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**ECOLOGIA DE ASSEMBLÉIAS
DE DROSOPHILIDAE (INSECTA, DIPTERA)
DE MANGUEZAIS DA ILHA DE SANTA CATARINA,
SUL DO BRASIL**

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sobre ombros de gigantes.

Isaac Newton.

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(E que desculpem minha miopia!)

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Sumário

Resumo	03
Abstract	04
Capítulo I	05
Introdução	06
Objetivos	15
Referências Bibliográficas	16
Capítulo II	25
Taxonomic survey of Drosophilidae (Insecta, Diptera) from mangrove forests of Santa Catarina Island, southern Brazil	
Resumo	28
Abstract	29
Introduction	30
Material and Methods	31
Results and Discussion	33
Literature Cited	46
Capítulo III	61
Ecology of assemblages of drosophilids (Diptera, Drosophilidae) in mangrove forests	
Abstract	63
Introduction	64
Material and Methods	66
Results	71
Discussion	74
References	82

Capítulo IV	98
Resultados e Discussão	99
Referências Bibliográficas	111
Anexos	115
Normas para publicação em Neotropical Entomology	116
Normas para publicação em Biological Journal of the Linnean Society	120

Resumo

Apesar de assembléias de drosófilos já terem sido estudadas em diversos ambientes, os manguezais ainda surgem como um ambiente inexplorado. Este trabalho teve como objetivo caracterizar as assembléias de drosófilos encontradas nos manguezais da ilha de Santa Catarina, sul do Brasil. Para isso, foram realizadas 28 coletas nos três principais manguezais da ilha – Itacorubi (13 coletas), Tavares (8 coletas) e Ratones (7 coletas) - entre o período de julho de 2002 e julho de 2005. Um total de 82.942 espécimes foi analisado, distribuídos em 69 espécies de seis gêneros. Foi encontrada uma grande dominância de *Drosophila simulans* Sturtevant, seguida por *D. malerkotliana* Parshad & Paika, *Zaprionus indianus* Gupta, *D. mediostriata* Duda, *D. willistoni* Sturtevant, *D. paulistorum* Dobzhansky & Pavan, *D. repleta* Wollaston, *D. polymorpha* Dobzhansky & Pavan e *D. mercatorum* Patterson & Wheeler. As demais espécies não atingiram 1% de abundância relativa. Não foram encontradas diferenças importantes entre os locais, mas as diferenças sazonais foram relevantes. A dinâmica populacional de várias espécies pareceu estar relacionada, experimentando picos de abundância no outono, embora haja algumas exceções importantes. O número de indivíduos e a riqueza de espécies observada também foram mais elevados nesta estação, mas a eqüitabilidade e a riqueza de espécies estimada por rarefação se mostraram mais elevadas no inverno. No entanto, algumas importantes variações temporais pareceram não ser relacionadas a fatores que operam sazonalmente. A composição das assembléias pareceu sofrer uma pequena modificação quando são comparadas as amostras de verão e outono com as de inverno e primavera. As assembléias de outono apresentaram uma estrutura típica, caracterizada pela abundância aumentada de *D. malerkotliana*, enquanto as demais estações se assemelharam mais aos períodos adjacentes do que aos mesmos períodos de anos diferentes.

Abstract

Notwithstanding assemblages of drosophilids have already been surveyed in different kinds of environments, mangrove forests are still an unstudied environment. The present work aimed to characterise the assemblages of drosophilids found in the mangrove forests of Santa Catarina Island, southern Brazil. It was based on 28 samples taken from the three main mangrove forests of the Island – Itacorubi (13 samples), Tavares (8 samples) and Ratones (7 samples) – in the period between July 2002 and July 2005. In total, 82.942 specimens were analysed, belonging to 69 species and six genera. A high dominance of *Drosophila simulans* Sturtevant was found, followed by *D. malerkotliana* Parshad & Paika, *Zaprionus indianus* Gupta, *D. mediostriata* Duda, *D. willistoni* Sturtevant, *D. paulistorum* Dobzhansky & Pavan, *D. repleta* Wollaston, *D. polymorpha* Dobzhansky & Pavan and *D. mercatorum* Patterson & Wheeler. Other species did not reach 1% of relative abundance. There was no important difference among sites, but seasonal differences were high. Population dynamics of many species seemed to be related, presenting abundance peaks in autumn, despite some important exceptions. The number of individuals and the observed species richness were higher in this season as well, while evenness and species richness estimated by rarefaction were higher in winter. In the other hand, some temporal variations appeared not to be related to seasons. The composition of the assemblages seemed to experience a slight modification when compared samples of summer and autumn with samples of winter and spring. Assemblages of autumn showed a typical structure, characterised by the increased abundance of *D. malerkotliana*, while structure of other seasons were more similar to adjacent periods, rather than to the same season in subsequent years.

CAPÍTULO I

Introdução

Os drosofilídeos formam uma família de moscas de pequeno porte que, especialmente nas regiões tropicais, compõe associações onde muitas espécies coexistem em um mesmo habitat. Ecologicamente, Carson (1971) define esses organismos como consumidores primários de microrganismos, principalmente leveduras, associados a frutos em estágios iniciais de decomposição.

A ciência tem dirigido bastante atenção a estes organismos. Pavan (1959) sugere que nenhum outro animal além do homem tenha sido alvo de tantos estudos como as moscas do gênero *Drosophila*. Remsen & O'Grady (2002) chegam a apontar *Drosophila melanogaster* Meigen como forte candidato ao título de organismo eucarionte mais amplamente pesquisado.

De fato, *Drosophila* se tornou o animal preferido do geneticista com os trabalhos clássicos da equipe de Thomas Morgan, no começo do século XX, quando foram desvendados aspectos cruciais da teoria cromossômica e da hereditariedade. A seguir, desempenhou papel central no estudo de princípios genéticos de transmissão dos caracteres, ligação cromossônica, efeitos da radiação, interação gênica, fenocópias, aberrações cromossômicas, mudanças evolutivas em populações e muitos outros estudos em genética, biologia celular e evolução (Freire-Maia & Pavan, 1949; Strickberger, 1962). Mais recentemente, o gênero *Drosophila* vem sendo promissor também na genômica (Rubin & Lewis, 2000), em estudos filogenéticos (Grimaldi, 1990; Remsen & O'Grady, 2002) e como modelo para estudos de genética do comportamento, desenvolvimento e até de doenças humanas (Ferveur, 2003).

Entretanto, Remsen & O'Grady (2002) chamam a atenção de que, apesar de seu freqüente uso em pesquisas biológicas, muitos cientistas não estão cientes de que a família Drosophilidae contém aproximadamente 65 gêneros, dos quais *Drosophila* é apenas um deles. Compreendendo mais de 3800 espécies (Bächli, 2006) descritas, esta família possui ecologia muito mais variada do que denota seu nome vulgar “moscas-das-frutas”. Além da preferência das larvas e adultos dos representantes mais conhecidos da família por frutos carnosos e

algumas flores e fungos, alguns de seus membros desenvolvem-se em guano de morcego (Tosi *et al.*, 1990), cladódios de cactos (Carson, 1971; Mizuguchi, 1978; Vilela, Pereira & Sene, 1983), carcaças de insetos e carne (Lachaise & Tsacas, 1983), fluxos de seiva e material vegetal em decomposição (Carson, 1971) ou exibem comportamento predatório (de homópteros ou larvas aquáticas de mosquitos), comensal (de caranguejos, aranhas, abelhas e homópteros), parasitário (de homópteros e de lagartas de lepidópteros) e até de canibalismo, no caso de larvas que se encontram em um recurso superpopulado (Carson, 1971; Ashburner, 1981; Lachaise & Tsacas, 1983).

A família Drosophilidae teve sua origem nas regiões tropicais, há cerca de 50 milhões de anos, e hoje tem representantes espalhados por todo o globo, de regiões equatoriais a temperadas, do nível do mar a grandes altitudes (Throckmorton, 1975). Taxonomicamente, é incluída na ordem Diptera, subordem Brachycera, infra-ordem Muscomorpha, divisão Schizophora, seção Acalyptratae e superfamília Ephydrioidea (Borror, Triplehorn & Johnson, 1992).

Como o estudo dos drosófilídeos é tradicionalmente ligado à genética, o conhecimento da ecologia e da taxonomia desses insetos foi, em grande escala, construído por geneticistas. Ecólogos e taxonomistas especializados no grupo surgiram mais recentemente. A taxonomia, feita inicialmente apenas através da morfologia externa, desenvolveu, no decorrer do tempo, técnicas mais elaboradas, como o uso da genitália masculina para diferenciação do grande número de espécies crípticas (Hsu, 1949; Vilela & Bächli, 1990).

Carson (1971) relata que, na década de 1940, *Drosophila* era vista com descrédito nos estudos ecológico-evolutivos. No entanto, este autor afirma estar convencido de que este é o organismo ideal para se desvendar os mecanismos da evolução. Apesar de tão amplamente estudados, ou talvez exatamente por isso, novas aplicações para os drosófilídeos na ciência não faltam. Alguns avanços têm sido feitos utilizando-se esses organismos na discussão sobre nichos ecológicos (Shorrocks, 1974), competição (Gilpin, Carpenter & Pomerantz, 1986; Shorrocks, 1991; Budnik *et al.*, 2001) mecanismos de coexistência de espécies (Atkinson & Shorrocks, 1981; Sevenster & van Alphen,

1993; Krijger, 2000), estresse climático (Parsons, 1989; Hoffmann *et al.*, 2003), biogeografia de ilhas (Jaenike, 1978), seleção (revisão em Harshman & Hoffmann, 2000), dispersão (Fontdevila & Carson, 1978) e colonização de novos ambientes por espécies exóticas (Brncic & Budnik, 1988; Tidon, Leite & Leão, 2003; Silva *et al.*, 2005a, b).

Outro motivo que vem atraindo a atenção para o estudo da ecologia de drosófilídeos é que esse grupo de animais preenche relativamente bem os critérios necessários para utilização como organismos bioindicadores de monitoramento ambiental, como os formulados por Pearson (1994): especialização ao habitat, taxonomia estável e bem conhecida, fácil manipulação e observação, biologia e história natural bem conhecidas, padrões de resposta refletidos em outros táxons, ampla distribuição geográfica e potencial econômico. Alguns resultados interessantes foram obtidos estudando-se drosófilídeos como bioindicadores de fragmentação de habitats (Martins, 2001), de urbanização (Avondet *et al.*, 2003) e de poluição do ar (Lucchese, Flores & Valente, 2002). Parsons (1991) observa ainda o potencial do grupo como bioindicador de mudanças climáticas globais.

Cunha & Magalhães (1965) já salientavam que é importante se estudar drosófilas tropicais para poder comparar organismos de um mesmo grupo vivendo em ambientes que oferecem condições bastante diversas. Com o passar de décadas, a ecologia de comunidades de drosófilídeos consolidou-se como uma linha de pesquisa fértil. Krijger (2000) defende que tais comunidades constituem excelentes modelos para o estudo do impacto da heterogeneidade ambiental sobre a diversidade de espécies.

Segundo Roughgarden & Diamond (1986), há muitas definições de comunidade. A mais inclusiva delas congrega todos os organismos que vivem juntos em uma determinada área. Este conceito é normalmente restringido de diversas formas, seja por critérios temporais, espaciais, tróficos ou taxonômicos. Este último critério é o que usamos para definir o termo assembléia no presente trabalho.

Para Diamond (1986), a ecologia de comunidades procura entender a abundância e a distribuição das espécies, que dependem de variáveis que são controladas por fatores físicos e bióticos. Compreender esses processos não é tarefa fácil, pois as respostas que se encontram nunca são universais. Krijger (2000) relata que explicar a diversidade de espécies de um local ainda representa um dos maiores desafios para a ciência e que os fatores e processos que mantém o número de espécies em uma dada localidade, na maior parte dos sistemas biológicos, ainda são desconhecidos.

Apesar das dificuldades, estudos sobre comunidades têm fornecido importantes contribuições para a compreensão da ecologia e da evolução dos grupos estudados (Begon, Harper & Townsed, 1990). Segundo Magurran (1988), a diversidade específica de uma comunidade está entre os parâmetros mais importantes para a determinação de seus elementos estruturais. Além disso, o levantamento do número de espécies nos permite descrever uma comunidade e compará-la com outra em função de sua riqueza de espécies (Begon *et al.*, 1990).

Shorrocks & Sevenster (1995) defendem que comunidades de drosófilídeos são dominadas por agregação intra-específica e não são saturadas. Petersen (1960) salienta que muitas espécies apresentam sazonalidade pronunciada. Benado & Brncic (1994), em um estudo de oito anos, mostraram que essas variações podem ser cíclicas. No entanto, a detecção de padrões nem sempre é fácil. Pipkin (1953) mostrou que variações irregulares podem ocorrer dependendo das variações no suprimento de recursos alimentares. Wolda (1992) afirma que o tamanho das populações de muitos insetos em florestas tropicais não permanece dentro de limites restritos, mesmo em locais inalterados e estáveis. Greig-Smith (1989) apresenta evidências da falta de organização das comunidades, sendo que, em muitos casos, sua composição pode ser bastante influenciada pelo simples acaso. Diante de tantas dificuldades, Gilpin *et al.* (1986) afirmam que o estudo de comunidades de drosófilídeos pode ser bastante importante como modelo para se entender a

competição e seus mecanismos, a amplitude de nicho das espécies e as respostas a mudanças ambientais.

A ecologia de drosofilídeos no Brasil começou no início da década de 1940, com a vinda do famoso evolucionista Theodosius Dobzhansky, quando, então, se formou uma equipe de especialistas no país. Datam deste período inicial trabalhos que mais tarde se tornariam clássicos para os drosófilistas brasileiros, como os de Dobzhansky & Pavan (1943), Freire-Maia & Pavan (1949), Dobzhansky & Pavan (1950), Frota-Pessoa (1954) e Pavan (1959), que incluem descrições de um grande número de espécies, grandes levantamentos taxonômicos, chaves de identificação e diversas abordagens ecológicas.

A fauna de drosofilídeos brasileira é riquíssima em número de espécies e em variações regionais na distribuição destas (Val, Vilela & Marques, 1981). A grande extensão territorial, a enorme biodiversidade e a variedade de ambientes torna esta linha de pesquisa atrativa ao se comparar comunidades que se estabelecem em diferentes locais. Trabalhos incluindo grandes extensões do território brasileiro foram realizados por Pavan (1959) e Sene *et al.* (1980). O primeiro deles fez várias abordagens ecológicas em diversas localidades do Brasil, enquanto o segundo englobou os domínios Mata Atlântica, Caatinga e Cerrado, incluindo áreas de dunas, restingas, o Pantanal e as bordas do Chaco.

Outros trabalhos concentraram-se em ambientes mais restritos. Abundante número de publicações dá atenção à mata atlântica, em especial nos estados do Rio Grande do Sul e de São Paulo. No Rio Grande do Sul, um importante estudo pioneiro foi o de Petersen (1960), que mais tarde foi seguido por Brncic & Valente (1978), Araújo & Valente (1981), Franck & Valente (1985), Valente & Araújo (1991), Saavedra *et al.* (1995), entre outros, que observaram variações temporais na composição das assembleias estudadas em várias regiões deste estado e determinaram alguns recursos utilizados como sítio de ovoposição. O estado de São Paulo foi extensamente estudado com as coletas de Dobzhansky & Pavan (1950) e Pavan (1959). Mais recentemente, Val & Kaneshiro (1988), trabalhando na Estação Biológica de Boracéia, estimaram a presença de 152 espécies naquele local. Já Tidon-Sklorz & Sene (1992)

focalizaram variações verticais na distribuição de drosófilídeos em uma floresta mesófila semidecídua no interior do estado. Apesar de esta ser a região mais bem estudada do País, Medeiros & Klaczko (2004) estimaram que metade das espécies existentes ainda permanece sem ser descrita.

Os primeiros estudos regulares no estado de Santa Catarina também pesquisaram a mata atlântica. De Toni & Hofmann (1995) realizaram o primeiro levantamento taxonômico em uma localidade da ilha de Santa Catarina, que foi seguido por estudos mais aprofundados englobando o continente próximo e outras ilhas (De Toni, 1998 e 2002). Estes estudos também verificaram os substratos de ovoposição que estavam sendo utilizados pelos drosófilídeos. Após tais estudos, sucederam-se os de Gottschalk (2002 e 2004) e Oliveira (2004), na ilha de Santa Catarina, e de Döge (2003), em Joinville.

A característica mais marcante evidenciada por estes trabalhos sobre as assembleias de drosófilídeos na mata atlântica é a dominância do grupo *willistoni* de *Drosophila*, em especial do subgrupo *willistoni*, além de outras espécies nativas.

Outro ambiente que vem sendo estudado é o urbano. Vários aspectos da ecologia de assembleias urbanas de drosófilídeos foram estudados em Olímpia (SP), por Bélo & Oliveira-Filho (1976 e 1978), Bélo & Gallo (1977), Bélo & Lemos (1978) e Bélo (1979). Trabalhos mais recentes foram realizados em Montevidéu (Uruguai) por Goñi, Martinez & Daguer (1997), em Porto Alegre (RS), por Silva *et al.* (2005a), em Brasília (DF), por Ferreira & Tidon (2005) e em Florianópolis (SC), por Gottschalk (2002 e 2004). Estes trabalhos evidenciam o predomínio de espécies exóticas no ambiente urbano, em especial as do grupo *melanogaster* de *Drosophila* e, mais recentemente, da invasora *Zaprionus indianus* Gupta.

Entre os ambientes estudados também se encontra o Cerrado, em trabalhos como os de Tidon-Sklorz *et al.* (1994) e Vilela & Mori (1999), na Serra do Cipó, e Tidon-Sklorz & Sene (1995), na Cadeia do Espinhaço. Posteriormente, Tidon (2006) comparou as assembleias de drosófilídeos presentes no cerrado *sensu stricto* e nas florestas de galeria.

Tidon-Sklorz & Sene (1995) também estudaram a caatinga e Mizuguchi (1978) pesquisou os substratos de ovoposição utilizados pelos drosófilídeos neste ambiente.

A Amazônia foi estudada por Martins (1987, 1995 e 2001). Nestes trabalhos, a autora pesquisou variações temporais e espaciais na distribuição de drosófilídeos, a exploração dos frutos de *Parahancornia amapa* (Huber) Ducke por estes insetos e o efeito da fragmentação da floresta sobre essas assembleias.

Além disso, a mata de araucárias e os campos sulinos receberam a atenção de Saavedra *et al.* (1995), no Rio Grande do Sul, enquanto o Chaco foi estudado por Vilela, Sene & Pereira (1980), na Argentina, o Pantanal por Val & Marques (1996) e a restinga por Bizzo & Sene (1982) em Peruíbe (SP) e Bizzo (2005) em Florianópolis (SC).

Embora estejam presentes nos litorais tropicais de todo o globo, os manguezais receberam pouca atenção quanto ao estudo sobre assembleias de drosófilídeos, mesmo no Brasil, país detentor da segunda maior área de manguezais do mundo. Talvez algumas características peculiares desta floresta tenham desestimulado tais pesquisas. A baixa diversidade florística parece não fornecer aos drosófilídeos grande variedade de recursos e o solo periodicamente alagado por água salgada pode ser um obstáculo a mais para esses insetos.

No entanto, Schmitz (2004) mostrou a ocorrência de 40 espécies de drosófilídeos no manguezal do Itacorubi, em Florianópolis (SC). Neste estudo, foi observado que a assembleia do local é dominada por espécies generalistas e há evidências de que o manguezal possa ser bastante vulnerável à invasão por indivíduos provindos dos ambientes adjacentes, em especial da cidade. Entre as espécies mais comuns no local estão *Drosophila simulans* Sturtevant, uma espécie exótica comum em ambientes alterados, *D. willistoni* Sturtevant, típica de ambientes de mata e *D. mediostriata* Duda, rara em outros locais. Além dos drosófilídeos, este autor encontrou grande número de curtonotídeos, um grupo de moscas proximamente relacionado a Drosophilidae e não encontrado em outros locais até então pesquisados na ilha de Santa Catarina.

Este ecossistema é constituído por uma floresta muito peculiar, situada nas planícies entremarés e possuindo fauna e flora com adaptações bastante curiosas para a sobrevivência em um local com características tão únicas, como as periódicas inundações, a salinidade, o solo instável e pouco oxigenado e a ação mecânica da água (Cintrón & Schaeffer-Novelli, 1980; Lacerda, 1984). A baixa diversidade florística dos manguezais se torna ainda mais pronunciada nos extremos da distribuição deste ecossistema, já que algumas espécies vegetais restringem-se aos trópicos e não alcançam latitudes mais altas como as de Santa Catarina, que se encontra em uma região subtropical. Neste estado, apenas três espécies de árvores habitam o interior dos manguezais: *Avicennia schaueriana* Stapf & Leechman (Verbenaceae), *Laguncularia racemosa* (L.) (Combretaceae) e *Rhizophora mangle* L. (Rhizophoraceae) (Souza Sobrinho, Bresolin & Klein, 1969; Souza *et al.*, 1994; Meloni, 2003).

Por sua localização costeira, os manguezais sofrem uma acelerada devastação em todo o mundo, com taxas de desmatamento muito superiores às das demais florestas tropicais, tão comuns na mídia. Um dado preocupante é o de que cerca de um terço dos manguezais do mundo foram perdidos nas últimas duas décadas (Valiela, Bowen & York, 2001).

Os manguezais impõem condições bastante distintas daquelas encontradas em outros ambientes, o que torna interessante a comparação das assembleias de drosófilídeos que vivem nesses locais. A necessidade de se estudar qualquer aspecto relativo aos manguezais torna-se mais evidente quando se considera o rápido processo de desmatamento e as fortes pressões antrópicas que tal tipo de floresta vem sofrendo. Encontrar drosófilídeos, insetos terrestres e associados à vegetação, em um ambiente tão pobre floristicamente e localizado no encontro da terra com o mar pode parecer surpreendente, mas retrata a versatilidade ecológica e a onipresença deste grupo de insetos. Analisar de modo mais profundo as assembleias de drosófilídeos que se estabelecem neste ambiente, além de contribuir para o conhecimento da ecologia desses organismos, pode servir como fonte de dados para um conhecimento mais aprimorado da diversidade, da biogeografia e dos

processos ecológicos envolvidos na formação da composição e da estrutura das comunidades.

Objetivos

Objetivo geral:

Caracterizar as assembléias de drosófilídeos existentes nos manguezais da ilha de Santa Catarina.

Objetivos específicos:

- Levantamento taxonômico das espécies de drosófilídeos que habitam os manguezais da ilha de Santa Catarina;
- Caracterização da estrutura das assembléias de drosófilídeos presentes nestes manguezais, através de aspectos como diversidade e abundância relativa de cada espécie;
- Investigar a variação espacial existente quanto à composição e estrutura das assembléias de drosófilídeos entre os três manguezais estudados, relacionando-a com as características de cada local;
- Acompanhar a variação temporal das assembléias e da abundância das espécies que as compõem no período estudado.

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CAPÍTULO II

(Artigo submetido ao periódico *Neotropical Entomology*)

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Taxonomic Survey of Drosophilidae (Insecta, Diptera)

from Mangrove Forests of Santa Catarina Island, Southern Brazil

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**Taxonomic Survey of Drosophilidae (Insecta, Diptera)
from Mangrove Forests of Santa Catarina Island, Southern Brazil**

Levantamento Taxonômico de Drosophilidae (Insecta, Diptera) de Manguezais da Ilha de Santa Catarina, Sul do Brasil

RESUMO – Assembléias de drosofilídeos têm sido caracterizadas em vários ambientes no Brasil, como mata atlântica, áreas urbanas, cerrados, caatingas, floresta amazônica e outros. Este trabalho é a primeira tentativa em caracterizar a fauna de Drosophilidae nos manguezais, um ambiente presente nos litorais tropicais de todo o mundo. Vinte e oito amostras foram coletadas nos três principais manguezais da ilha de Santa Catarina, sul do Brasil, utilizando-se armadilhas com isca de banana suspensas em árvores. As amostras foram obtidas nos meses de janeiro (verão), abril (outono), julho (inverno) e outubro (primavera), no período entre julho de 2002 e julho de 2005. Um total de 82.942 indivíduos foi coletado, incluindo 69 espécies de seis gêneros – *Amiota* Loew, *Drosophila* Fallen, *Leucophenga* Mik, *Scaptodrosophila* Duda, *Zaprionus* Coquillett e *Zygothrica* Wiedemann. Mostrou-se marcante a alta abundância de *D. simulans* Sturtevant, com alguns picos pronunciados de *D. malerkotliana* Parshad & Paika nas amostras de outono. Outras espécies comuns foram *Zaprionus indianus* Gupta, *D. mediotriata* Duda e *D. willistoni* Sturtevant. Também foram coletados 45.826 espécimes da família Curtonotidae, grupo irmão de Drosophilidae, virtualmente ausente em outros ambientes. As assembléias de drosofilídeos mostraram-se bastante homogêneas entre os três manguezais pesquisados, apesar das diferenças nos ambientes que os circundam. Em geral, as espécies encontradas nos manguezais são as mesmas encontradas nos ambientes vizinhos, porém suas abundâncias são bastante modificadas, sugerindo que várias espécies estejam respondendo diferentemente às pressões ambientais em ação nos manguezais, que podem ser mais restritivas para algumas do que para outras.

PALAVRAS-CHAVE: Biodiversidade, fauna de manguezais, assembléias de insetos, *Drosophila*, *Zaprionus*.

ABSTRACT – Assemblages of drosophilids have been characterised in several environments of the Brazilian territory, like Atlantic Rain Forest, urban areas, *cerrados*, *caatingas*, Amazon Forest and others. The present survey is the first attempt to characterise the fauna of Drosophilidae in mangrove forests, an environment present in tropical coasts of the whole world. Twenty-eight samples were collected from the three main mangrove forests of Santa Catarina Island, southern Brazil, using banana-baited traps hung in trees. The samples were taken in January (summer), April (autumn), July (winter) and October (spring), in the period between July 2002 and July 2005. In total, 82,942 specimens of drosophilids were caught, belonging to 69 species of six genera – *Amiota* Loew, *Drosophila* Fallen, *Leucophenga* Mik, *Scaptodrosophila* Duda, *Zaprionus* Coquillett and *Zygothrica* Wiedemann. It was remarkable the high abundance of *D. simulans* Sturtevant, with some notable peaks of *D. malerkotliana* Parshad & Paika in autumn samples. Other common species were *Zaprionus indianus* Gupta, *D. mediotriata* Duda and *D. willistoni* Sturtevant. We also collected 45,826 flies of family Curtonotidae, sister-group of Drosophilidae and virtually absent in other environments. The assemblages of drosophilids were very similar in the three mangrove forests surveyed, despite differences of the surrounding environments. In general, the same species found in the neighbouring environments were sampled, but with different abundances, suggesting that environmental pressures operating in the mangroves are perceived as more restrictive for some species than for others.

KEY-WORDS – Biodiversity, fauna of mangroves, insect assemblages, *Drsoophila*, *Zaprionus*.

The family Drosophilidae comprises more than 3,800 species (Bächli 2006) of small flies widespread throughout the world, in a variety of climates and environments. The best known members of the family are defined by Carson (1971) as primarily consumers of the micro-organisms, yeasts and bacteria, which are associated with the initial stages of decaying plant materials. Although these flies have emerged as a paradigm organism to a great amount of researches, most of the ecological features of their natural populations and assemblages are poorly known.

Researches on species of drosophilids in Brazil had their start in the 1940's, when Theodosius Dobzhansky first visited Brazil and a research program on Neotropical species of *Drosophila* was established (Pavan & Cunha 2003). Later on, many descriptions of new species, taxonomic surveys and studies on genetics and chromosomal polymorphism were carried out. In addition, several aspects of the ecology of these flies were investigated.

In the subsequent decades, assemblages of drosophilids were characterised in a variety of environments of the Brazilian territory. The best studied environment is Atlantic Rain Forest, especially in the states of São Paulo (Dobzhansky & Pavan 1950, Pavan 1959, Val & Kaneshiro 1988, Tidon-Sklorz & Sene 1992, Medeiros & Klaczko 2004) and Rio Grande do Sul (Petersen 1960, Brncic & Valente 1978, Araújo & Valente 1981, Franck & Valente 1985, Valente & Araújo 1991, Saavedra *et al.* 1995). The urban environment was also examined by Bélo & Oliveira-Filho (1976, 1978), Bélo & Gallo (1977), Bélo & Lemos (1978) and Bélo (1979), in Olímpia, São Paulo, and, after, by Goñi *et al.* (1997), in Montevideo (in Uruguay), Silva *et al.* (2005) in Porto Alegre, Rio Grande do Sul, and Ferreira & Tidon (2005) in Brasília, Distrito Federal. In recent years, the *Cerrado* of Central Brazil have received attention from Tidon-Sklorz *et al.* (1994), Tidon-Sklorz & Sene (1995), Vilela & Mori (1999) and Tidon (2006). *Caatinga* was also target of some studies (Mizuguchi 1978, Tidon-Sklorz & Sene 1995) as well as *Pantanal* (Val & Marques 1996) and *restingas* (Bizzo & Sene 1982). Furthermore, Amazon forest was studied by Martins (1987, 1989,

2001) and Chaco (in Argentina) was surveyed by Vilela *et al.* (1980), while Saavedra *et al.* (1995) included the southern grasses and the forest with *Araucaria* in their researches.

In Santa Catarina state, besides a few earlier collections, this area of research was effectively inaugurated by De Toni & Hofmann (1995), who studied a site covered by Atlantic Rain Forest in Santa Catarina Island. After that, these authors and his colleagues established a research group interested in assemblages of drosophilids in different environments of Santa Catarina state, studying Atlantic Rain Forest, urban environment, *restinga* and, with the present paper, mangrove forests. This last environment is a *terra incognita* on the knowledge of ecology of Drosophilidae. Present in tropical and subtropical coasts around the world, at the intertidal plains, they form a very peculiar forest, subjected to the flood of tides, instable soil and salinity. Such harsh conditions lead to a low diverse but exclusive flora, and the encounter of marine and terrestrial faunas. Finding drosophilids in this environment may be surprising, but reflects the versatility and ubiquity of these insects. The present work comes as the first effort to know the assemblages of drosophilids in such environment.

Material and Methods

The samples were collected from the three main mangrove forests of Santa Catarina Island: Itacorubi ($27^{\circ}34'34''S$; $48^{\circ}31'23''W$), a forest situated inside the most populated urban zone of the city of Florianópolis; Tavares ($27^{\circ}39'13''S$; $48^{\circ}32'12''W$), bordered by regions of medium level of urbanisation, pastures and some forested areas; and Ratones ($27^{\circ}27'45''S$; $48^{\circ}30'28''W$), located in Estação Ecológica de Carijós, an area where the mangrove is the main component of a complex vegetation, within a mosaic of Atlantic forest, *restingas*, fresh-water marshes and transitional formations. The climate of the region is type cfa of Köeppen (1948), i. e., subtropical with hot summer, the temperatures of summer above $22^{\circ}C$ and precipitation superior to 30mm in the driest month.

The mangrove forests of Santa Catarina Island have similar vegetation composition. The forests are very homogeneous, dominated by *Avicennia schaueriana* (Verbenaceae), and having also *Laguncularia racemosa* (Combretaceae) and *Rhizophora mangle* (Rhizophoraceae) (Souza Sobrinho *et al.* 1969). These three species are the only plants that inhabit the interior of the woods, forming a forest with almost no stratification, canopy not thick or continuous, relatively open and well lit. The soil is muddy, salty, wet and periodically flooded by the tides. Owing to the low floristic diversity and the particularities of the environment, the mangrove forests seem to offer few food resources and harsh abiotic conditions to the drosophilid fauna.

The sampling method consisted of capturing adult flies with banana-baited traps (Tidon & Sene 1988). In each collection, 5kg of banana were mashed, seeded with baker's yeast and distributed in 50 traps, which were hung in trees, at around 1.5m above the ground, and kept there for 3-4 days.

The collections were done in the months of January (summer), April (autumn), July (winter) and October (spring). Itacorubi was sampled between July 2002 and July 2005 (13 collections), Tavares from October 2003 until July 2005 (8 collections) and Ratones between January 2004 and July 2005 (7 collections). Flies were identified by external morphology and male terminalia, consulting specialised literature (Freire-Maia & Pavan 1949, Breuer & Pavan 1950, Malogolowkin 1952, Wheeler 1952, Frota-Pessoa 1954, Burla 1956, Magalhães & Björnberg 1957, Bock & Wheeler 1972, Val 1982, Vilela 1983, Vilela 1984, Vilela & Val 1985, Grimaldi 1987, Pereira & Vilela 1987, Vilela & Bächli 1990, Vilela 1992, Bächli *et al.* 2000, Vilela & Bächli 2000). Females of sibling species were separated in culture tubes for analysing their male offspring. For analyses of male terminalia (and in some cases female spermathecae) the flies were prepared with potassium hydroxide (KOH) 10% and acid fuchsin, and dissected in glycerol (Wheeler & Kambyellis 1966).

Voucher specimens of the material collected were deposited at Museu de Ciências Naturais of Fundação Zoobotânica, in Porto Alegre.

Results and Discussion

A total of 82,942 drosophilid flies were collected in all the samples done, distributed in 69 species of six genera. Table 1 shows the complete species list and the sites where each of them was found. It was found 51 species in Itacorubi, 48 in Tavares and 45 in Ratones. Though, these values may be result of the different number of samples.

Besides the drosophilids, we collected 45,826 specimens of flies belonging to Curtonotidae, a related family, considered sister-group of Drosophilidae by Grimaldi (1990). Taken altogether, drosophilids and curtonotids totalised 128,768 individuals, being 65% Drosophilidae and 35% Curtonotidae. In some occasions, the number of curtonotids even surpassed the number of drosophilids. The presence and the impressive abundance of these flies may be considered an exclusive characteristic of mangrove forests, because they were not collected in other environments surveyed by our research team. As this taxon is not the scope of the present work, it will be treated in a further paper.

Figures 1 to 3 summarises the structure of all the samples taken, with the relative abundance of the most common species (that reached 10% in at least one sample), in each locality. It was remarkable the high abundance of *D. simulans*, with some notable peaks of *D. malerkotliana*, *D. mediostriata* and *D. sgr. willistoni*. Except for the samples of April (autumn), characterised by the increased abundance of *D. malerkotliana*, the other seasons did not show typical patterns. *D. mediostriata* has very irregular oscillations, while *D. sgr. willistoni* and *D. repleta* seemed to show differences more related to inter-year variations.

Below, it is discussed some information about each taxa collected. The order of the taxa follows the same criteria of table 1, organised alphabetically within the higher taxonomic categories.

Subfamily Drosophilinae

Genus *Drosophila*

Fifty-eight out of the 69 species collected belong to genus *Drosophila*. It is the most diverse genus of Drosophilidae and also the best studied and most attracted to banana-baited traps. A total of 78,484 individuals of this genus were caught, consisting of almost 95% of the sample, distributed in four subgenera.

Subgenus *Dorsilopha*

This subgenus comprises only three species of *busckii* group. All of them have Oriental origin, but *D. busckii* achieved status of cosmopolitan and is present in Neotropical region.

busckii group

Sixteen individuals of *D. busckii* were collected. This species is mostly found associated with man, being rare in natural environments of South America (Val *et al.* 1981), very generalist (Carson 1971) and well adapted to low temperatures (Goñi *et al.* 1998).

Subgenus *Drosophila*

This is the most diverse subgenus of genus *Drosophila*. Thirty-six of the species found belong to it, distributed in 11 groups, besides two ungrouped species. On the other hand, it comprised just about 9% of the individuals collected, being the majority of the species, rare.

annulimana group

Three species of this group were caught, but in low numbers. *D. schineri* is known only for Brazil and was represented by three specimens. The other two species caught, *D. annulimana* and *D. arassari*, are found preferentially in forests (Val *et al.* 1981). The former is widespread in South

America and was represented by two individuals. A single specimen of *D. arassari* was collected. This species is distributed only in south-eastern and southern Brazil and in Uruguay. It is found rather in high altitudes (Val *et al.* 1981), but in the southern part of its distribution, it can be caught in lower altitudes, as in Uruguay (150m) (Goñi *et al.* 1998) and Santa Catarina Island (300m) (De Toni & Hofmann 1995). In the present work, it was captured at sea level, during winter.

bromeliae group

Just one species of this group was caught: five specimens of *D. bromelioides*. This is a widespread species in Brazil but is only occasionally attracted to banana baits. On the other hand, it is quite common in flowers (Frota-Pessoa 1952, Schmitz & Hofmann 2005). Contrasting to its rarity in our trap samples, a great number of individuals were reared from flowers of *Hibiscus tiliaceus*, *Ipomoea cairica* and *I. aff. chilantha*, collected in the borders of the mangroves, even in Itacorubi, where it was absent in the traps.

cardini group

The four collected species belonging to this group are widespread in Neotropics. The most common was *D. polymorpha*, which is relatively abundant in many kinds of environments, except in the driest ones (Sene *et al.* 1980). A total of 853 individuals of this species were collected, comprising 1% of the sample, with maximums of 6% in some collections. Besides it, *D. neocardini* was represented by 44 specimens, while *D. cardini*, a species better adapted to driest environments (Vilela *et al.* 2002) counted with 24 individuals. The rarer species was *D. cardinoides*, with only four individuals.

calloptera group

Two individuals of *D. atrata* and two of *D. quadrum* were collected in the mangroves. Val & Kaneshiro (1988) collected the same species but by sweeping over forest litter or over the slime flux of freshly cut or fallen fruits. Probably they are not so well attracted to banana baits. The species of this group seem to prefer living in forests (Val *et al.* 1981). The two species collected here are until now known only in South America.

coffeata group

Two out of the four species of this group were found. *D. fuscolineata* seems to be the most widespread species in Neotropics and was represented in our collection by seven specimens. A single individual of *D. coffeata* was collected. This species were restricted, as far as known, to West Antilles (Vilela 1984) and is now recorded in South America.

guarani group

It was proposed many times that the subgroups of *guarani* group should be raised to group level. Two species of the *guaramunu* subgroup were found. *D. griseolineata*, a widespread species in South America, was the most common, with 45 individuals. *D. maculifrons* were rarer, with just one specimen. From *guarani* subgroup, three species were found: a single specimen of *D. guaraja*, three individuals of *D. ornatifrons* and two individuals of *D. aff. ornatifrons*. This last one is an undescribed species, with external morphology very similar to *D. ornatifrons*, but with slight differences in morphology of aedeagus.

immigrans group

This group has Oriental origin, but *D. immigrans* is a cosmopolitan species, found in Neotropical region, so, as an exotic element. A total of 28 individuals of this species were collected in the mangroves.

pallidipennis group

The only species of this group, *D. pallidipennis*, is widespread in Neotropics and found preferentially in open formations (Val *et al.* 1981). Thirty individuals were caught in our collections.

repleta group

This is the most diverse group of *Drosophila* in Neotropics and was represented in our collections by six species (2.5% of the total of individuals) of four subgroups. *D. hydei* (*hydei* subgroup) has got the status of cosmopolitan and is rather a species associated with synanthropic and xeric environments (Vilela *et al.* 1983), being collected 33 individuals. *D. mercatorum* (*mercatorum* subgroup) is a widespread species especially in open environments (Sene *et al.* 1980, Vilela *et al.* 1983) and has achieved subcosmopolitan status. It was the second most abundant species of this group in our collections, with 802 specimens, representing 1% of the total, reaching a maximum of 7%. The *fasciola* subgroup was represented by two species, *D. onca* and *D. pictilis*. *D. onca* (12 specimens collected) is a preferentially forest-dwelling fly, found in southern and south-eastern Brazil (Vilela *et al.* 1983) and *cerrados* (Tidon 2006). *D. pictilis* was represented by a single specimen. It was previously known only for Central America (Vilela 1983) and São Paulo state, in south-eastern Brazil (Medeiros & Klaczko 2004). This is, so, its first record in Santa Catarina state, what constitutes a new southernmost locality for the species. The other two species belong to *repleta* subgroup. *D. repleta* was the most abundant species of the group (876 individuals, 1% of total, with maximum of 26%) (Figs. 1 to 3) and is also a cosmopolitan species, associated mainly with xeric and disturbed environments (Vilela *et al.* 1983). It is interesting to note, however, that this species was not so abundantly collected previously in Santa Catarina as it was in the mangrove forests, even when compared with urban environments (data not published).

Finally, six individuals of *D. zottii* were caught. This species is found in forested areas of southern and south-eastern Brazil (Tidon-Sklorz & Sene 1999). As the identification of species of *repleta* group is many times difficult due to the existence of sibling species, 340 out of 2,070 individuals were not classified at species level.

tripunctata group

It was the most diverse group in our collections, with eight species. However, only *D. mediostriata* was common, representing 96.6% (4,056 specimens) of the individuals of the group. This species comprised 5% of the total sample, what can be considered a striking feature of the assemblage of drosophilids in the mangrove forests, yet it was collected only in very low numbers by researches carried out in other environments. It showed also very strong oscillations, ranging from 0 to 72% of relative abundance among the samples (Figs. 1 to 3). The peaks of abundance, however, were very irregular, occurring at different seasons in different years, and sometimes, in just one or two sites, but not in all of them. Its surprisingly high abundance in the mangrove forests is very probably associated with the presence of *H. tiliaceus*. This plant does not reach the interior of the mangrove forests, but is a typical (but not exclusive) inhabitant of the borders of this kind of environment, being present in the three localities surveyed. Decaying flowers of this plant taken to laboratory and maintained at glass vials bred high number of individuals of *D. mediostriata*. However, some irregularities are not easy to explain. Maybe the fluctuations of abundance of this fly are linked to the phenology of the host plant, but in some occasions it was reared in great number from the flowers but remained rare in the traps; in others, few flowers were observed, but it was common in traps; and in other times, it was common both in flowers as in traps. At least, it was never abundant in April (autumn), when the flowers were always absent. Although it is not a true flower-breeding drosophilid, yet it is more commonly found in fruits (Heed 1957, De Toni *et al.* 2001), it was already found in some other flowers (Pipkin *et al.* 1966). The other species of the

group were collected in low numbers. *D. mediopicta* (three individuals), *D. mediopunctata* (20 individuals) and *D. paraguayensis* (11 individuals) are widespread species in Neotropics and commonly found in Santa Catarina state (De Toni & Hofmann 1995). In the other way, *D. cuaso* (five individuals), *D. roehrae* (four individuals) and *D. trapeza* (one individual) were collected only recently in Santa Catarina (Döge *et al.* 2006). A single individual of *D. gr. tripunctata* sp, probably an undescribed species, was collected. Because of the difficult identification of sibling species, 96 individuals were classified only at group level (but certainly they were not *D. mediostriata*, which can be easily distinguished from the others).

virilis group

Just two individuals of *D. virilis* were found. It is probably native to China, but is found as a domestic and exotic species around the world and is the only species of its group to enter Neotropical region (Throckmorton 1982).

ungrouped species

Drosophila caponei is a species of uncertain affinities so far known only in Brazil, from states of Minas Gerais and São Paulo (Vilela 2001), and now, in Santa Catarina. A total of 245 specimens of this fly were collected in the mangroves. Another species of doubtful affinities within the subgenus *Drosophila* is *D. sp. 1*, an undescribed species (six individuals collected).

Subgenus *Siphlodora*

This subgenus includes just two species, and only *D. flexa* is present in Neotropical region. Twelve specimens were collected. This species is associated to maize (*Zea mays*), being abundantly collected from ears and tassels of that plant, but rare in baits (Vilela & Bächli 2000). It is

distributed from Mexico to Brazil and Argentina and the present record constitutes its southernmost locality, as far as known (Schmitz *et al.* 2004).

Subgenus *Sophophora*

Three groups and 14 species of this subgenus were represented. This subgenus was also highly representative in number of individuals, with 85% of the total.

melanogaster group

The *melanogaster* group is native to Oriental and Afrotropical regions, but five species are cosmopolitan or subcosmopolitan, present in Neotropical region as exotic elements of the fauna (Lemeunier *et al.* 1986). All of them were collected in this survey. Altogether, they comprised 77% of the total sample. *D. simulans* was by far the most abundant species, with 46,522 individuals, representing 56% of the total of drosophilids collected, reaching a maximum of 86% (Figs. 1 to 3). It is a very generalist and versatile species, cosmopolitan and already present in Brazil during the first collections, being most common in open and disturbed areas, but also well adapted to the natural ones (Sene *et al.* 1980, Val *et al.* 1981). Its sibling species, *D. melanogaster* (both of them belong to *melanogaster* subgroup, originated in Afrotropical region), also cosmopolitan, synanthropic and present in Brazil for a long time, was rarer (379 individuals). The other species found were *D. kikkawai* (*montium* subgroup), *D. ananassae* and *D. malerkotliana* (*ananassae* subgroup) and have Oriental origin. The first two were rare, with four and 30 individuals, respectively. On the other hand, *D. malerkotliana* was the second most abundant species, representing about 21% of the total sample (17,139 individuals). Nevertheless, its abundance varied very much, reaching until 45% in April (autumn) samples and decreasing to low numbers in other seasons (Figs. 1 to 3). In contrast to the other species of the group, *D. malerkotliana* invaded

Neotropics only in the 1970's (Val & Sene 1980), but as the others, is more abundant in open and disturbed environments.

saltans group

Four species were found. Seven individuals of *D. neoelliptica* and a single one of *D. neosaltans*, two species that occur mainly in forests (Sene *et al.* 1980) and are restricted to Brazil, were collected in the present work. In the other hand, *D. prosaltans* and *D. sturtevanti* are widespread in Neotropics. Twenty-five individuals of *D. prosaltans* were caught, while *D. sturtevanti* was by far the most abundant of the group, represented by 198 specimens. Five specimens of the group could not be identified at species level.

willistoni group

This is one of the most conspicuous and well studied groups of *Drosophila* of Neotropical region. The five species collected belong to two subgroups. The *bocainensis* subgroup was represented by *D. nebulosa* (121 individuals), *D. capricorni* (68 individuals) and *D. fumipennis* (four individuals). *D. nebulosa* is the only species of the group that is more abundant in open areas, being typical of *cerrados* and *caatingas* (Sene *et al.* 1980). The others are preferentially inhabitants of forests. Two species of the *willistoni* subgroup were found, *D. willistoni* and *D. paulistorum*. These species are cryptic and of difficult identification, so that not all the individuals were identified at species level. Taken in sum, this subgroup was responsible for about 8% of the total sample (6,367 individuals) (Figs. 1 to 3). In general, this taxon is highly dominant in tropical and subtropical forested areas in Neotropics (Dobzhansky & Pavan 1950, Ehrman & Powell 1992, De Toni & Hofmann 1995). An estimate of the proportion between the two species were done by morphology of hypandrium (Malogolowkin 1952), showing that *D. willistoni* was more abundant (about 63%) than *D. paulistorum*. The species of the group collected here are those which, as

reported by Val *et al.* (1981), frequently enter traps in large numbers, while the other species come to baits only occasionally. These species are also widespread in Neotropics, especially *D. willistoni*.

unidentified species

Besides the previous discussed species, it was collected six species of *Drosophila* of uncertain taxonomic position and probably undescribed. *D. sp2*, *D. sp3*, *D. sp4*, *D. sp5* and *D. sp7* were represented by single individuals, while *D. sp6* was represented by one specimen in each of the three sites. We place these species tentatively in genus *Drosophila*, but with some reservations, especially for *D. sp5* and *D. sp7*.

Genus *Scaptodrosophila*

This genus is composed by species found especially in the Oriental, Australasian and Afrotropical regions (Bock & Parsons 1978). Just one species are commonly found in Brazil.

latifasciaeformis group

S. latifasciaeformis is an exotic species, originated from Africa (Bock & Parsons 1978), present in Brazil at least since the first collections, frequently associated to disturbed environments. A total of 29 individuals of this species were found.

Genus *Zaprionus*

This genus is a dominant element of the Afrotropical drosophilid fauna (Tsacas *et al.* 1981), but just one species is found in Neotropics, belonging to *armatus* group.

armatus group

One species of this group, *Z. indianus*, expanded its geographical distribution recently and reached the status of subcosmopolitan (Chassagnard & Kraaijeveld 1991). The colonisation of Neotropical region succeeded in very rapidly. It was first recorded in São Paulo state (south-eastern Brazil) by Vilela (1999), where became a pest in fig crops. Soon after, the species was found in the southern states of Santa Catarina (De Toni *et al.* 2001) and Rio Grande do Sul (Castro & Valente 2001), in Uruguay (Goñi *et al.* 2001), in *cerrado*, in Central Brazil (Tidon *et al.* 2003), and in the north of Brazil, in Pará (M. Martins, personal communication). In fact, this fly became one of the most abundant species of drosophilids in open and disturbed areas (Tidon *et al.* 2003, Silva *et al.* 2005). In the present work, we collected 4,401 individuals of *Z. indianus*, about 5% of the total sample (Figs. 1 to 3). The abundance of this fly in mangrove forests was higher than in Atlantic Rain Forest, but lower than in *cerrados* (Tidon *et al.* 2003) and urban environments (Ferreira & Tidon 2005, Silva *et al.* 2005). It is interesting to compare *Z. indianus* with *D. simulans*, the two most common species in urban areas of Santa Catarina Island (M. Gottschalk, personal communication). While the latter is also very abundant in mangrove forests, the former has its abundance very reduced. So, notwithstanding the huge colonisation power shown by *Z. indianus* in its invasion of Neotropical region, it seems to have some relative difficulty to spread to mangrove forests, at least until now.

Genus *Zygothrica*

Species of this genus show strong association with fungi, especially bracket fungi growing in rainforests (Grimaldi 1987). They are not common in fruit baits. Just 13 individuals, belonging to six species, were collected in traps. Two of these species, each of them represented by a single specimen (*Z. sp1* and *Z. sp2*) could not be identified. The other four species are allocated in three groups, listed below. An additional species, also not identified, were reared (eight individuals) from

a fungus of genus *Auricularia* collected in Itacorubi (as this species was not found in traps, it was not included in the general counts of this work).

dispar group

Two species of this group were found, both in Tavares: three individuals of *Z. dispar* and one of *Z. prodispar*, both of them widespread in Neotropics.

orbitalis group

Four specimens of *Z. orbitalis* were collected. This species was known previously only in Panama (Grimaldi 1997), but is being recently collected in several localities in Santa Catarina.

vittimaculosa group

Just *Z. vittimaculosa* was collected (three individuals). This species was already found in Brazil, inclusive in Santa Catarina state (Val & Kaneshiro 1988).

Subfamily Steganinae

Genus *Amiota*

Two species of this genus were found. Both of them belong to subgenus *Amiota*, according to diagnosis of Wheeler (1952), but could not be identified at species level. We found five individuals of *A. sp1* and nine of *A. sp2*.

Genus *Leucophenga*

Only a single individual of an unidentified species of this genus was caught. Flies of this genus rarely enter banana-baited traps.

Despite the difference of the surrounding environments, the fauna of Drosophilidae of the three mangrove forests investigated was similar in respect to the species composition and their abundances. Some particularities, however, were detected, for instance, the striking abundance of flies of the related genus *Curtonotum* (Curtonotidae), virtually absent in all other environments so far studied by our colleagues from Laboratório de Drosofilídeos (Universidade Federal de Santa Catarina).

In general, the same species found in neighbouring environments (urban, Atlantic forest, *restinga*) were sampled in mangrove forests. However, their abundances were different, suggesting that environmental pressures operating in the mangroves are perceived as more restrictive for some species than for others. The environmental pressures that can be evoked for explain these findings can be humidity, salinity, wind, tidal regime, unpredictability of feeding and breeding resources and the own dispersion ability of the species.

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Table 1. List of Drosophilidae species collected in the mangrove forests of Santa Catarina Island.

Group	Species	Itacorubi	Tavares	Ratones
Subfamily Drosophilinae (S=66)				
Genus <i>Drosophila</i> Fallen (S=58)				
Subgenus <i>Dorsilopha</i> Sturtevant (S=1)				
<i>busckii</i>	<i>D. busckii</i> Coquillett	x	x	x
Subgenus <i>Drosophila</i> Fallen (S=36)				
<i>annulimana</i>	<i>D. annulimana</i> Duda	x	x	
	<i>D. arassari</i> Cunha & Frota-Pessoa	x		
	<i>D. schineri</i> Pereira & Vilela	x	x	
<i>bromeliae</i>	<i>D. bromelioides</i> Pavan & Cunha		x	x
<i>calloptera</i>	<i>D. atrata</i> Burla & Pavan	x		
	<i>D. quadrum</i> (Wiedemann)		x	
<i>cardini</i>	<i>D. cardini</i> Sturtevant	x	x	x
	<i>D. cardinoides</i> Dobzhansky & Pavan	x	x	x
	<i>D. neocardini</i> Streisinger	x	x	x
	<i>D. polymorpha</i> Dobzhansky & Pavan	x	x	x
<i>coffeata</i>	<i>D. coffeata</i> Williston		x	
	<i>D. fuscolineata</i> Duda	x	x	x
<i>guarani</i>	<i>D. griseolineata</i> Duda	x	x	x
	<i>D. guaraja</i> King	x		
	<i>D. maculifrons</i> Duda		x	
	<i>D. ornatifrons</i> Duda		x	x
	<i>D. aff. ornatifrons</i>			x
<i>immigrans</i>	<i>D. immigrans</i> Sturtevant	x	x	x
<i>pallidipennis</i>	<i>D. pallidipennis</i> Dobzhansky & Pavan	x	x	x
<i>repleta</i>	<i>D. hydei</i> Sturtevant	x	x	
	<i>D. mercatorum</i> Patterson & Wheeler	x	x	x
	<i>D. onca</i> Dobzhansky & Pavan	x		
	<i>D. pictilis</i> Wasserman			x
	<i>D. repleta</i> Wollaston	x	x	x
	<i>D. zottii</i> Vilela	x		x
<i>tripunctata</i>	<i>D. cuaso</i> Bächli, Vilela & Ratcov	x	x	x
	<i>D. mediopicta</i> Frota-Pessoa	x		
	<i>D. mediopunctata</i> Dobzhansky & Pavan	x	x	x
	<i>D. mediostriata</i> Duda	x	x	x
	<i>D. paraguayensis</i> Duda	x	x	x
	<i>D. roehrae</i> Pipkin & Heed	x	x	x

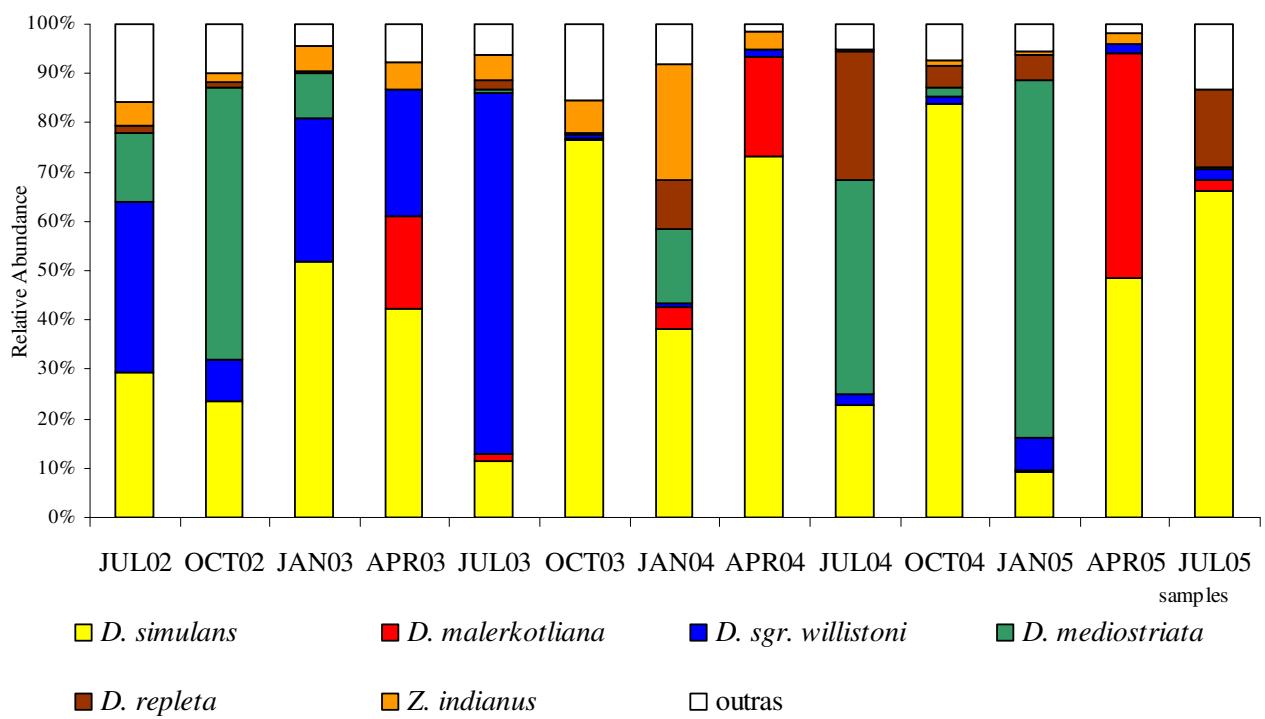
	<i>D. trapeza</i> Heed & Wheeler <i>D. gr. tripunctata</i> sp		x	
<i>virilis</i>	<i>D. virilis</i> Sturtevant	x		
ungrouped	<i>D. caponei</i> Pavan & Cunha	x	x	x
ungrouped	<i>D. sp1</i>	x	x	
Subgenus <i>Siphlodora</i> Patterson & Mainland (S=1)				
-	<i>D. flexa</i> Loew	x	x	x
Subgenus <i>Sophophora</i> Sturtevant (S=14)				
<i>melanogaster</i>	<i>D. ananassae</i> Doleschall	x	x	x
	<i>D. kikkawai</i> Burla	x	x	
	<i>D. malerkotliana</i> Parshad & Paika	x	x	x
	<i>D. melanogaster</i> Meigen	x	x	x
	<i>D. simulans</i> Sturtevant	x	x	x
<i>saltans</i>	<i>D. neoelliptica</i> Pavan & Magalhães	x	x	
	<i>D. neosaltans</i> Pavan & Magalhães			x
	<i>D. prosaltans</i> Duda	x	x	x
	<i>D. sturtevanti</i> Duda	x	x	x
<i>willistoni</i>	<i>D. capricorni</i> Dobzhansky & Pavan	x	x	x
	<i>D. fumipennis</i> Duda	x		
	<i>D. nebulosa</i> Sturtevant	x	x	x
	<i>D. paulistorum</i> Dobzhansky & Pavan	x	x	x
	<i>D. willistoni</i> Sturtevant	x	x	x
Unidentified				
	<i>D. sp2</i>			x
	<i>D. sp3</i>	x		
	<i>D. sp4</i>			x
	<i>D. sp5</i>		x	
	<i>D. sp6</i>	x	x	x
	<i>D. sp7</i>			x
Genus <i>Scaptodrosophila</i> Duda (S=1)				
<i>latifasciaeformis</i>	<i>S. latifasciaeformis</i> (Duda)	x	x	x
Genus <i>Zaprionus</i> Coquillet (S=1)				
Subgenus <i>Zaprionus</i> Coquillet (S=1)				
<i>armatus</i>	<i>Z. indianus</i> Gupta	x	x	x
Genus <i>Zygothrica</i> Wiedemann (S=6)				
Subgenus <i>Zygothrica</i> Wiedemann (S=6)				
<i>dispar</i>	<i>Z. dispar</i> (Wiedemann)		x	
	<i>Z. prodispar</i> Duda		x	

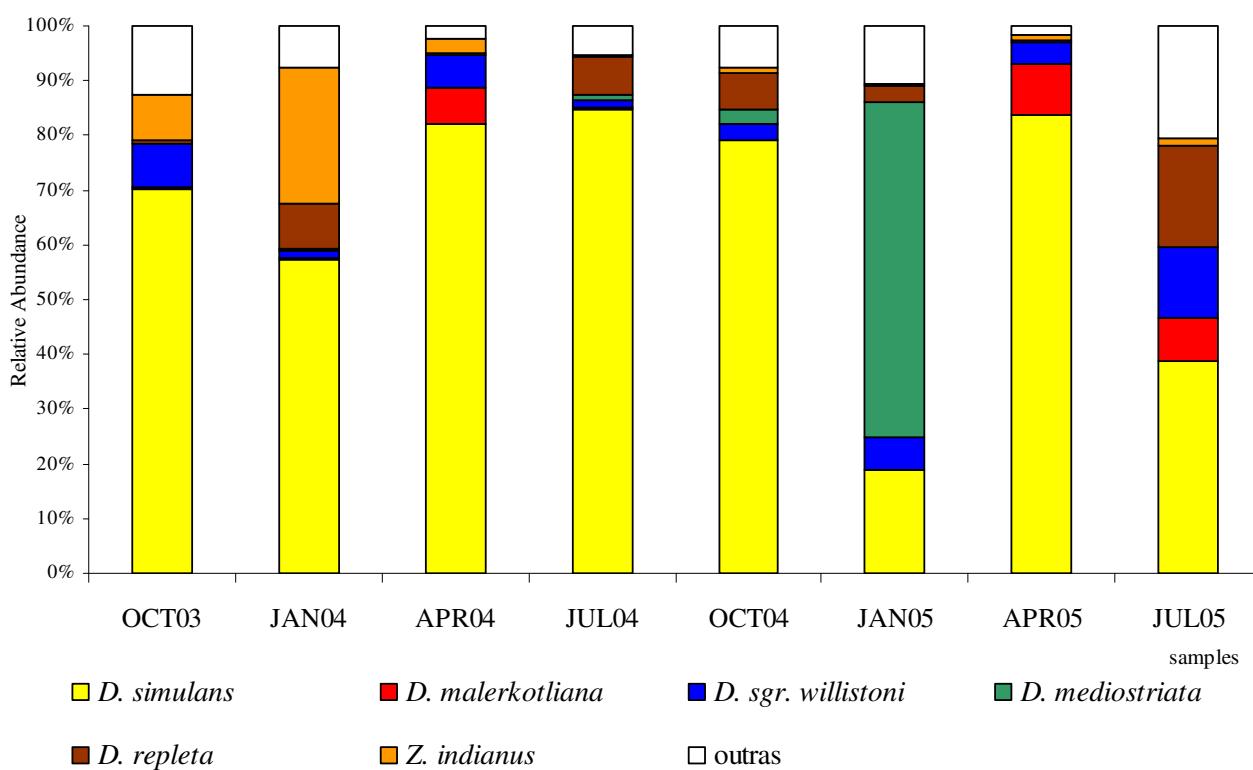
<i>orbitalis</i>	<i>Z. orbitalis</i> (Sturtevant)	x	x
<i>vittimaculosa</i>	<i>Z. vittimaculosa</i> Burla	x	
?	<i>Z. sp1</i>	x	
?	<i>Z. sp2</i>		x
Subfamily Steganinae (S=3)			
Genus <i>Amiota</i> Loew (S=2)			
Subgenus <i>Amiota</i> Loew (S=2)			
?	<i>A. sp1</i>	x	x
	<i>A. sp2</i>	x	x
Genus <i>Leucophenga</i> Mik (S=1)			
?	<i>L. sp1</i>		x

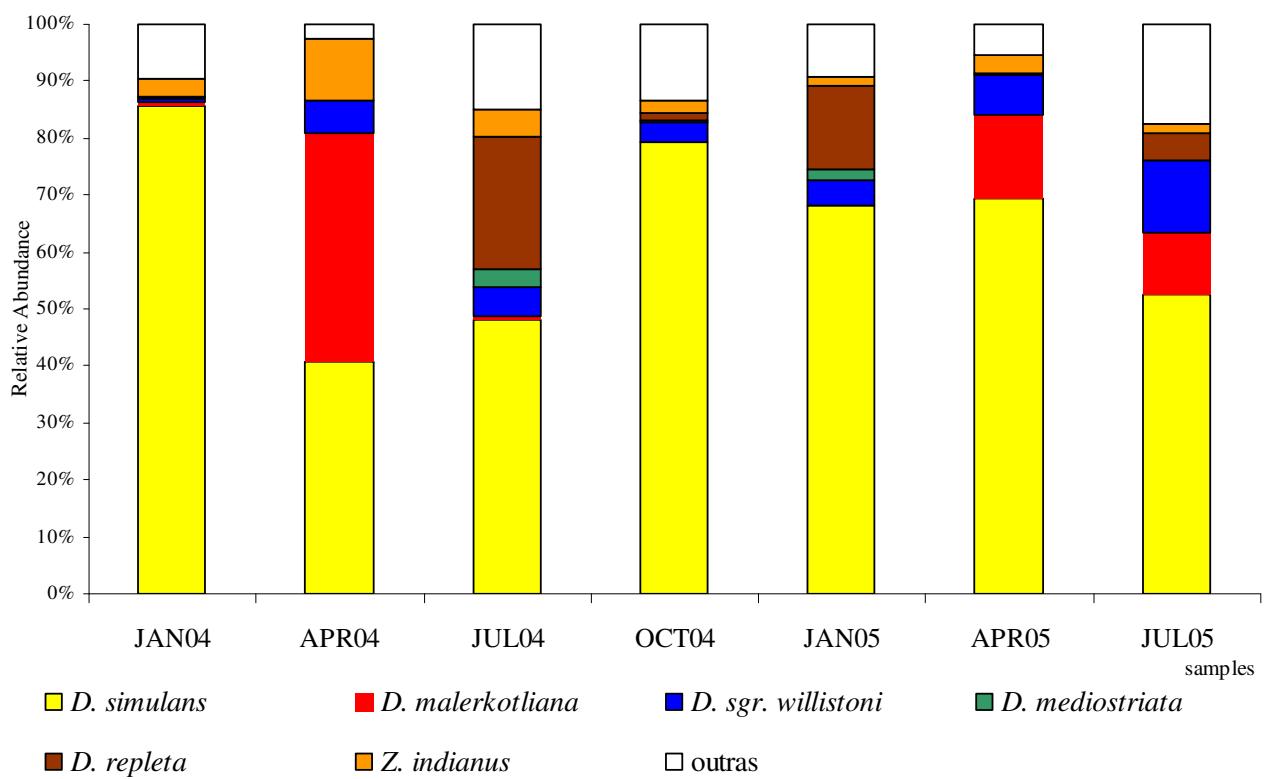
Figure 1. Relative abundances of the most common species in samples from mangrove of Itacorubi.

Figure 2. Relative abundances of the most common species in samples from mangrove of Tavares.

Figure 3. Relative abundances of the most common species in samples from mangrove of Ratones.







CAPÍTULO III

(Artigo a ser submetido ao periódico *Biological Journal of the Linnean Society*)

**Ecology of assemblages of drosophilids (Diptera, Drosophilidae)
in mangrove forests**

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Running Title: Drosophilids in mangrove forests

Abstract: Notwithstanding researches on assemblages of drosophilids have focused different environments, mangrove forests have been neglected in such studies. The present work is the first effort to characterise the ecology of drosophilids in that environment, based in 28 samples taken from three mangrove forests in Santa Catarina Island, southern Brazil. Sixty-nine species were collected, and the seasonal fluctuations of some of them were characterised. Several species presented peaks of abundance in autumn and seemed to respond similarly to temporal changes. Important exceptions were *Drosophila medostriata* Duda and *D. repleta* group. Diversity measures also showed seasonal fluctuations. Evenness and species richness estimated by rarefaction increased in winter, while number of individuals and observed species richness in autumn. Spatial variation among the three sites surveyed was little. Coefficient of Jaccard showed that species composition modifies slightly between summer/autumn and winter/spring. Morisita index evidenced a typical structure of autumn assemblages, characterised by high abundance of *D. malerkotliana* Parshad & Paika, but the lack of typical features of winter, spring and summer. The unpredictability of the mangrove drosophilid assemblages was supposed to be high and processes of migration from other environments were suggested.

Additional Key Words: biodiversity – Brazil – community ecology - diversity measures - *Drosophila* - Neotropics – population dynamics – similarity analysis

Introduction

Community ecology has provided important contributions to the deeper understanding of evolution of the organisms (Begon, Harper & Townsed, 1990). Some properties of communities that have been considered evidence for their structure are species abundance relations, distribution of species in ecomorphological space and diversity (Roughgarden & Diamond, 1986). *Drosophila* has been used intensively in several areas of study, but the solution for many genetical and evolutionary problems must be found within an adequate ecological framework and this area has received less attention (Shorrocks, 1975). Cunha & Magalhães (1965) emphasised the importance of studying tropical assemblages of *Drosophila* as an opportunity to compare organisms of the same group living in environments that offer different conditions. Furthermore, several studies have been proved the adequacy of the use of *Drosophila* in ecological subjects, as competition (Gilpin, Carpenter & Pomerantz, 1986; Shorrocks, 1991; Budnik *et al.*, 2001), climatic stress (Parsons, 1989; Hoffmann, Sørensen & Loeschcke, 2003), coexistence of species (Sevenster & van Alphen, 1993 and 1996), diversity (Shorrocks & Sevenster, 1995; Krijger & Sevenster, 2001), selection (Harshmann & Hoffmann, 2000), speciation (Sawamura & Tomaru, 2002), response to urban gradients (Avondet *et al.*, 2003; Ferreira & Tidon, 2005), invasion of exotic species (Brncic & Budnik, 1987; Huey *et al.*, 2000; Tidon, Leite & Leão, 2003), migration (Coyne *et al.*, 1982; Coyne, Bryant & Turelli, 1987) and many others.

Understanding processes in community ecology is not a simple task, because the answers found are never universal (Diamond, 1986). Explaining the local species diversity remains a great challenge and the factors and processes that maintain the species richness are, in general, unknown (Krijger, 2000). Studying tropical forest

insects, Wolda (1992) suggested that many populations are not kept within narrow abundance limits, oscillating greatly even in undisturbed and stable environments. Greig-Smith (1989) presented evidences of lack of organisation of some communities, emphasising the influence of chance in their structure.

Regarding to drosophilid assemblages, Shorrocks & Sevenster (1995) concluded that they are dominated by intraspecific aggregation and are not fully saturated. Brncic & Valente (1978) found evidence that species of *Drosophila* have strong gregarious tendency and those who coexist in the same fruit seem to facilitate one another, instead of a negative interference. These same authors called attention to the fact that species of *Drosophila* form complex associations in the same microhabitat. Dobzhansky & Pavan (1950) emphasised the great diversity of Brazilian *Drosophila* fauna and verified that the abundances of the species vary significantly in space and time.

The huge Brazilian biodiversity is reflected in the immense variety of habitats, what permits the study of the impact of spatio-temporal heterogeneity in the structure and composition of drosophilid assemblages. Neotropical drosophilid fauna is highly diverse (Val, Vilela & Marques, 1981) and some works have focused this subject in different types of environments (Sene *et al.*, 1980; Martins, 1987; Val & Kaneshiro, 1988; De Toni & Hofmann, 1995; Saavedra *et al.*, 1995; Medeiros & Klaczko, 2004; Tidon, 2006). The present study is the first attempt to characterise such assemblages in the mangrove forests.

This ecosystem is a very peculiar forest that covers tropical and subtropical intertidal plains all over the world. The floristic diversity is low, compounded of trees presenting extreme adaptations to live in an environment dominated by the tidal regime, subjected to periodical flooding, salinity and muddy and poor-oxygenated soil (Cintrón & Schaeffer-Novelli, 1980). Due their coastal localisation, mangroves suffer an

accelerated deforestation and human impact, constituting one of the most threatened environments of the world (Valiela, Bowen & York, 2001).

Material and Methods

Study Area

Santa Catarina Island lies in the coast of the state of Santa Catarina, in southern Brazil, having an area of 431km², where is situated the municipality of Florianópolis, the capital of the state. The climate is type cfa of Köeppen (1948), i. e., subtropical with hot summer, the temperatures of summer above 22°C and precipitation superior to 30mm in the driest month. Its landscape is heterogeneous, comprising different types of environments, like Atlantic forest, *restingas* (beaches, dunes and strand vegetation), urbanised regions and mangrove forests. Extending in a north-south axis, its eastern coast is dominated by sandy beaches facing the open sea, but the western coast is sheltered in calm-water bays edged by the island and the mainland. The three main hydrographical basins flow to the western coast, where the mouths form intertidal plains covered by mangrove forests. Santa Catarina state has special importance to the biogeography of mangrove forests for representing the southernmost limits of the distribution of this ecosystem both in American continent and Atlantic Ocean (Woodroffe & Grindod, 1991).

The three major areas of mangrove forests of Santa Catarina Island were surveyed in this study. Itacorubi (27°34'34"S; 48°31'23"W) is located at the central region of the island and is surrounded by the main urban zone of the city of Florianópolis, having subjected to a very high human influence. Tavares (27°39'13"S;

48°32'12" W) is situated in the southern portion of the island, being surrounded by areas of medium urbanisation, pastures and some forested areas. Finally, Ratones (27°27'45"S; 48°30'28"W) is protected by an ecological station (Estação Ecológica de Carijós) in the north of the island, and is relatively far from urban areas, being surrounded by other natural environments as the Atlantic forest, *restingas*, fresh-water marshes and transitional types of vegetation, that form in some places a mosaic of environments.

The floristic composition of these mangroves is very similar, with only three species of trees constituting the forest: *Avicennia schaueriana* Stapf & Leechman (Verbenaceae), which widely dominates the physiognomy, *Laguncularia racemosa* (L.) (Combretaceae) and *Rhizophora mangle* L. (Rhizophoraceae) (Souza Sobrinho, Bresolin & Klein, 1969; Souza *et al.*, 1994), with almost no other plant living in the interior of the forest, neither grasses nor lianas or epiphytes. The forest canopy is not thick or continuous, so that the forest is rather well lit. The tidal marshes, dominated by the grass *Spartina alterniflora* Loisel. (Poaceae), stand on the sea edges and more flooded areas.

Field and laboratory methods

A collection site was established in each of the three mangroves studied, in the interior of the forest. The flies were captured by banana-baited traps (Tidon & Sene, 1988) hung in the trees at about 1.5m above the ground. In each collection, it was utilised 50 traps in which were distributed 5kg of mashed banana seeded with baker's yeast. The traps were kept in field for 3-4 days and, after that, they were taken to laboratory to be processed. The collections were performed every three months, always

in the second half of January (summer), April (autumn), July (winter) and October (spring). This study has begun initially in Itacorubi and, later on, we could carry out collections also in the other mangroves. So, all the collection were concluded in July 2005, but in Itacorubi they started in July 2002 (totalising 13 collections), in Tavares in October 2003 (8 collections) and in Ratones in January 2004 (7 collections).

For the identification, flies were analysed by their external morphology and male genitalia features. Specialised literature was consulted. For analysis of male genitalia (and in some cases, female spermathecae), flies were dissected in glycerol after preparation with potassium hydroxide (KOH) 10% and acid fuchsine (Wheeler and Kambyrellis, 1966). Females of sibling species were, when possible, kept alive in culture tubes so as to obtain male offspring for identification. Not all the specimens of the sibling *willistoni* subgroup could be identified, so the total abundances of the two species, *D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky and Pavan, were estimated by the proportion found considering the identified specimens. However, for statistical analysis, they were considered together, as *D. sgr. willistoni*, like in other studies.

Statistical analyses

Kruskal-Wallis tests, followed by Dunn tests in case of significant difference at 0.05 level, were performed with data of absolute abundance of the species with a minimum of thirty individuals, in order to detect differences within sites and seasons. The data of absolute abundances of each species in each sample was used to perform Spearman correlation tests to verify if the abundances variations of these species are correlated or not. This same data was used to carry out an analysis of niche overlap,

using Morisita index (Krebs, 1999) as distance coefficient to construct a dendrogram by UPGMA method, with software package Past version 1.34 (Hammer, Harper & Ryan, 2001). Morisita index was used for calculating an unbiased niche overlap because it is almost not influenced by different sample sizes (Smith & Zaret, 1982). The combination of these analyses provides an idea on the similarity of distribution of the different species in space and time.

Species accumulation curves were constructed for each site investigated. Species abundance distribution was graphed as a Whittaker plot (Krebs, 1999). The goodness-of-fit to the observed distribution were assessed for geometric, logarithmic series and lognormal distributions, using Past 1.34 (Hammer *et al.*, 2001).

Diversity was measured by the following ways: 1. Observed species richness (S_{obs}); 2. Estimative of species richness by rarefaction method (S_{rar}); 3. Shannon-Wiener index of diversity (H'); and 4. Smith-Wilson index of evenness (E_{var}). The observed species richness (S_{obs}) is simply the number of species counted in an assemblage. The estimative of species richness by rarefaction method (S_{rar}) is used to compare assemblages of different sample sizes (Magurran, 1988; Krebs, 1999). All assemblages were standardised to a common sample size of 101 individuals, using BiodiversityPro version 2 (McAleece *et al.*, 1997). The Shannon-Wiener index of diversity is based on information theory and is a heterogeneity index, which combines species richness and evenness (Magurran, 1988; Krebs, 1999). Evenness measures attempt to quantify the unequal representation against a hypothetical assemblage in which all species are equally common (Krebs, 1999). Smith-Wilson index (E_{var}) was selected due to its independence of species richness and equal sensitivity to minor and abundant species (Smith & Wilson, 1996). The calculations of these last two measures were done in the software Ecological Methodology (Krebs, 1999), but we preferred log base e (\ln) for H' ,

because it is best encountered in this form in the literature about Drosophilidae ecology. The correlation among S_{obs} , S_{rar} , H' , E_{var} and N (number of individuals) was tested by Pearson correlation tests. Number of individuals was transformed to $\ln(N+1)$ in order to normalise data. Shapiro-Wilk test was used to verify normality and Levene's test for homogeneity of variances.

The influence of several variables on assemblage diversity was estimated by the calculations $H'_{between} = H'_{total} - (\sum N_j H'_j)/N_t$; 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_t is the total number of individuals in all samples, N_j is the number of individuals in category j , H'_j is H' within category j . The components considered were year (with categories 1, 2, 3), season (winter, spring, summer, autumn), residual (Jul 2002, Oct 2002, Jan 2003, Apr 2003 and so on) and local (Itacorubi, Tavares and Ratones).

The similarity among the samples was investigated with a cluster analysis using UPGMA method, in Past 1.34 (Hammer *et al.*, 2001). As similarity measures it was used: 1. Coefficient of Jaccard; and 2. Morisita index of similarity. Coefficient of Jaccard is a binary coefficient (deals with presence/absence data), so it was used to compare the similarities in species composition among samples. In the other hand, Morisita index deals with quantitative data, so it was used to compare samples in respect to the relative abundance of each species. As the original Morisita index showed little discrimination among our samples, we used it after a logarithmic transformation [$\ln(x+1)$], as recommended by Wolda (1981) and Krebs (1999) in communities with few common species and many rare species, as are ours.

Results

A total of 82,942 drosophilids were collected, belonging to 69 species of five genera – 58 species of *Drosophila* (N=78,484), six of *Zygothrica* (N=13), two of *Amiota* (N=14), and one of *Leucophenga* (N=1), *Scaptodrosophila* (N=29) and *Zaprionus* (N=4,401). The most common species were *D. simulans* Sturtevant (56% of the total sample), *D. malerkotliana* Parshad & Paika (21%), *Zaprionus indianus* Gupta (5%), *D. medostriata* Duda (5%), *D. willistoni* Sturtevant (5%), *D. paulistorum* (3%), *D. repleta* Wollaston (1%), *D. polymorpha* Dobzhansky and Pavan (1%) and *D. mercatorum* Patterson and Wheeler (1%). Ten species found are exotic in Neotropical Region: *D. ananassae* Doleschall, *D. busckii* Coquillet, *D. immigrans* Sturtevant, *D. kikkawai* Burla, *D. melanogaster* Meigen, *D. malerkotliana*, *D. simulans*, *D. virilis* Sturtevant, *S. latifasciaeformis* (Duda) and *Z. indianus*.

Besides the drosophilids, we collected 45,826 specimens of Curtonotidae, an unusual finding, because this family was not found in other environments searched by our lab team in Santa Catarina state. It is considered the sister group of Drosophilidae (Grimaldi, 1990), but very little is known on its natural history and taxonomy.

Species used to statistical analysis of absolute abundance were the following: *D. ananassae*, *D. caponei* Pavan and Cunha, *D. capricorni* Dobzhansky and Pavan, *D. griseolineata* Duda, *D. hydei* Sturtevant, *D. medostriata*, *D. mercatorum*, *D. melanogaster*, *D. malerkotliana*, *D. nebulosa* Sturtevant, *D. neocardini* Streisinger, *D. pallidipennis* Dobzhansky and Pavan, *D. polymorpha*, *D. repleta*, *D. simulans*, *D. sturtevanti* Duda, *D. sgr. willistoni* and *Z. indianus*. For comparisons among the three sites surveyed, just *D. mercatorum* showed a significant difference ($H_c=9.12$, $p=0.011$), with lower abundances in Ratones than in Itacorubi ($Q=2.675$, $p<0.05$) and Tavares

($Q=2.708$, $p<0.05$). On the other hand, nine species showed significant differences in abundance in accordance to seasons, as shown in box-plots of Figure 1. *D. caponei*, *D. malerkotliana*, *D. polymorpha*, *D. simulans*, *D. sturtevanti*, *D. sgr. willistoni* and *Z. indianus* reached peaks in samples of April (autumn), while *D. hydei* had higher abundances in October (spring) and *D. repleta* in July (winter).

Spearman correlation tests among the absolute abundance of the predominant species showed 53 significant correlations, out of 153 comparisons. From them, 47 were positive (not shown) and just six were negative. The significant negative correlations involved *D. medostriata* with *D. malerkotliana* ($r=-0.387$, $p=0.042$) and *D. repleta* with *D. polymorpha* ($r=-0.574$, $p=0.001$), *D. simulans* ($r=-0.557$, $p=0.002$), *D. sturtevanti* ($r=-0.515$, $p=0.005$), *D. sgr. willistoni* ($r=-0.463$, $p=0.013$) and *Z. indianus* ($r=-0.416$, $p=0.028$). Comparable results were found with the analysis of niche overlap, showed in the dendrogram of Figure 2. Eleven out of the 18 species considered formed a group with overlap above 0.60, while the other seven species showed more differentiated patterns, especially *D. medostriata* and the species of *repleta* group – *D. hydei*, *D. mercatorum* and *D. repleta*.

Species accumulation curves for each site are shown in Figure 3A. They did not reach a plateau, suggesting that more species would be collected if more samples were done. The species abundance distribution of the total sample can be viewed in Whittaker plot in Figure 3B. It can be noticed the large proportion of rare species in the samples. The observed curve did not fit to geometric and log-series models, but to a lognormal distribution ($\text{mean}=-1.492$, $\text{variance}=4.454$, $p=0.580$). However, we must treat this adjustment with some restriction, as there is not a mode in the curve, fact that can produce inaccurate estimates (Krebs, 1999). For this reason, we did not calculate them.

Magurran (1988) affirmed that this model is commonly found by community ecologists, especially for large, mature and varied natural communities.

ANOVA tests comparing values of S_{obs} , S_{rar} , H' , E_{var} and N did not find any significant difference among sites. In the other hand, some significant differences were found when comparing such parameters among seasons. As seen in box-plots of Figure 4, S_{obs} and N reached peaks in April (autumn) samples, while S_{rar} and E_{var} showed an opposite pattern, with peaks in July (winter) and lower values in April (autumn). H' , however, did not vary with seasons.

The significant correlations found by Pearson tests among the diversity measures can be seen in Figure 5. As can be observed, the higher the values of N , higher the values of S_{obs} , but lower the S_{rar} . The concomitant increase of N and S_{obs} also was accompanied by a decrease in evenness (E_{var}). In the other hand, E_{var} and S_{rar} varied greatly together. H' was correlated only with S_{rar} , positively.

Table 1 shows the partitioning of diversity for temporal and spatial changes. The spatial component showed less importance than the temporal one. Within the temporal changes, the seasonal variation was greater than the annual, but a large amount of variation was due to factors not related to seasons or years. Additionally, more than half of the diversity could not be explained by the components analysed.

Figure 6 depicts the similarity among the samples. Accordingly to coefficient of Jaccard, despite some exceptions, two major groups can be recognised, split at about 0.40 of similarity, one containing mainly the samples of January (summer) and April (autumn) and another mainly the samples of July (winter) and October (spring). In the other hand, the dendrogram with Morisita index showed another aspect of the assemblages. The samples were distributed roughly in four groups at about 0.80 of similarity, that we named groups 1 to 4. All the samples of April (autumn) clustered

together, but the samples of other seasons were mixed among the groups. With the both indexes, there was no clear tendency in clustering by site.

Discussion

It would be imagined that the harsh abiotic conditions and the very low floristic diversity of the mangrove forests could lead to a low diversity of drosophilids. The 69 species collected in the present survey and the species accumulation curves indicating that more species could be found (Figure 3A) deny such supposition. The species richness found in the mangrove forests of Santa Catarina Island were higher than, for example, that found until now in Chile (Brncic, 1987) and in Uruguay (Goñi *et al.*, 1998) and also in the majority of similar papers published with data of other environments in Brazil (Tidon-Sklorz & Sene, 1992; Saavedra *et al.*, 1995; Vilela & Mori, 1999). Nevertheless, it was lower than found in other types of environments surveyed by our lab team in Santa Catarina Island (data not published). Perhaps the drosophilid fauna of mangroves could be considered a bit depleted, but only when compared to other environments of the same biogeographical area, indicating that its diversity could be limited primarily by regional factors, rather than by local ones. Flies are mobile organisms, so many of the components of an assemblage can be occasional visitants. For this reason, maybe species accumulation curves would not stabilise before that all the species of the region are collected.

It was remarkable, as well, the presence and abundance of the phylogenetically related family Curtonotidae, a feature not found in collections of drosophilids in other environments. The natural history of this group of flies is very obscure and maybe studies in mangrove forests could make some attempts to clarify several aspects of it.

Mangrove forests of Santa Catarina Island have a typical assemblage of drosophilids. This can be concluded by the lack of significant differences for all diversity measures and for all the species, except one, among the three sites. The low contribution to diversity of the spatial component (Table 1) and the lack of clustering by site in dendograms of similarity, regarding both to species composition (Coefficient of Jaccard) and to assemblage structure (Morisita index) (Figure 6), go in the same direction. Also there was no significant difference in abundance of all native species (ANOVA: $F=1.131$; $p=0.337$) and all exotic species ($F=0.251$, $p=0.780$) by sites. Despite the three mangroves can be classified as high, medium and low-disturbed (Itacorubi, Tavares and Ratones, respectively), it was observed no effect of such human disturbance gradient in the drosophilid assemblages, as seen in other environments by Avondet *et al.* (2003) in the city of Oxford, USA, and Ferreira & Tidon (2005) in Brasília, in Brazilian Cerrado.

The population peak of *Drosophila* in autumn was already known for a long time (Basden, 1953). It was also the case of the present work, as seen by the significant higher N in this season (Figure 4). Several of the predominant species showed significant peaks in April (autumn) samples (Figure 1). The most remarkable peak was that from *D. malerkotliana*, which reached very high abundances in that season but became very rare or even absent in the others. *D. simulans* had also a conspicuous peak in autumn, but kept common all over the year, with an apparent secondary peak in spring. This behaviour, with a higher peak in autumn and a secondary one in spring, was already observed for this species in southern Brazil, by Franck & Valente (1985). In turn, *D. caponei*, besides the higher abundance in autumn, was abundant also in summer, becoming very rare or absent during winter and spring. Other species - *D. polymorpha*, *D. sturtevanti*, *D. sgr. willistoni* and *Z. indianus* – showed less steep

fluctuations, but also with significant peaks in autumn. Even some species with not statistically significant differences seemed to experiment less pronounced population expansions in autumn, as it was the case of *D. ananassae*, *D. capricorni* and *D. nebulosa*.

Overall, this autumn peak was more striking for exotic species, yet number of individuals of exotic species were significantly greater in autumn (ANOVA: $F=12.38$; $p<0.0001$; Tukey: APR>JUL $Q=4.167$, $p<0.001$ and APR>JAN $Q=3.084$, $p<0.02$) but the total number of individuals of native species did not ($F=0.584$, $p=0.631$).

The high number of positive correlations found for abundance of species by Spearman correlation tests may indicate that, in general, the species respond in the same way to temporal changes. The main exceptions were *D. mediostriata* and *D. repleta*. The niche overlap analysis showed a similar pattern, with almost all the species clustering close together, including exotic and native ones, with the exceptions again of *D. mediostriata* and *D. repleta* and, moreover, *D. hydei* and *D. mercatorum*. These last three species belong to *repleta* group and, in spite of being cosmopolitan or subcosmopolitan, they are native from Neotropics. This group, so, seemed to behave differently from the most of the species. Some authors have related peaks of *repleta* group in spring, not in autumn (Bélo & Oliveira-Filho, 1978; Bizzo & Sene, 1982; Franck & Valente, 1985). It was the case of *D. hydei* in our collections, although *D. repleta* reached higher abundances during winter. *D. mercatorum* too, although not significantly, appeared to have more pronounced abundances in spring. Some species, in the other hand, seemed to be little influenced by seasons, as *D. melanogaster*, *D. neocardini*, *D. pallidipennis* and, maybe, *D. griseolineata*, that kept abundances relatively even along the year. In turn, *D. mediostriata* showed very irregular oscillations, but also appearing not to be related with seasons, since its peaks happened

in different seasons in different years. It is a rare species in other environments, representing one of the most unusual features of the mangrove assemblages. Probably, this fact is related to an association with decaying flowers of *Hibiscus tiliaceus* L., a plant that can be found in borders of mangroves, although not in the interior of the forest.

The seasonality could be observed not only in the abundance of species but also in the diversity measures (Figure 4). The only parameter that did not show seasonal pattern was H' . The season of greater abundances, the autumn, was also the moment of more elevated species richness, when considered S_{obs} . In the other hand, winter was the season of higher S_{rar} and evenness (E_{var}). It could be observed that when populations of drosophilids increased in autumn, more species could be detected in samples, but such increase was disproportionately distributed among species, i. e., few species were responsible for almost the whole boost, causing a decrease in evenness (E_{var}) and S_{rar} .

Diversity defined as H' can be comprehended as the combination of two ideas: species richness and evenness (Krebs, 1999). So, it is interesting to check which of these factors have a stronger influence on the diversity of the studied assemblage. In mangrove drosophilid data, H' was correlated significantly only with S_{rar} (Figure 5), positively. Although not significantly, it was correlated positively with E_{var} and negatively with S_{obs} . So, in our data, an estimative of species richness as S_{rar} was a better outline of diversity than S_{obs} , which was strongly influenced by N. The higher N, the higher S_{obs} , but the lower S_{rar} and E_{var} , and H' showed more influenced by the latter pair than by the former.

The analysis of partitioning of diversity (Table 1) showed that temporal heterogeneity was more important than spatial in contributing to the value of H' . The lower influence of sites in this case can be understood because the three mangrove

forests are very homogeneous in floristic compositions and abiotic conditions. The differences in human disturbance seemed not to play an essential role. In turn, the factors associated with seasons were stronger than those associated with years. However, the proportion for seasons found here (12.18%) is very lower than what was found by Shorrocks (1975) in Leeds, England (35.69%), and Brncic, Budnik & Guiñez (1985) in Quilicura, Chile (46.23%), but similar to findings of Silva *et al.* (2005) in Porto Alegre, southern Brazil (14.14%). A possible reason for this, already stated by the last authors, could be differences in methodology, yet the other studies carried out monthly collections, while Silva *et al.* (2005) and our work have done only seasonal ones. Another possible cause is the climate, temperate in England and Chile, but subtropical in Porto Alegre and Santa Catarina Island. The contribution of year changes, although lower than the seasonal, seemed to be proportionally higher herein than in the cited papers. While in those papers, this component was remarkably lower than the seasonal, in the mangroves it represented more than half of the value of the seasonal. Finally, there was still a considerable amount of variation not related to years or seasons, which we called residual. In addition, more than half of the diversity has to be attributed to other factors that not those exposed here. In temperate climates, the temporal changes explain almost all the diversity (Shorrocks, 1975; Brncic *et al.*, 1985), but the more complex assemblages of Neotropics seem to be more unpredictable.

Analysis of coefficient of Jaccard (Figure 6) showed that the composition of the assemblages of drosophilids in the mangroves suffers a slightly modification throughout the year, suggesting a scenario like the following. The composition of the summer is, in general, similar in the subsequent autumn, but changes until winter. The composition in spring is similar to the preceding winter, but so, the assemblage changes again until the

next summer. The factors that lead these processes are unknown, but changes in temperature and breeding/feeding resources can be suggested.

Not transformed Morisita index showed little discrimination among most of the samples, giving similarities very close to 1 in many cases (not shown). As this index is very affected by a dominant species (Wolda, 1981; Krebs, 1999), the fact can be explained by an evident characteristic of drosophilid assemblages of the mangroves: the always-high relative abundance of *D. simulans*. As the dominant species was almost always the same, very high similarities were obtained; the few samples more differentiated were those when other species reached prominent peaks, even surpassing *D. simulans* (it was the case of *D. mediotriata* and *D. sgr. willistoni*). The analysis with logarithmic transformation showed another pattern (Figure 6). It evidenced that there was a typical autumn assemblage structure, but the other seasons did not have such a typical structure. Comparing the dendrogram with relative abundances of each sample, we could perceive that those constituting what we called Group 1 (Figure 6), that comprised all samples from autumn, were clearly characterised by a high relative abundance of *D. malerkotliana* (this group had a mean of 18.5% of relative abundance of the mentioned species, contrasting to a mean less than 1% in the other samples). However, no conspicuous characteristic could be noticed in the other seasons, and their samples did not form clusters for that reason. Samples from spring, summer and winter were more similar to preceding or subsequent seasons than to the same season of other years. Group 2 of samples can be characterised by increased relative abundance of *Z. indianus* (mean of 11%, against 2.5% of others). It consists principally of samples from July 2003 to January 2004. Group 3, in its turn, comprised the irregular peaks of *D. mediotriata* (mean of 48% of relative abundance of such species in this group of samples, while the mean was inferior to 2% in other samples), that occurred in October

2002, July 2003 and January 2004. Finally, Group 4 included samples with prominent relative abundances of *D. repleta* (mean of 12% within this group and 3% outside it). It is constituted only by samples from period between July 2004 and July 2005.

Although some important seasonal events occurred, as those shown in population dynamics of species (Figure 1) and changes in diversity measures (Figure 4), the drosophilid assemblages of mangrove forests seemed to be largely affected by factors not related to seasons. Some events looked as if they were non-cyclic and related to definite periods, as the increased abundance of *Z. indianus* and *D. repleta*, in the periods cited above. Also *D. sgr. willistoni* showed this trait, being more abundant between July 2002 and October 2003, but clearly decreasing in the subsequent period, and *D. nebulosa*, which experienced a boost in April 2004. It was noticeable also, the irregular peaks of *D. medostriata*, happening in different seasons in different years. All of this has brought a high amount of unpredictability of the drosophilid assemblages in this environment. Dobzhansky & Pavan (1950) already had paid attention in seasonal behaviours that vary from year to year in Brazilian species of *Drosophila*; the number of factors acting may be so great, that it is difficult the same abundances be repeated in the same seasons of different years. Pipkin (1953) stated that irregular fluctuations of a species are probably non-cyclic and depend upon variations in the local food supply. Maybe the unpredictability of the mangrove drosophilid assemblages is result of the typical unpredictability of an environment poor in food resources and due also to other possible complex processes.

According to our observations, there is a lack of resources for feeding and breeding sites inside the mangrove forests. We could not rear any fly from fruits and flowers of the three species of trees that form the forests. Some fleshy fungi collected inside the forests and flowers of terrestrial plants that live in the borders showed to be

used by specialised species, not collected in our traps. No other potential resource was recognised and, actually, flies were never observed inside the mangroves far from traps. So, we concluded that the apparent lack of resources for drosophilid fauna is real, and, so, that the flies collected probably were migrants using the traps opportunistically. However, even if the drosophilid fauna does not reside inside the mangroves, the flies apparently can, at least, reach them easily, what can be concluded by the high number of individuals collected. Coyne *et al.* (1982 and 1987) showed that flies living in deserts can disperse randomly, including to desolate areas, many kilometres far from favourable areas. Maybe a random dispersion is also involved in the presence of flies in mangroves. They could be migrants from any other more favourable environment, and the heterogeneous nature of Santa Catarina Island offers a great variety of possible sites of origin. Nonetheless, different species of drosophilids may perform this putative dispersion to mangroves more or less successfully, maybe due to their dispersion power, behaviour or adaptability to abiotic conditions, so that the result is a typical mangrove assemblage, with the relative abundance of each species altered after the process.

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Figure Legends

Figure 1. Seasonal fluctuations in absolute abundance of predominant species. Only species with significant differences at 0.05 level with Kruskal-Wallis tests are graphed, showing also the significant differences of the pair comparisons with Dunn tests. Species with no significant difference were: *D. ananassae* ($H_c=12.46$, $p=0.066$), *D. capricorni* ($H_c=6.654$, $p=0.238$), *D. griseolineata* ($H_c=8.41$, $p=0.092$), *D. mediostriata* ($H_c=1.71$, $p=0.640$), *D. melanogaster* (0.282 , $p=0.971$), *D. mercatorum* ($H_c=6.547$, $p=0.088$), *D. nebulosa* ($H_c=8.388$, $p=0.082$), *D. neocardini* ($H_c=6.782$, $p=0.106$) and *D. pallidipennis* ($H_c=3.405$, $p=0.457$).

Figure 2. Niche overlap among predominant species, following Morisita index of niche overlap.

Figure 3. A. Species accumulation curve for each collection site. B. Whittaker plot for global data.

Figure 4. Seasonal fluctuations of diversity measures. Only significant differences at 0.05 level with ANOVA tests are graphed, showing also the significant differences of the pair comparisons with Tukey tests. H' did not present significant difference ($F=2.65$, $p=0.072$).

Figure 5. Correlations between diversity measures. Only significant correlations at 0.05 level with Pearson tests are graphed. Not significant correlations were: $H' \times E_{var}$

($r=0.267$, $p=0.170$), $H' \times S_{obs}$ ($r=-0.130$, $p=0.510$), $H' \times N$ ($r=-0.331$, $p=0.085$) and $S_{obs} \times S_{rar}$ ($r=-0.177$, $p=0.367$).

Figure 6. Similarity among samples accordingly to species composition (Coefficient of Jaccard) and assemblage structure (Morisita index of similarity).

Table 1. Niche analysis for mangrove data, showing partitioning of diversity for temporal and spatial changes.

Niche component	Contribution to diversity	
	H'	%total
Year to year	0.098	6.91
Season to season	0.172	12.18
Residual	0.281	19.88
Spatial	0.110	7.80
Not explained	0.752	53.23
Total	1.413	100.00

Figure 1

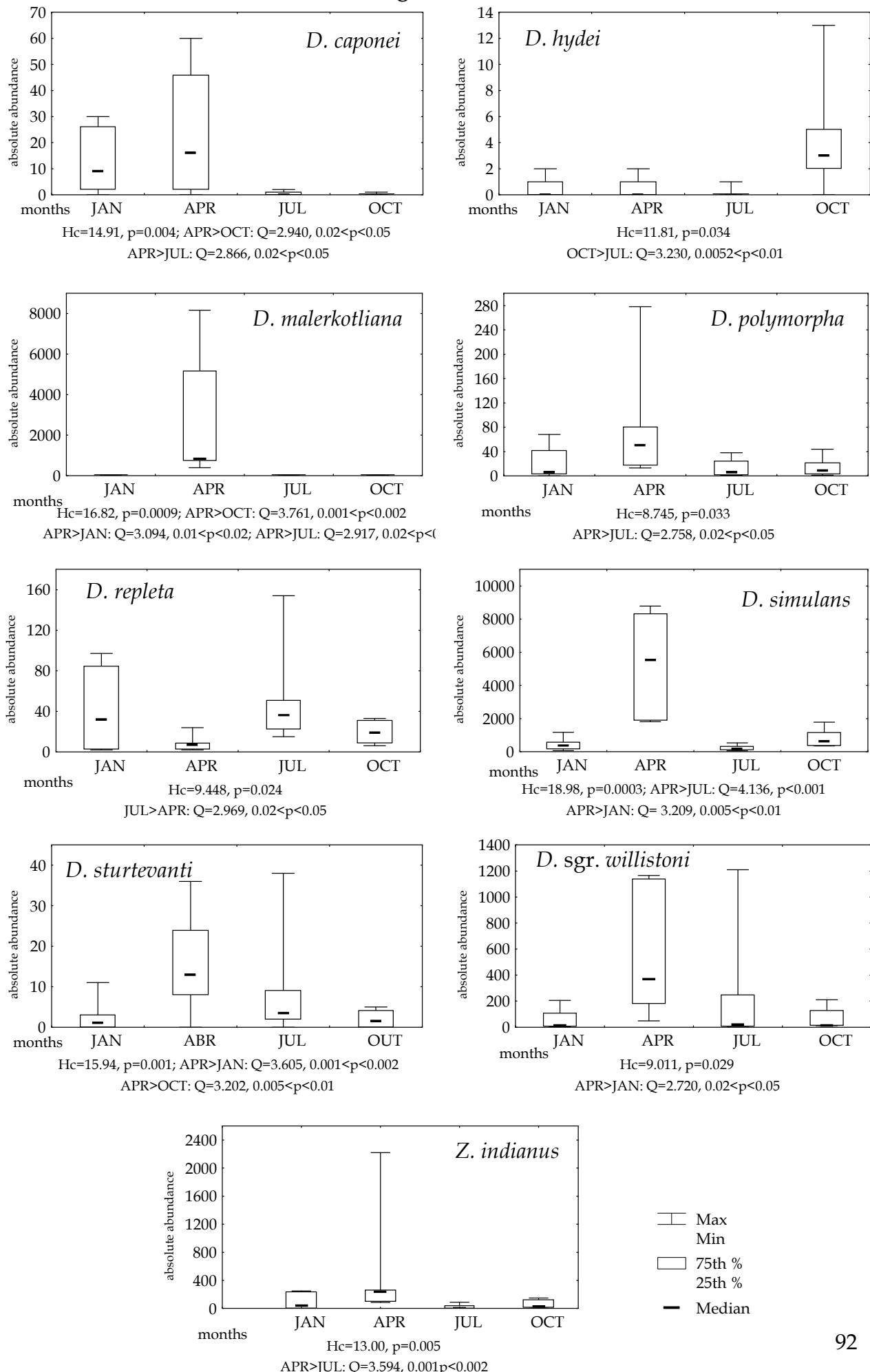


Figure 2

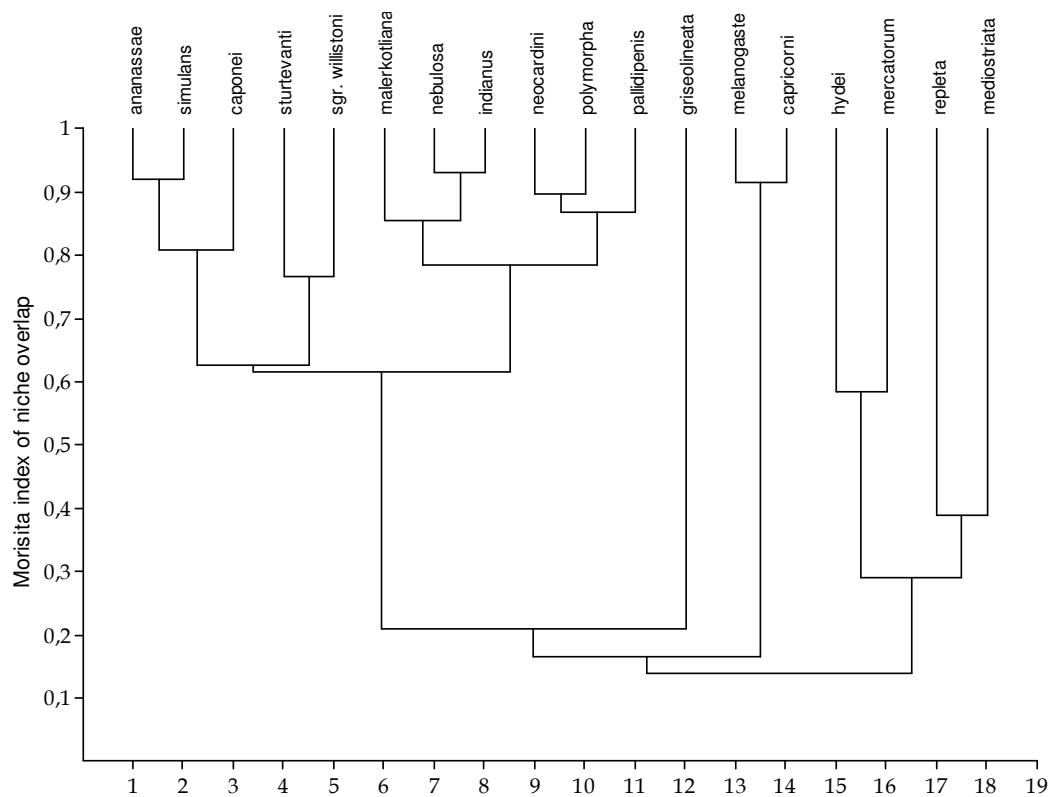


Figure 3

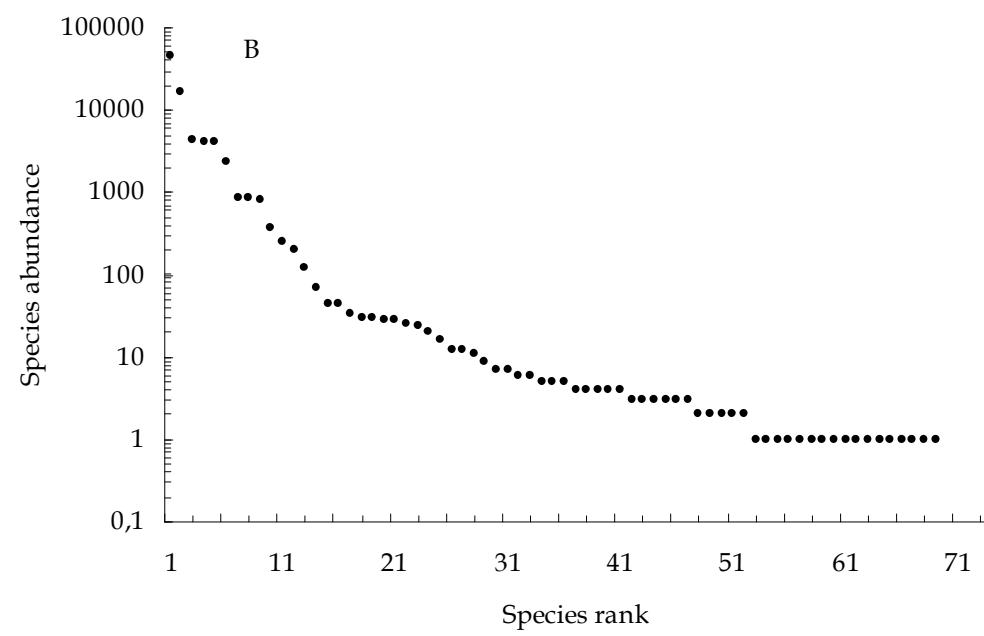
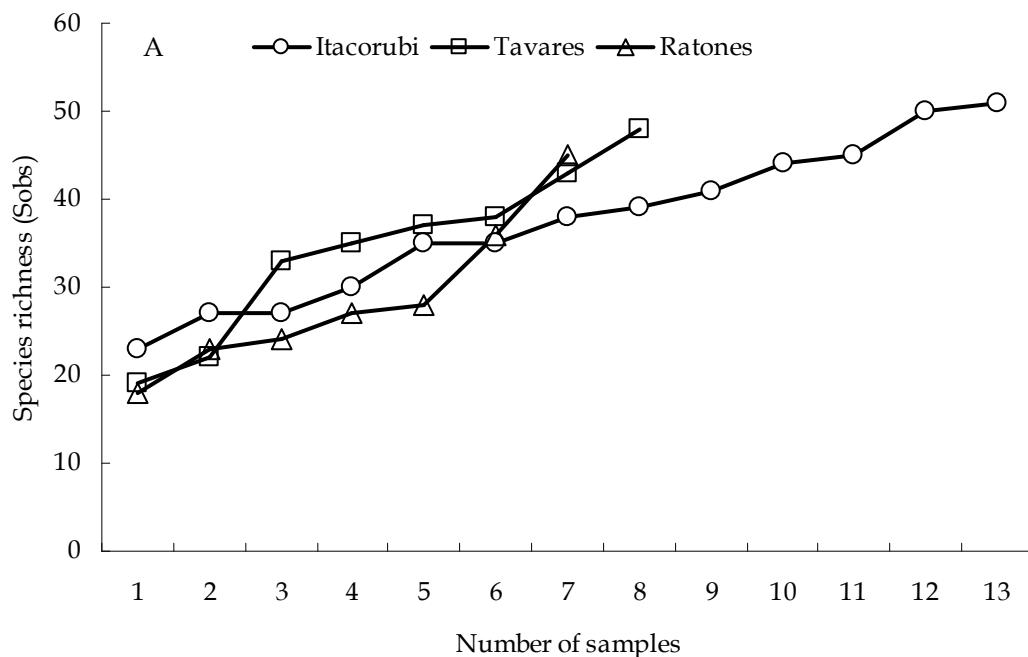


Figure 4

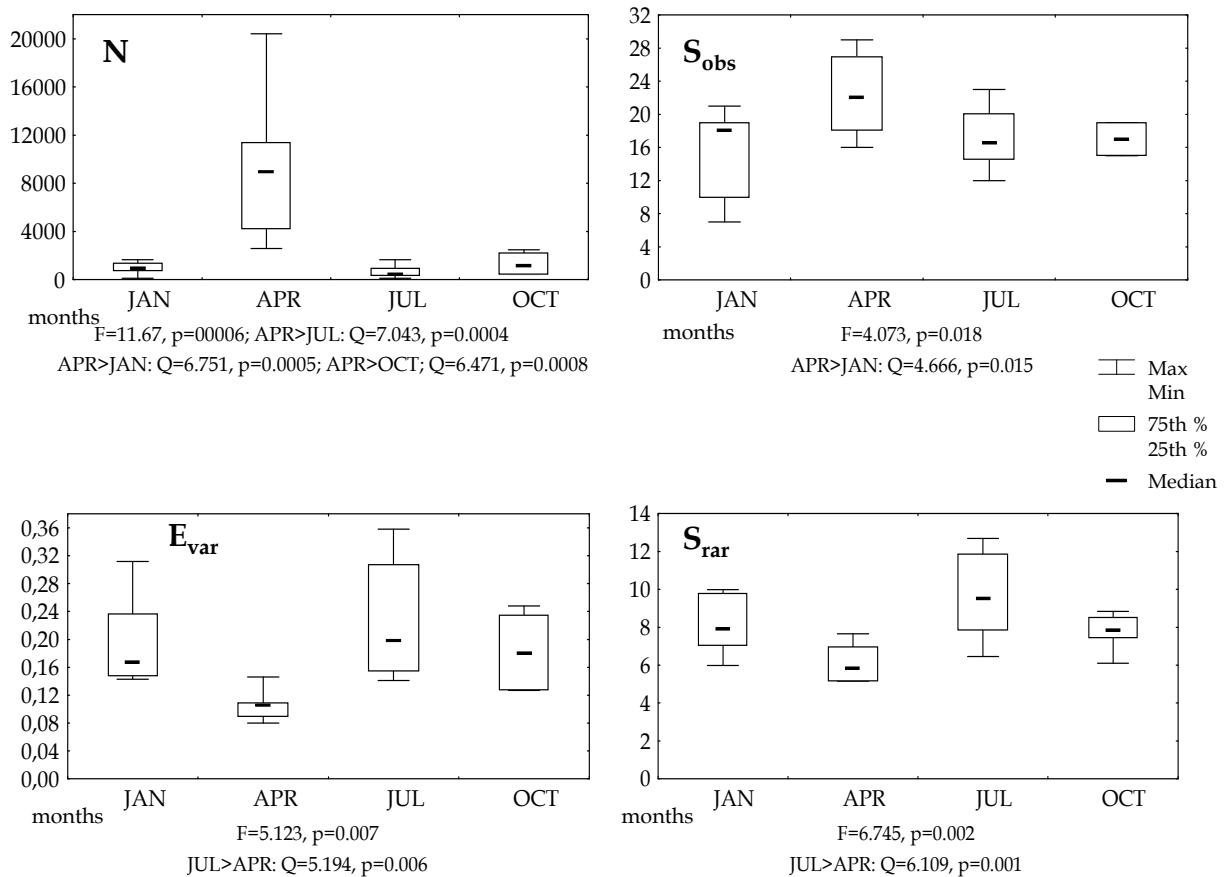


Figure 5

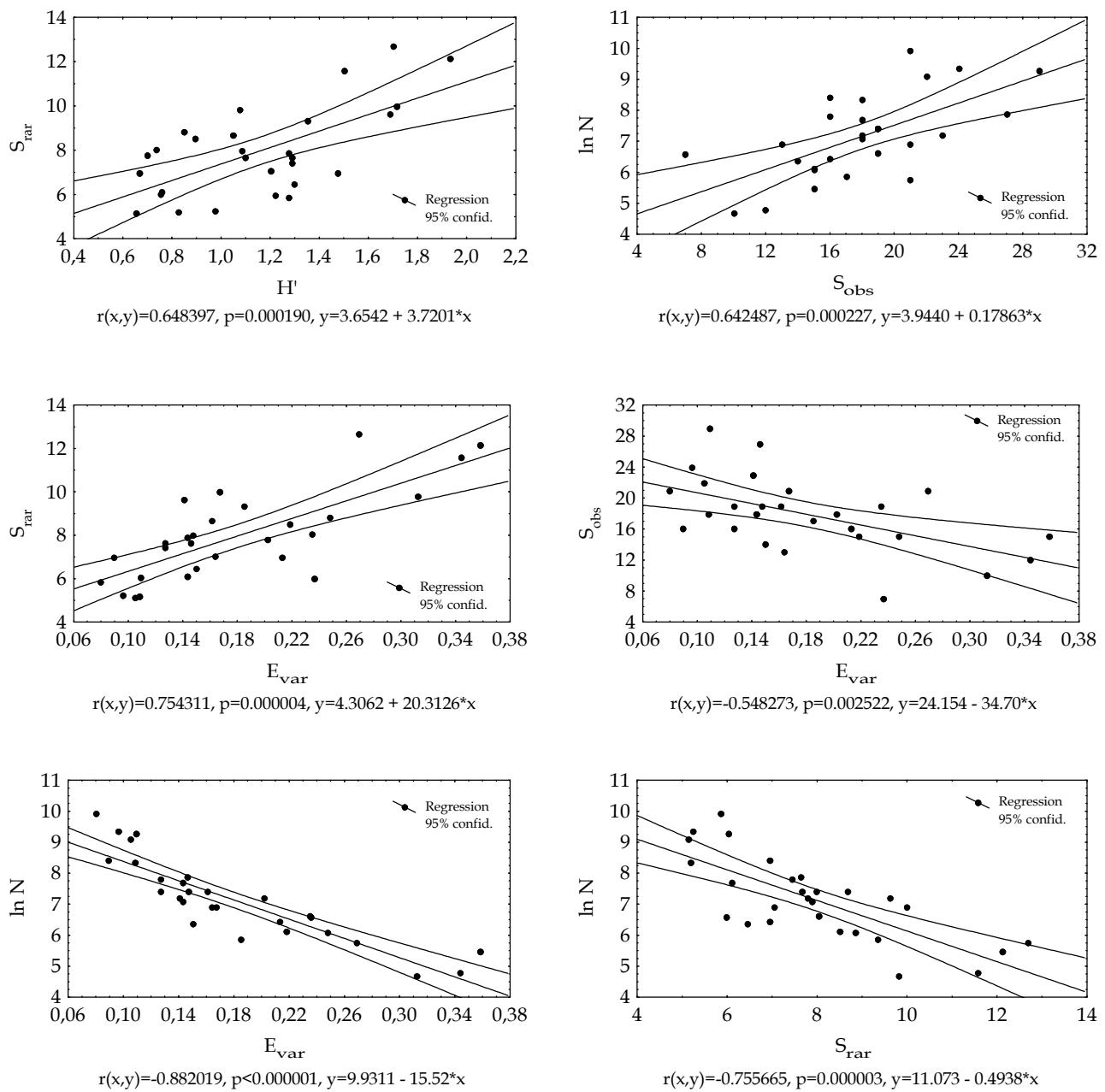
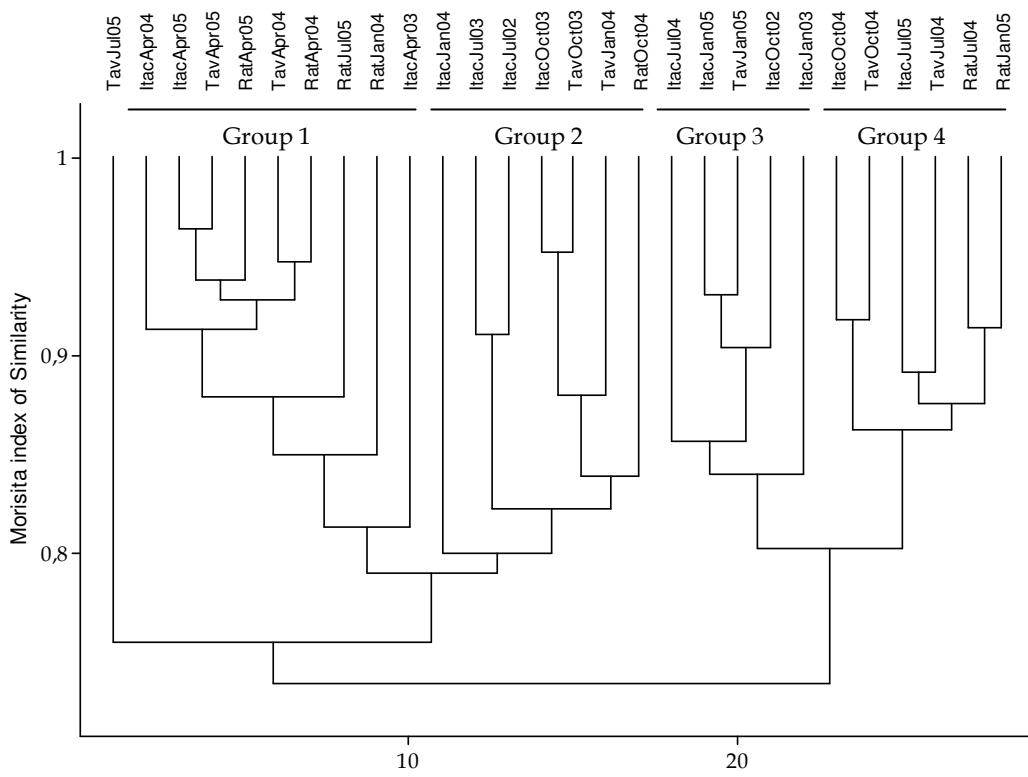
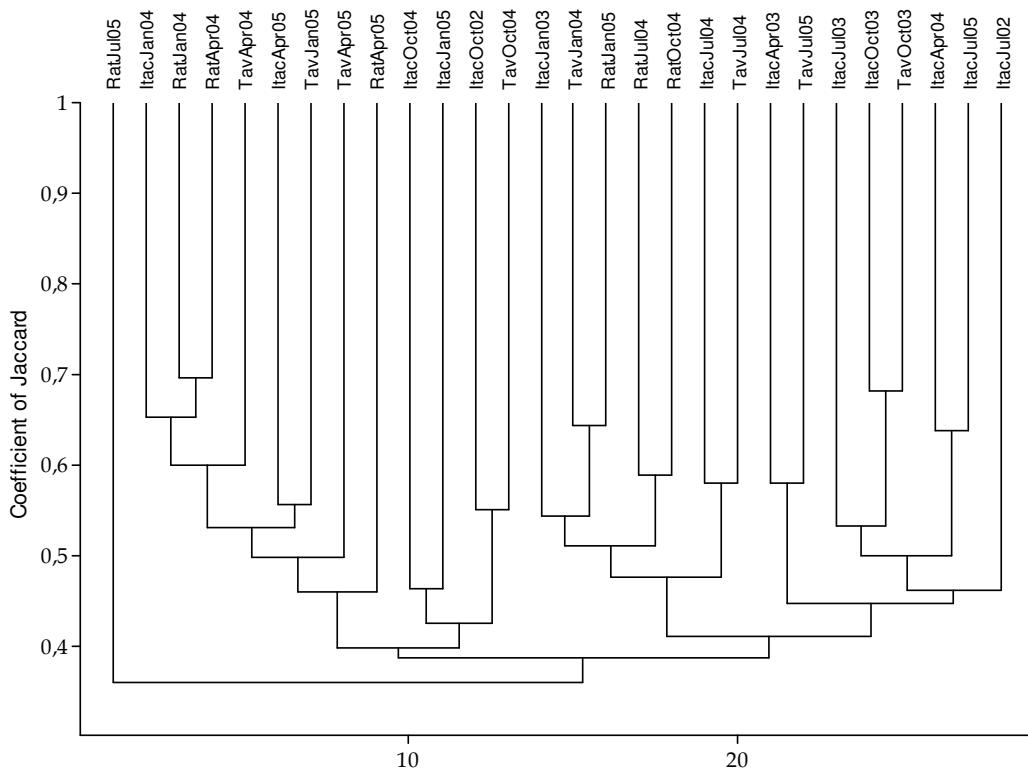


Figure 6



CAPÍTULO IV

Resultados e Discussão

Um total de 82.942 drosófilídeos foi analisado neste trabalho, a partir de uma série de 28 amostras coletadas nos três principais manguezais da ilha de Santa Catarina, SC, sul do Brasil, com o intuito de caracterizar as assembléias deste grupo de insetos existentes em tal ambiente. As principais conclusões, de acordo com os objetivos do trabalho são as que se seguem.

1. Levantamento taxonômico

Sessenta e nove espécies de drosófilídeos foram encontradas, distribuídas em seis gêneros. Da subfamília Drosophilinae ocorreram *Drosophila*, com 58 espécies, *Zygothrica*, com seis espécies, e *Scaptodrosophila* e *Zaprionus*, com uma espécie cada. Da subfamília Steganinae ocorreram duas espécies de *Amiota* e uma de *Leucophenga*.

Quatro subgêneros de *Drosophila* foram encontrados. O subgênero *Drosophila* foi o mais diverso, com 36 espécies de 11 grupos, além de duas não agrupadas. Os grupos presentes foram: *annulimana* (três espécies), *bromeliae* (uma espécie), *cardini* (quatro), *calloptera* (duas), *coffeata* (duas), *guarani* (cinco), *immigrans* (uma), *pallidipennis* (uma), *repleta* (seis), *tripunctata* (oito) e *virilis* (uma). O subgênero *Sophophora* teve 14 espécies e 3 grupos: *melanogaster* (cinco), *saltans* (quatro) e *willistoni* (cinco). Além disso, ocorreram *D. busckii* Coquillett e *D. flexa* Patterson & Mainland, únicas espécies presentes na região neotropical dos subgêneros *Dorsilopha* e *Siphlodora*, respectivamente. Seis espécies não determinadas não foram classificadas em nível subgenérico. Estas, juntamente com uma espécie do grupo *guarani*, outra do grupo *tripunctata* e uma não agrupada do subgênero *Drosophila* são muito provavelmente espécies não descritas.

Três grupos do gênero *Zygothrica* estiveram presentes, além de duas espécies não identificadas. Os grupos coletados foram *orbitalis* e *vittimaculosa*, com uma espécie cada, e *dispar*, com duas espécies. Os gêneros *Scaptodrosophila* e *Zaprionus* foram representados por *S. latifasciaeformis* (Duda) e *Z. indianus*

Gupta, respectivamente. As duas espécies de *Amiota* e a espécie de *Leucophenga* não foram determinadas e podem, também, ser espécies não descritas.

De acordo com as curvas do coletor de cada um dos locais, o número de espécies não se estabilizou, o que indica que mais espécies poderiam ser encontradas caso mais coletas fossem realizadas. A riqueza de espécies final de cada manguezal pesquisado foi de 51 para o Itacorubi, 48 para Tavares e 45 para Ratones. Esta diferença pode ser reflexo do diferente esforço amostral em cada um dos pontos: Itacorubi foi amostrado 13 vezes, Tavares, oito, e Ratones, sete.

Em geral, a composição das assembleias de drosófilídeos dos manguezais é semelhante à encontrada em outros ambientes já pesquisados em Santa Catarina (De Toni & Hofmann, 1995; De Toni 1998 e 2002; Döge, 2003; Gottschalk, 2004; Oliveira, 2004; Bizzo, 2005), mas as abundâncias das espécies são alteradas. No entanto, a riqueza de espécies parece ser um pouco depauperada, já que, em geral, ela é mais elevada nos outros ambientes. Mesmo assim, a riqueza de espécies encontrada aqui pode ser considerada alta se comparada com trabalhos realizados em outras regiões (Brncic, 1987; Goñi *et al.*, 1998, Tidon, 2006).

Um importante diferencial das coletas de drosófilídeos realizadas nos manguezais foi a presença e grande abundância de um grupo relacionado de moscas, a família Curtonotidae, considerada por Grimaldi (1990) grupo-irmão de Drosophilidae. Estas moscas não têm sido encontradas em nenhum outro ambiente estudado por nosso grupo de pesquisa em Santa Catarina e não há relatos de alguma associação semelhante na literatura sobre drosófilídeos. É comum ocorrer a presença de uma fauna associada às coletas de drosófilídeos, como outros dipteros, lepidópteros, coleópteros, neurópteros, aranhas e outros, mas não de forma tão acentuada como no caso dos curtonotídeos em manguezais, que várias vezes chegaram a ultrapassar os drosófilídeos em abundância. Três morfoespécies foram identificadas. As moscas foram determinadas como pertencentes à família Curtonotidae segundo a chave de Borror, Triplehorn & Johnson (1992) e ao gênero *Curtonotum* de acordo com

Sturtevant (1921), Malloch & McAtee (1924), Malloch (1930), Patterson & Mainland (1944) e Delfinado (1969). Até o momento nenhuma das morfoespécies encontradas foi reconhecida como alguma das espécies já descritas. As abundâncias de cada uma delas, por local, estão mostradas na tabela 1.

Tabela 1. Abundâncias das morfoespécies de *Curtonotum* encontradas, por local.

	Itacorubi	Tavares	Ratones
<i>Curtonotum</i> sp1	7.374	38.188	1
<i>Curtonotum</i> sp2	123	23	5
<i>Curtonotum</i> sp3	-	-	112

A família Curtonotidae comprehende apenas três gêneros, dos quais muito pouco se conhece. Sobre sua história natural, há relatos de comportamento crepuscular, de preferência por ambientes pouco iluminados, de utilização de tocas de mamíferos como abrigo e de ocorrência em ambientes próximos à água (Meier, Kotrba & Barber, 1997; Pollock, 2002). Seus hábitos alimentares são igualmente pouco conhecidos. Os raros registros citam fezes, insetos mortos e frutos ("sand cherries") para adultos e posturas em decomposição de gafanhoto para larvas, embora não se possa ainda considerar tal comportamento como regra geral (Meier *et al.*, 1997).

Exemplares adultos de *C. sp1* coletados em campo e mantidos vivos em laboratório foram observados alimentando-se em banana e em meio de cultura padrão para *Drosophila*. No entanto, estas moscas não puderam ser mantidas em cultura, pois os adultos morreram sem deixar descendência. Ovos puderam ser observados no papel de pouso e nas paredes dos tubos de cultura, mas estes não se desenvolveram. Este comportamento de ovoposição em laboratório é diferente dos drosófilídeos, que ovopositem no meio de cultura. Se isto for reflexo do que ocorre na natureza, é possível que os curtonotídeos, apesar de os adultos serem atraídos pelas iscas de banana, se utilizem de outro recurso que não os frutos fermentados para a ovoposição.

São registradas 21 espécies de *Curtonotum* para a região Neotropical (Wirth, 1975). No entanto, informações novas praticamente não são obtidas desde a década de 1930. Exemplares de todas as morfoespécies e dos ovos de *C. sp1* foram mantidos em etanol 70% para posterior análise. Atualmente estão sendo analisados em comparação com as espécies descritas e caracterizados de acordo com a morfologia externa e de genitálias masculina e feminina.

2. Estrutura das assembléias

As assembléias de drosófilídeos dos manguezais mostraram-se bastante dominadas por uma espécie: *D. simulans* Sturtevant. Esta espécie, pertencente ao grupo *melanogaster* e com *status* de cosmopolita, é bastante comum em ambientes antropizados (Val, Vilela & Marques, 1981; Gottschalk, 2004), mas, das espécies exóticas, é a que melhor se adaptou aos ambientes naturais do Brasil (Sene *et al.*, 1980). Neste trabalho, representou 56% dos drosófilídeos coletados, sendo quase sempre a espécie mais comum. Outra espécie do mesmo grupo, *D. malerkotliana* Parshad & Paika, totalizou 21% dos indivíduos coletados. É também uma espécie exótica, que invadiu a região Neotropical apenas recentemente (Val & Sene, 1980). Em Santa Catarina, é comum na cidade (Gottschalk, 2004), mas rara na mata (Döge, 2003; Oliveira, 2004). Com abundância relativa de 5% apareceram três espécies: *Z. indianus*, *D. mediostriata* Duda e *D. willistoni* Sturtevant. *Z. indianus* é uma espécie exótica, invasora muito recente do Neotrópico (Vilela, 1999; De Toni, Hofmann & Valente, 2001) e bastante comum em ambientes abertos (Tidon, Leite & Leão, 2003) e urbanizados (Gottschalk, 2004), mas rara nas matas (Döge, 2003; Oliveira, 2004). Já *D. mediostriata* é uma espécie nativa, rara em outros ambientes. Sua grande abundância no manguezal pode estar relacionada com a utilização de flores em decomposição de *Hibiscus tiliaceus* L. como sítio de ovoposição, já que muitos adultos desta espécie de mosca emergiram destas flores que foram coletadas e levadas ao laboratório. Esta planta, embora não esteja presente no interior do manguezal, é a que mais penetra na floresta a partir das bordas, estando em uma situação intermediária entre as espécies de manguezal e as demais

comunidades vegetais. Por sua vez, *D. willistoni* costuma ser dominante nas áreas florestadas do Neotrópico (Dobzhansky & Pavan, 1950, Ehrman & Powell, 1992), o que ocorre também em Santa Catarina (De Toni & Hofmann, 1995; Döge, 2003; Oliveira 2004). Outras espécies que atingiram abundância relativa total igual ou superior a 1% foram *D. paulistorum* Dobzhansky & Pavan (3%), *D. repleta* Wollaston (1%), *D. polymorpha* Dobzhansky & Pavan (1%) e *D. mercatorum* Patterson & Wheeler (1%), todas neotropicais.

A distribuição das abundâncias das espécies, com poucas espécies dominantes e muitas raras, mostrou-se ajustar a um modelo lognormal (média=-1,492, variância=4,454, $p=0,580$), que segundo Magurran (1988) é bastante comum em comunidades biológicas e normalmente se aplica a assembleias grandes, maduras e variadas.

A figura 1 mostra o número de indivíduos (N) capturado em cada amostra. Em média, o valor de N foi de 2.962,2, mas houve uma variação bastante grande (desvio padrão: $s=4.735,56$; coeficiente de variação: CV%=159,87%), com amplitude entre 109 e 20.410 indivíduos.

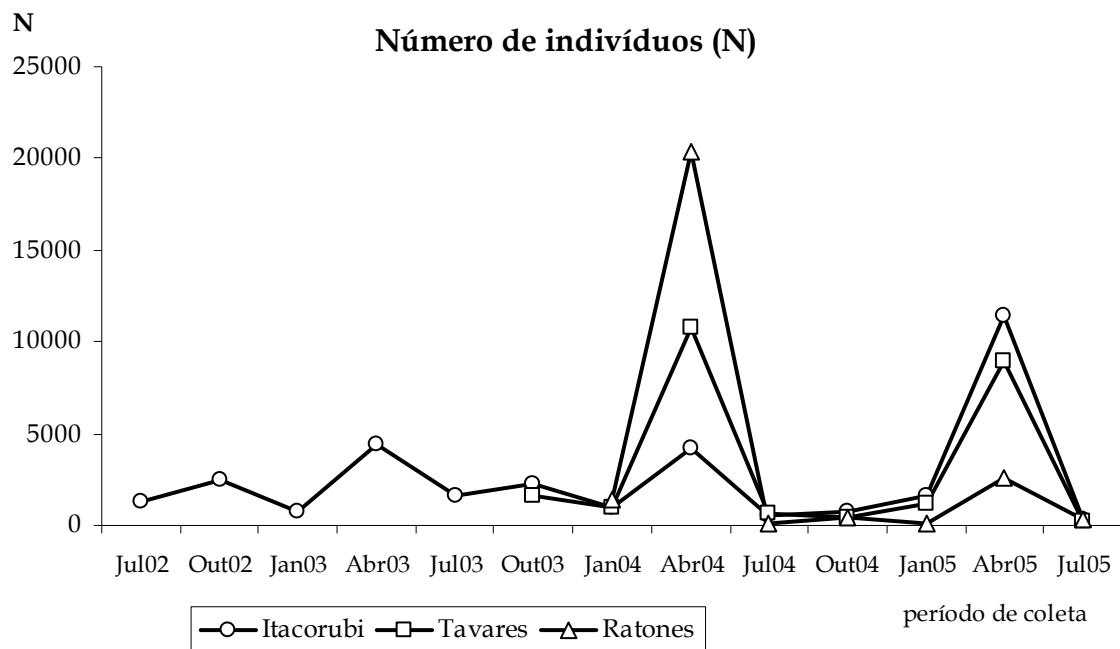


Figura 1. Oscilações no número de indivíduos (N) coletados em cada amostra.

Foi observada uma média de 17,5 espécies por amostra ($s=4,54$; $CV\%=25,94\%$), com um mínimo de sete e um máximo de 29. As flutuações na riqueza de espécies observada (S_{obs}) podem ser vistas na figura 2.

No entanto, de acordo com a estimativa de riqueza de espécies pelo método de rarefação (S_{rar}), a média foi de 7,8 espécies por amostra padronizada em 101 indivíduos ($s=1,87$; $CV\%=23,97\%$), com amplitude entre 5,2 e 12,2. As variações neste parâmetro entre as amostras podem ser vistas na figura 3.

O índice de diversidade de Shannon e Wiener (H') apresentou valor médio de 1,14 ($s=0,349$; $CV\%=34,42\%$), variando de 0,65 a 1,93. A figura 4 mostra os valores deste índice para cada amostra analisada.

Já o índice de eqüitabilidade de Smith e Wilson (E_{var}) atingiu média de 0,18 ($s=0,076$; $CV\%=42,22\%$), com valores entre 0,08 e 0,36. As variações na eqüitabilidade entre as amostras podem ser vistas na figura 5.

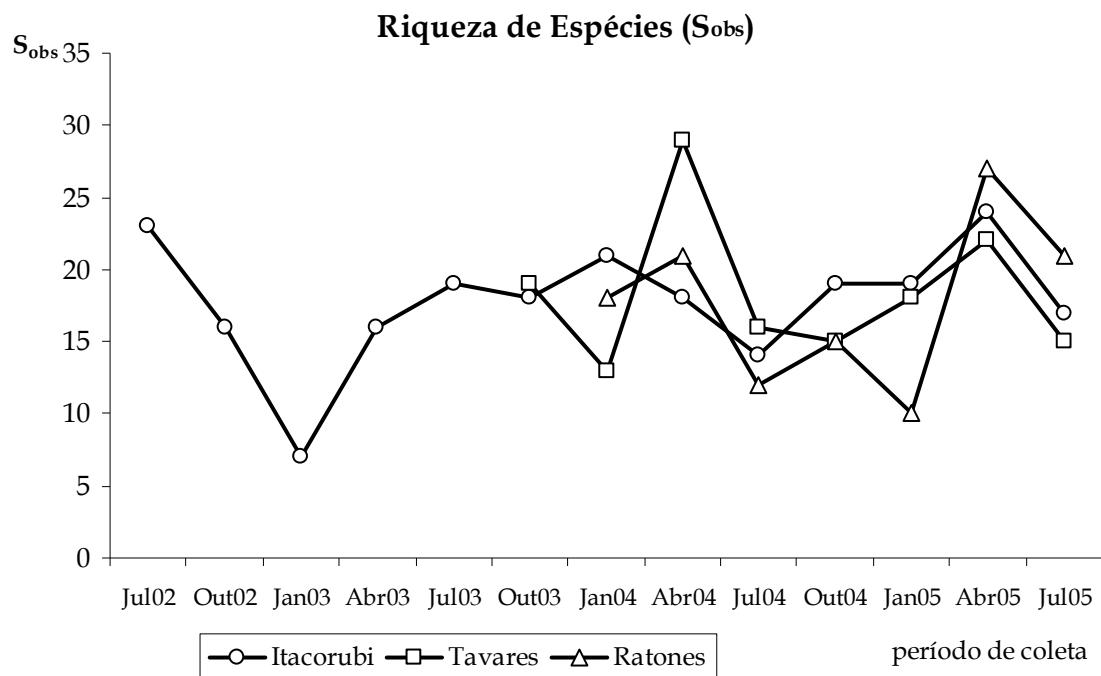


Figura 2. Oscilações na riqueza de espécies observada (S_{obs}) em cada amostra.

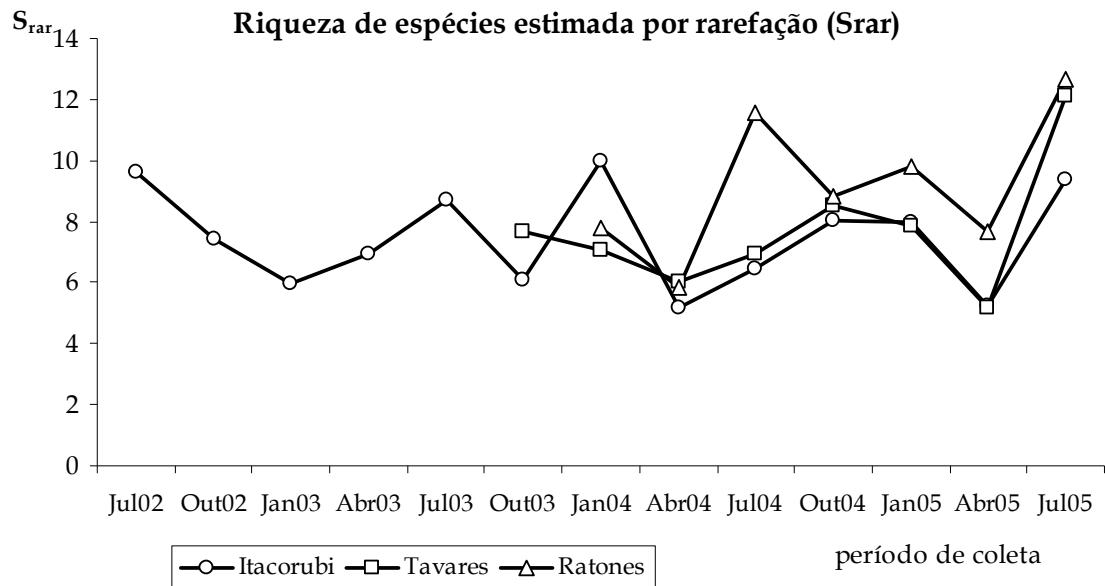


Figura 3. Oscilações na riqueza de espécies estimada por rarefação (S_{rar}), para 101 indivíduos, em cada amostra.

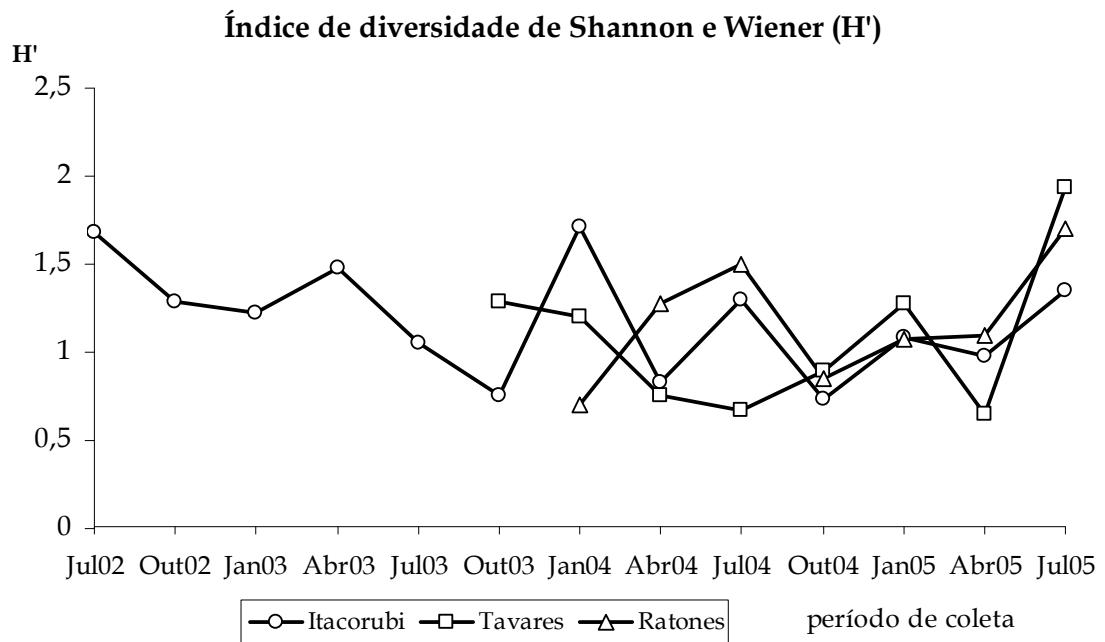


Figura 4. Oscilações no índice de diversidade de Shannon e Wiener (H') em cada amostra.

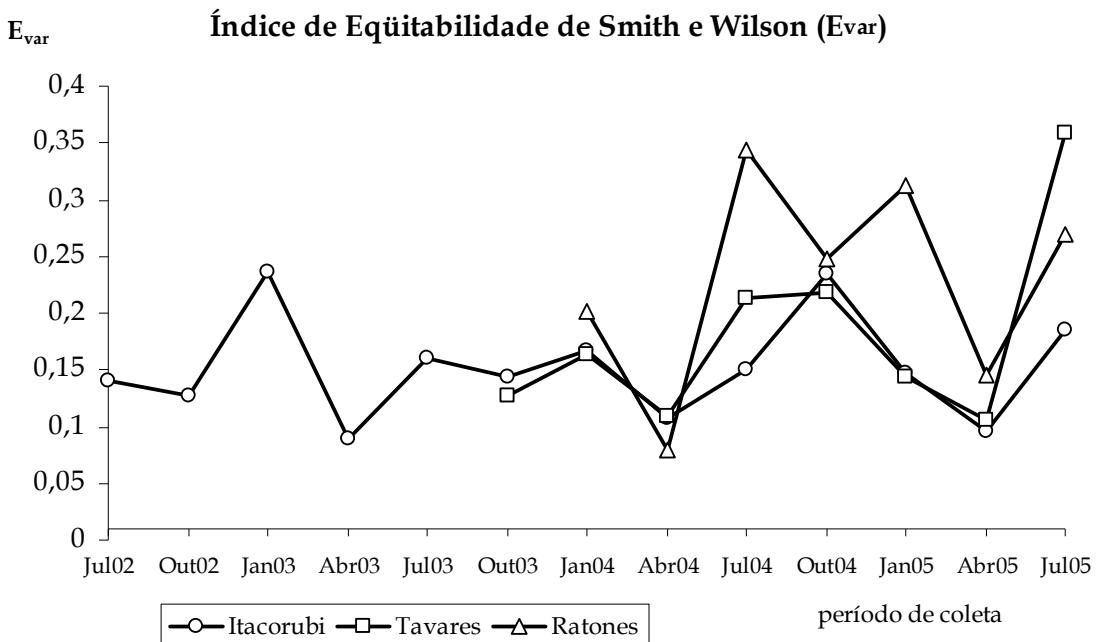


Figura 5. Oscilações no índice de eqüitabilidade de Smith e Wilson (E_{var}) em cada amostra.

3. Variação espacial

Os três manguezais mostraram-se bastante homogêneos quanto aos aspectos relacionados às assembleias de drosófilídeos. O componente espacial explicou apenas 7,8% da diversidade observada e amostras dos diferentes locais apresentaram alta similaridade na composição de espécies, medida pelo coeficiente de Jaccard, e na estrutura, medida pelo índice de Morisita.

Todas as espécies, exceto uma, apresentaram abundâncias semelhantes nos três manguezais. A única exceção foi *D. mercatorum* ($H_c=9,12$, $p=0,011$), mais rara em Ratones do que em Itacorubi ($Q=2,675$, $p<0,05$) e Tavares ($Q=2,708$, $p<0,05$). Também não foi encontrada diferença significante na abundância quando consideradas as espécies exóticas em conjunto, bem como as nativas.

As medidas de diversidade também se mostraram homogêneas entre os locais, não havendo variação espacial no índice de diversidade de Shannon e Wiener (H'), no índice de eqüitabilidade de Smith e Wilson (E_{var}), na riqueza de

espécies observada (S_{obs}), na riqueza de espécies estimada pelo método de rarefação (S_{rar}) e no número de indivíduos (N).

Os manguezais estudados diferem em seus ambientes vizinhos e no grau de perturbação apresentado. O manguezal do Itacorubi está rodeado pela principal zona urbana de Florianópolis e sofre intensa ação antrópica. Já, o manguezal do Tavares localiza-se em uma região de média urbanização, enquanto o manguezal de Ratones situa-se em uma estação ecológica, rodeado por outras formações vegetais como mata atlântica, restinga e brejos. Respostas a gradientes de urbanização têm sido encontradas em assembleias de drosófilídeos de diversos locais, como na cidade de Oxford, EUA (Avondet *et al.*, 2003), em Brasília-DF, no cerrado brasileiro (Ferreira & Tidon, 2005) e mesmo em Florianópolis, na ilha de Santa Catarina (Gottschalk, 2004). No entanto, nenhum gradiente foi encontrado nas assembleias dos manguezais. A homogeneidade dos manguezais quanto à composição florística e condições abióticas parece desempenhar um papel mais importante na formação das assembleias de drosófilídeos deste ambiente que os diferentes graus de perturbação antrópica e os ambientes vizinhos. Mesmo que os indivíduos encontrados no interior dos manguezais sejam migrantes dos ambientes vizinhos, como sugerido pela falta de recursos no local, o manguezal parece impor um filtro seletivo na chegada destes migrantes, de modo que a abundância de cada espécie é alterada, diferindo da encontrada em outros ambientes, mas sendo semelhante entre os manguezais. A presença nos manguezais parece exigir uma performance mais versátil e oportunista, como a de espécies exóticas. Além disso, embora bastante úmido, a salinidade e a luminosidade existente nos manguezais deve impor condições relativamente severas para o controle hídrico das moscas, o que selecionaria espécies adaptadas a ambientes mais áridos, como a maior parte das espécies mais abundantes encontradas.

4. Variação temporal

A variação temporal mostrou-se importante nas assembleias de drosófilídeos dos manguezais da ilha de Santa Catarina, tanto em relação às abundâncias de espécies quanto aos valores de parâmetros de diversidade.

Várias espécies mostraram sazonalidade marcante. Destas, a maior parte experimentou expansões populacionais durante o outono, representado pelas amostras de abril. Foi o caso da espécie dominante, *D. simulans*, que apresentou ainda, aparentemente, um pico secundário na primavera (amostras de outubro). Semelhante comportamento sazonal já havia sido descrito por Franck & Valente (1985), em Bento Gonçalves, no estado do Rio Grande do Sul. No entanto, a sazonalidade mais acentuada entre todas as espécies foi a de *D. malerkotliana*, que se mostrou uma das espécies dominantes no outono, mas manteve-se rara nas demais estações. Outras espécies também se mostraram mais abundantes durante o outono. Foi o caso de *D. caponei* Pavan & Cunha, *D. polymorpha*, *D. sgr. willistoni*, *D. sturtevanti* Duda e *Z. indianus*. Por outro lado, *D. repleta* teve abundâncias mais baixas nesta estação e mais altas durante o inverno (amostras de julho), enquanto *D. hydei* Sturtevant apresentou picos na primavera.

Algumas espécies mostraram picos não significantes do ponto de vista estatístico, talvez por serem menos acentuados. Foi o caso de *D. ananassae* Doleschall, *D. capricorni* Dobzhansky & Pavan e *D. nebulosa* Sturtevant, no outono, e *D. mercatorum*, na primavera. Já *D. melanogaster* Meigen, *D. neocardini* Streisinger, *D. pallidipennis* Dobzhansky & Pavan e *D. griseolineata* Duda mostraram pouca variação de abundância no período amostrado. Por fim, uma espécie de comportamento peculiar foi *D. mediostriata*, que apresentou picos bastante acentuados em algumas ocasiões, mas parecendo não ter relação com fatores sazonais, já que se repetiram em estações diferentes a cada ano - outubro de 2002, julho de 2003 e janeiro de 2004. Alguma relação com a utilização de flores de *Hibiscus tiliaceus* como sítio de ovoposição, como observado a partir de flores coletadas nos locais, pode estar envolvida na dinâmica de populações desta espécie. As demais espécies foram consideradas raras ($N < 30$) e não foram analisadas.

Análises de sobreposição de nicho e de correlação entre abundâncias das espécies mais comuns revelaram que a maior parte delas responde de forma semelhante às variações temporais. As exceções mais marcantes foram *D. mediotriata*, que embora apresente fortes flutuações no tamanho das populações, não parece responder a fatores que operam sazonalmente, e as espécies do grupo *repleta* - *D. repleta*, *D. mercatorum* e *D. hydei* - que apresentaram comportamento sazonal oposto à maioria das espécies.

Também foram observadas fortes variações sazonais em parâmetros como número de indivíduos (N), riqueza de espécies observada (S_{obs}) e estimada por rarefação (S_{rar}) e eqüitabilidade (E_{var}). Enquanto N e S_{obs} atingiram valores mais elevados no outono, S_{rar} e E_{var} mostraram-se mais elevados no inverno, e menores no outono. Por outro lado, o índice de diversidade de Shannon e Wiener (H') não mostrou sazonalidade marcada.

Fatores temporais que não operam de forma sazonal também parecem afetar as assembléias de drosófilídeos nos manguezais. Estimou-se que a variação sazonal seja responsável por 12,18% da diversidade, enquanto a variação anual contribui com 6,91% e outras variações temporais com 19,88%. Variações não-sazonais parecem ter sido importantes, por exemplo, na dinâmica das populações de *D. mediotriata*, anteriormente citada. Variações de abundância aparentemente não cíclicas também foram observadas em outras espécies. *D. repleta* teve um período de maior abundância entre julho de 2004 e julho de 2005, enquanto *Z. indianus* teve um crescimento populacional entre julho de 2003 e janeiro de 2004. *D. sgr. willistoni* mostrou-se mais abundante entre julho de 2002 e julho de 2003 e *D. nebulosa* pareceu ter tido um pico populacional em abril de 2004.

A análise de similaridade entre as amostras de acordo com o coeficiente de Jaccard, ou seja, com a composição de espécies, mostrou que parece haver uma pequena modificação nas assembléias comparando os períodos de verão e outono, por um lado, e inverno e primavera, por outro. Já o índice de Morisita evidenciou estruturas típicas das assembléias no outono, marcadas pela alta abundância de *D. malerkotliana*. Entretanto, as demais estações não

apresentaram estruturas típicas, sendo mais semelhantes com os períodos adjacentes do que com a mesma estação de anos seguintes. Estes resultados dão às assembléias de drosófilídeos dos manguezais um alto grau de imprevisibilidade. A dominância de *D. simulans* durante todo o ano e a de *D. malerkotliana* no outono são aspectos estáveis de tais assembléias, mas as abundâncias de espécies secundárias são bem menos previsíveis.

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ANEXOS

INSTRUÇÕES AOS AUTORES

- [Política editorial](#)
- [Forma e preparação de manuscritos](#)
- [Normas para publicação](#)

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Burr FA, Evert RF. 1982. A cytochemical study of the wound-healing proteins in *Bryopsis hypnoides*. *Cytobios* **6**: 199-215.

Gould SJ. 1989. *Wonderful life: the Burgess Shale and the nature of history*. New York: W.W. Norton.

Dow MM, Cheverud JM, Rhoads J, Friedlaender J. 1987b. Statistical comparison of biological and cultural/history variation. In: Friedlaender J, Howells WW, Rhoads J, eds. *Solomon Islands project: health, human biology, and cultural change*. New York: Oxford University Press, 265-281.

Gay HJ. 1990. The ant association and structural rhizome modifications of the far eastern fern genus *Lecanopteris* (Polypodiaceae). Unpublished D. Phil. Thesis, Oxford University.

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