhansky & Pavan						1			1	0.0003
D. hydei Sturtevant			1		1			1	3	0.0009
D. immigrans Sturtevant	2			7		8	2		19	0.0055
D. kikkawai Burla					2	3			5	0.0014
D. malerkotliana Parshad & Paika	32				1				33	0.0095
D. mediopicta Frota-Pessoa	3		1			12			16	0.0046
D. mediopunctata Dobzhansky & Pavan	6	1	2		1	11			21	0.0060
D. mediostriata Duda	1			37	11				49	0.0141
D. melanogaster Meigen	17			4		18		110	149	0.0427
D. mercatorum Patterson & Wheeler	14			19	3	4	2	17	59	0.0169
D. neocardini Streisinger	6		3	49	18			1	77	0.0221
D. onca Dobzhansky & Pavan			7	3				4	14	0.0040
D. pallidipennis Dobzhansky & Pavan						4			4	0.0011
D. paraguayensis Duda	26		2	1	1	5	13	4	52	0.0149
D. neosaltans Pavan & Magalhaes							2		2	0.0006
D. polymorpha Dobzhansky & Pavan	50	11	28	23	22	197	10	31	372	0.1067
D. prosaltans Duda				1					1	0.0003

Continue

Table 8. Continuation.

Species	H1	H2	H3	H4	H5	H6	H7	H8	ni	pi
D. quadrum Wiedemann					1				1	0.0003
D. repleta Wollaston	1								1	0.0003
D. nappae Vilela, Valente & Basso						1			1	0.0003
D. sellata Sturtevant				1			2	2	5	0.0014
D. serido Vilela & Sene				3					3	0.0009
D. simulans Sturtevant	195	13	33	57	129	198	7	18	650	0.1865
D. sturtevanti Duda	1			4	4			4	13	0.0037
D. zottii Vilela				1					1	0.0003
Rhinoleucophenga obesa Loew	1	1	1				42		45	0.0129
Leucophenga sp.1	1	1							2	0.0006
D. willistoni sp. subgroup Pavan	152	72	239	196	271	267	61	435	1693	0.4857
D. sp 1							2		2	0.0006
Zaprionus indianus Gupta				4	15	5			24	0.0069
Zygothrica dispar Duda			1						1	0.0003
Total	528	103	348	432	484	767	187	637	3486	1.0000