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UTILIZAÇÃO DE RECURSOS TRÓFICOS POR ESPÉCIES NEOTROPICAIS DE DROSOPHILIDAE (DIPTERA)

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Área de Concentração: Biodiversidade

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SUMÁRIO

RESUMO

O estudo da interação entre os indivíduos de uma mesma espécie ou de espécies diferentes é essencial para o entendimento das dinâmicas envolvidas na manutenção das comunidades ou assembléias na natureza. Assim, o estudo das preferências alimentares das larvas dos drosofilídeos, refletidas no padrão de emergência das mesmas dos sítios de oviposição, é de suma importância, uma vez que este grupo de organismos tornou-se um excelente modelo para o estudo de padrões ecológicos. Assim, esta tese busca identificar como as larvas de espécies de Drosophilidae se relacionam na utilização dos recursos tróficos, identificando quais os principais fatores que podem estar atuando na manutenção da diversidade de espécies de suas assembléias em áreas de Mata Atlântica e urbanas de Florianópolis (SC). Realizamos coletas de frutos em onze localidades do Estado de Santa Catarina, onde montamos uma listagem das espécies vegetais hospedeiras utilizadas como sítio de oviposição e das espécies de Drosophilidae que as utilizam. Observamos que as espécies de Drosophilidae colonizam os ambientes urbanos estudados, mas há uma perda de diversidade de espécies, evidenciada pela ausência de espécies raras nestas amostras. Ainda, as espécies de Drosophilidae coletadas apresentaram um caráter generalista quanto à utilização dos recursos tróficos, onde, nas assembléias de Mata Atlântica, verificou-se a formação de grupos ecológicos funcionais. Este tipo de organização não foi observado nas assembléias urbanas, onde há uma grande sobreposição dos nichos e uma menor diversidade de espécies.

Além dos frutos, foram coletados também corpos de frutificação de fungos a fim de verificarmos as espécies de Drosophilidae emergentes dos mesmos. Dentre as espécies de moscas emergentes estão as dos gêneros *Drosophila*, *Hirtodrosophila*, *Mycodrosophila* e *Leucophenga*. Cabe ressaltar que as espécies neotropicais da radiação *immigrans-tripunctata*

(gênero *Drosophila*) possuem a capacidade de colonizar fungos em ambientes preservados e alterados do bioma Mata Atlântica.

Em outro estudo, buscamos verificar como a limitação de recursos alimentares para as larvas de drosofilídes pode influenciar a interação competitiva entre as mesmas. Para tal, foram coletados frutos de *Buchenavia tomentosa* (Combretaceae) e submetidos a dois tratamentos, um deles com uma suplementação alimentar. Assim, obtivemos evidências de que há restrições alimentares ou nutricionais em recursos naturais, que aumentam a interação competitiva entre espécies da família Drosophilidae. Entretanto, estas espécies possuem diferentes respostas à esta limitação, e o aumento da competição interespecífica parece ser maior que da intraespecífica.

Finalmente, foi realizada uma revisão da ocorrência das espécies de Drosophilidae no Brasil, onde foram levantadas 304 espécies coletadas em nosso território. A maioria dos registros é de espécies do gênero *Drosophila*, o mais bem estudado da família. Os estados mais bem amostrados até o momento são São Paulo, Rio de Janeiro, Rio Grande do Sul e Santa Catarina, além do Distrito Federal, onde há grupos de pesquisa enfocando a ecologia e taxonomia das espécies de Drosophilidae. Esta revisão auxiliou na avaliação dos objetivos anteriores, contribuindo com um panorama do conhecimento e distribuição desta moscas no Brasil.

ABSTRACT

The study of the interaction among the individuals of a same species or of different ones is essential for the understanding of the dynamics involved in the communities or assemblies maintenance in nature. Thus, the study of the alimentary preferences of the drosophilids larvae, evidenciated by their emergency pattern of the breeding sites, is of highest importance once that this group of organisms became an excellent model for the study of ecological patterns. So, this thesis aimed to identify how the larvae of the Drosophilidae species use the trophic resources, identifying the main factors that can be acting in the maintenancement of the species diversity of assemblies in areas of Atlantic Rain Forest and urbanized of Florianópolis (SC). We collected fruits in eleven locations of the State of Santa Catarina, and we listed the vegetable host species used as breeding sites and the Drosophilidae species emerged of them. We observed that the Drosophilidae species colonize the studied urban environments, but there is a loss of species diversity, evidenced by the absence of rare species in these samples. Although, the collected Drosophilidae species presented a generalist character for the use of the trophic resources, where, the formation of functional ecological groups was verified in the assemblies of Atlantic Rain Forest. This kind of organization was not observed in the urban assemblies, where there are a high niche overlap and lower species diversity.

Besides fruits collections, were carried out collections of fungi bodies of fructification in order to verify their emerging Drosophilidae species. Among the emerging fly species are the ones of the *Drosophila*, *Hirtodrosophila*, *Mycodrosophila* and *Leucophenga* genera. It to be useful to emphasize that the Neotropical species of the *immigrans-tripunctata* radiation (*Drosophila* genus) have capacity to colonize mushrooms in preserved Atlantic Rain Forest and antropic environments.

In another study, we search for how the limitation in trophic resources for drosophilid larvae could influence the competitive interaction among them. For such, fruits of *Buchenavia tomentosa* (Combretaceae) were collected and submitted to two treatments, one of them with an alimentary supply. Thereby, we obtained evidences that there are alimentary or nutritional restrictions in natural resources, which increase the competitive interaction among species of the family Drosophilidae. However, these species have different answers to this limitation, and the increase of the interspecific competition seems to be larger than of the intraspecific.

Finally, a revision of the occurrence of the Drosophilidae species in Brazil was accomplished, where were found 304 species recorded in our territory. Most of the records is of species of the *Drosophila* genus, the best studied of the family. The better evalueted states until the moment are São Paulo, Rio de Janeiro, Rio Grande do Sul and Santa Catarina, besides Distrito Federal, where there are research groups focusing the ecology and taxonomy of the Drosophilidae species. This revision helped us in the evaluation of the previous objectives, contributing with a panorama of the knowledge and distribution of these flies in Brazil.

CAPÍTULO 1

INTRODUÇÃO E OBJETIVOS

APRESENTAÇÃO

Quando proposto, meu projeto de doutorado visava estudar as interações entre espécies de Drosophilidae (Diptera), especificamente em ambientes urbanos de Florianópolis (SC) pois, durante o levantamento da fauna desta família em um gradiente de urbanização, realizado durante o meu mestrado, registrou-se um número bastante elevado de espécies em área urbana. Esses resultados foram de encontro ao descrito na literatura a respeito da fauna urbana de insetos, inclusive a de drosofilídeos, onde a cidade é considerada pobre em espécies. Assim, a princípio, o objetivo do projeto se restringia a buscar indicativos de que as espécies frugívoras de drosofilídeos poderiam estar se mantendo no ambiente urbano e de quais seriam os fatores que influenciariam em sua sobrevivência.

Entretanto, à medida que o projeto foi sendo executado, foram se abrindo oportunidades para desenvolver a temática da interação estas espécies de forma mais abrangente. Uma destas oportunidades foi a disponibilização dos dados obtidos durante o doutoramento da Prof^{a}. Dr^{a}. Daniela C. De Toni (colaboradora de nossos estudos), a quem eu tive o prazer de ajudar nas coletas durante a minha graduação e mestrado. Estes dados consistem numa listagem de espécies de drosofilídeos e dos frutos dos quais eles emergiram, em coletas realizadas nos anos de 1999 e 2000, em oito áreas de Mata Atlântica de Florianópolis. Somados a elas, foram realizadas coletas de frutos, em ambientes de Mata Atlântica e urbanos de Florianópolis, entre os anos de 2002 e 2003, concomitantemente às minhas coletas do mestrado e, mais recentemente, em 2005, durante o meu doutorado. Portanto, esta tese apresenta um levantamento das espécies de Drosophilidae e suas plantas hospedeiras na região de Florianópolis, tanto para áreas de Mata Atlântica como para ambientes urbanos (Capítulo 2), que difere da maioria dos trabalhos que vêem sendo realizados e que utilizam iscas de bananas nos levantamentos. Além disso, buscamos traçar relações entre o padrão de colonização das plantas hospedeiras pelos drosofilídeos com as variações ambientais, espaciais, sazonais e de disponibilidade de recursos.

Em outra abordagem, buscamos demonstrar a influência da quantidade de recursos tróficos disponíveis sobre as interações entre espécies de Drosophilidae em frutos no campo (Capítulo 3). Parte da comunidade estudada foi transportada ao laboratório e submetida a diferentes níveis de disponibilidade de alimento. Este experimento foi realizado em Tangará da Serra (MT), com um fruto nativo – *Buchenavia tomentosa* (Combretaceae) – em colaboração com a Prof^{a}. M.Sc. Monica L. Blauth, que auxiliou na coleta e análise dos dados, e possibilitou o uso dos laboratórios da Universidade do Estado de Mato Grosso (UNEMAT). Encontramos um aumento na interação competitiva entre as duas principais espécies coletadas no estudo em função da diminuição da disponibilidade de alimento. Um manuscrito foi gerado e submetido à apreciação pela revista *Oecologia*.

Outra oportunidade foi de estudar a colonização de corpos de frutificação de fungos por espécies de Drosophilidae, com a colaboração do M.Sc. Luís E. M. Bizzo (doutorando da Universidade de São Paulo – USP), do Prof. M.Sc. Jonas S. Döge (UFRGS) e do Biólogo Marcos S. Profes (enquanto acadêmico da UFRGS). Muito pouco se sabe sobre as espécies de Drosophilidae que colonizam fungos na região Neotropical, principalmente no Brasil. Assim, foram realizadas coletas de fungos e levantadas as espécies que deles emergiram (Capítulo 4). As coletas foram conduzidas em três estados brasileiros – São Paulo, Santa Catarina e Rio Grande do Sul – em ambientes de Mata Atlântica e urbanizados, onde foram relatadas diferenças nas espécies colonizadoras em função do ambiente onde o fungo se desenvolvia e da espécie de fungo coletada. Este levantamento resultou em um manuscrito que foi submetido à apreciação pela revista *Iheringia*, *série Zoologia*.

Já o Capítulo 5 apresenta uma revisão das espécies de Drosophilidae que possuem ocorrência no Brasil. Este trabalho foi desenvolvido e apresentado como Qualificação do Doutorado, sendo submetido à apreciação pela revista *Checklist*, e surgiu da necessidade, minha e de vários colegas, de uma listagem atualizada dos drosofilídeos ocorrentes no Brasil. Nele, é relatado o registro de 308 espécies da família no Brasil, com uma concentração maior de coletas e registros nas regiões Sudeste e Sul, onde se encontram os maiores grupos de pesquisa de Drosophilidae.

A influência da urbanização em assembléias de drosofilídeos na cidade de Florianópolis é o tema abordado no Capítulo 6 desta tese. Este artigo foi publicado em colaboração com a Prof^{a}. Dr^{a}. Daniela C. De Toni na revista *Neotropical Entomology* e é fruto das coletas realizadas durante meu mestrado, às quais tive a oportunidade de enriquecer com novas análises durante o Doutorado.

Finalmente, o último Capítulo discute os principais resultados obtidos nesta tese e as perspectivas para estudos futuros.

NICHO ECOLÓGICO E COMPETIÇÃO

Desde a primeira vez que foi usado por Ernest Haeckel, em 1869, o termo **Ecologia** foi conceituado diversas vezes por diferentes autores (BEGON *et al.* 2006). Atualmente, vem sendo atribuído à Ecologia o estudo da distribuição e da abundância dos organismos, incluindo as interações que as determinam (ODUM & BARRET 2005, BEGON *et al.* 2006). Estas interações podem ocorrer entre organismos que coabitam uma determinada área ou entre organismos e os fatores ambientais que o cercam, como o tipo de solo, temperatura, umidade, luminosidade.

Diretamente associado ao segundo tipo de interação mencionado, organismo *vs.* ambiente, originou-se o conceito do **nicho ecológico**. Este conceito, assim como o da própria ecologia, já passou por diversas mudanças até chegar ao que é hoje, e mesmo hoje em dia há variações em sua definição. Alguns autores atribuem ao nicho as respostas fisiológicas dos organismos às variações ambientais, ou o designam como o papel do organismo no ambiente, ou ainda vinculam o nicho ao ambiente onde um organismo é capaz de sobreviver (UDVARDY 1959, DEBACH 1966, STATZNER *et al.* 2001). Mas, desde Justus von Liebig, as definições de nicho ecológico vêm relacionando os organismos ao ambiente que os cercam. Este autor, em 1840, propôs a **lei do mínimo**, onde nicho ecológico é definido como as condições ambientais que um organismo necessita para sobreviver; Joseph Grinell, em 1924, atribuiu ao seu conceito a limitação na distribuição das diferentes espécies às barreiras físicas e climáticas; Charles S. Elton, em 1927, propôs o que chamamos hoje de nicho eltoniano e que significa o "lugar" do organismo no ambiente abiótico, suas relações com o alimento e com seus inimigos; e George E. Hutchinson propôs pela primeira vez, em 1957, o conceito do **nicho multidimensional** ou **nicho hipervolumétrico**, e que atualmente é o mais difundido pela comunidade acadêmica (DEBACH 1966, VANDERMEER 1972).

O **nicho multidimensional** de HUTCHINSON (1957) é definido como as condições ambientais em que os organismos de uma espécie ou população toleram ou persistem. Assim, considerando uma variável ambiental x, que possa ser ordenada ao longo de um eixo, podemos definir os valores mínimo (x') e máximo (x'') entre os quais os indivíduos da espécie em questão são capazes de sobreviver e reproduzir. A este eixo, podemos acrescentar um segundo eixo perpendicular, vinculado a uma segunda variável ambiental y, também com seus próprios valores de mínimo (y') e máximo (y''). Ligando estes quatro pontos teremos um retângulo (isto se estas variáveis forem independentes, senão teríamos outra forma), cuja área representa as possíveis combinações entre essas variáveis que permitem a persistência da espécie. Podemos continuar a acrescentar variáveis ambientais e, conseqüentemente, eixos até atingirmos um sistema ortogonal com as n variáveis que são importantes para tal espécie. Portanto, o nicho de uma espécie é definido como os pontos que se encontram dentro deste hipervolume n-dimensional e que podem proporcionar sua persistência indefinida. Entretanto, como lembrado por BEGON *et al.* (2006), temos que ter em mente que o nicho não é um local, e sim um conjunto de condições que são toleráveis e que preenchem todos os requisitos para o organismo sobreviver.

Normalmente, as interações entre espécies com nichos semelhantes são mutuamente negativas, isto é, diminuem o valor adaptativo dos indivíduos pela diminuição na quantidade de recursos disponíveis (DEBACH 1966, VANDERMEER 1972). Este tipo de interação é denominado **competição**. Em relação a este tipo de interação, HUTCHINSON (1957) foi o primeiro a aplicar o **princípio de Gause** ou das **leis da exclusão competitiva** (HARDIN 1960, MACARTHUR & LEVINS 1964, BARKER 1983, GOTELLI 2007) à idéia de nicho, que até então englobava principalmente a parte física do ambiente. O conceito apresentado no parágrafo anterior é o do **nicho fundamental**, que engloba toda a variação ambiental que permite uma espécie sobreviver (HUTCHINSON 1957, VANDERMEER 1972, ODUM & BARRET 2005, BEGON *et al.* 2006). Entretanto, os organismos não podem viver isolados e duas ou mais espécies podem acabar por sobrepor seus nichos, de forma a terem que disputar entre si as condições necessárias para suas sobrevivências, competindo. Neste caso, o nicho de uma espécie é deslocado por outra (DEBACH 1966). Este é o **nicho realizado**, onde as interações entre as espécies são levadas em conta e limitam as distribuições umas das outras (HUTCHINSON 1957, VANDERMEER 1972, ODUM & BARRET 2005, BEGON *et al.* 2006). Claro que podemos observar outros tipos de interações não competitivas, como o comensalismo, parasitismo e a predação, que diferem da competição em relação ao tipo de resposta (se negativa ou positiva) de uma espécie ao estímulo de outra, e vice-versa (ODUM & BARRETT 2005). Estes outros tipos de interação podem influenciar igualmente no nicho das diferentes espécies ou mesmo ajudá-las a coexistir (CHESSON 2000, MITSUI & KIMURA 2000).

Ainda, a competição não ocorre somente entre indivíduos de espécies diferentes. Na realidade, em certas circunstâncias, é mais provável que ocorra em indivíduos de uma mesma espécie. Neste caso, a competição é dita **intraespecífica**. Já, quando a competição ocorre entre indivíduos de espécies diferentes, ela é dita **interespecífica** (ODUM & BARRETT 2005).

Há três tipos de variáveis que devem ser consideradas no estudo do nicho das diferentes espécies (WHITTAKER *et al.* 1973): as **variáveis intercomunidades** ou **do hábitat**, as **variáveis intracomunidades** ou **do nicho** e as **variáveis de resposta da população**. As variáveis intercomunidades estão relacionadas com os padrões encontrados entre diferentes comunidades, pois atuam em uma grande escala espacial, como, por exemplo, as diferenças ambientais encontradas com o aumento da altitude ou latitude, a fertilidade e a umidade do solo, além dos gradientes entre as comunidades formados pelas respostas a estas variações. Já, as variáveis intracomunidades são localizadas e relacionadas com os padrões encontrados dentro das comunidades como, por exemplo, sua variação diária ou sazonal, o tamanho da presa ou a taxa de consumo de determinada planta por um consumidor primário. Por último estão as variáveis de resposta da população – a densidade, a distribuição, o sucesso reprodutivo ou a adaptabilidade (*fitness*) dos indivíduos. Todas estas variáveis são contínuas uma em relação à outra e, muitas vezes, não conseguimos distinguir as variáveis intracomunidades das intercomunidades. Quando isso ocorre, estas últimas variáveis podem ser chamadas de **variáveis ambientais** (WHITTAKER *et al.* 1973). Mesmo essas variáveis podem ser subdivididas durante a análise dos dados obtidos do estudo das comunidades, onde podemos encontrar referências ao nicho espacial, nicho temporal ou nicho trófico, por exemplo, dependendo do tipo de recurso ou variável a ser mensurado (DEBACK 1966, PIANKA 1973, KREBS 1999, KRONFELD-SCHOR & DAYAN 2003).

Dentro deste contexto, o estudo da competição entre as espécies tornou-se um dos grandes focos da Ecologia. Os primeiros estudos que buscaram mensurar esta interação em termos numéricos foram os de Alfred J. Lotka e de Vito Volterra. Estes autores propuseram, quase que concomitantemente, entre 1925 e 1926, as equações que modelam o crescimento populacional de determinada espécie sob a influência da interação com outras espécies – o **modelo de competição de Lotka-Volterra** (BEGON *et al.* 2006, GOTELLI 2007). Segundo o modelo de crescimento populacional logístico, dois fatores podem influenciar em uma população – sua **taxa de crescimento** (r) e a **capacidade suporte do ambiente** (K). O valor de r é dependente da taxa de natalidade e mortalidade da população em questão, assim como as taxas de emigração e imigração. O valor de K indica o número de indivíduos de determinada espécie que um ambiente consegue manter. Assim, a presença de uma segunda espécie, com nicho semelhante ao da primeira, pode alterar tanto a taxa de crescimento populacional quanto o valor de K, para a primeira espécie. Estas mudanças podem não ser recíprocas (e normalmente não são), e uma espécie pode ter uma capacidade competitiva maior do que outra. Diz-se que, nestes casos, a competição é assimétrica.

Há basicamente duas formas dos indivíduos competirem, por **interferência** ou por **exploração** (BIRCH 1957, CASE & GILPIN 1974, ODUM & BARRET 2005). A competição por interferência é caracterizada pela existência de uma interação direta de um indivíduo sobre outro, acarretando em uma mudança em sua distribuição e/ou fazendo com que o outro indivíduo responda a tal estímulo. Já, na competição por exploração um mesmo recurso é utilizado por mais de uma espécie e, como não há interação entre os indivíduos, a competição é dita indireta (CASE & GILPIN 1974, BARKER 1983, ODUM & BARRET 2005). Assim, dependendo do quanto os nichos são similares, podemos encontrar, teoricamente, condições em que populações de duas espécies podem não coexistir por muitas gerações, uma levando a outra à extinção (GOTELLI 2007).

Entretanto, em comunidades megadiversas encontramos um grande número de espécies coexistindo, sendo muitas delas próximas filogeneticamente e, conseqüentemente, possuindo nichos bastante similares (FUTUYMA & MITTER 1996, WIENS & GRAHAM 2005). A maioria das explicações dadas para a coexistência entre estas espécies é que elas não sobrepõem completamente seus nichos. Neste caso, haveria uma **partição dos recursos**, onde as espécies conseguiriam diferir de alguma forma seus nichos realizados (mesmo sobrepondo grandemente seus nichos fundamentais). Haveria, assim, uma grande **heterogeneidade ambiental** capaz de abrigar tais nichos (MACARTHUR 1958, HUTCHINSON 1959, MACARTHUR & LEVINS 1967, SCHOENER 1974, HOLT 1997, KRONFELD-SCHOR & DAYAN 2003), além de outros processos locais que poderiam estar atuando. Estes processos estariam vinculados à instabilidade e colonização do ambiente, uma vez que eles não são estáticos (embora possam ser estáveis) (ATKINSON & SHORROCKS 1981, 1984, HANSKI 1981, 1983, WILLIAMSON 1987, HOLT 1997, AMARASEKARE 2000, CHESSON 2000, BONSALL *et al.* 2002), ou à predação e parasitismo dos indivíduos da comunidade (HOLT 1977, HOLT & LOWTON 1994, KRIJGER 2000).

A FAMÍLIA DROSOPHILIDAE

A família Drosophilidae possui, atualmente, 3.991 espécies (BÄCHLI 2008) e, com exceção de regiões árticas, ela é encontrada em todo o globo, sendo registrada em todas as regiões biogeográficas (PATTERSON & STONE 1952, THROCKMORTON 1975). Várias delas são cosmopolitas ou subcosmopolitas (PARSONS & STANLEY 1981, MARKOW & O'GRADY 2005). Os membros desta família são muscoformes, possuindo de um a oito milímetros de comprimento e coloração variada, que vai do amarelo ao preto, passando pelo marrom (WHEELER 1981). Muitos gêneros podem apresentar diferentes graus de dimorfismo sexual, como hipercefalia e modificações no primeiro par de patas ou peças bucais (GRIMALDI & FENSTER 1989; MARKOW & O'GRADY 2005).

Drosophilidae é tradicionalmente subdividida em duas subfamílias monofiléticas, Steganinae e Drosophilinae (WHEELER 1981, GRIMALDI 1990, BÄCHLI *et al.* 2004). A subfamília Steganinae é composta por membros que compartilham um número maior de características pleisiomórficas para a família (THROCKMORTON 1975, GRIMALDI 1990) e inclui 29 gêneros, enquanto que Drosophilinae abriga nos seus 44 gêneros a maior parte das espécies da família, sendo *Drosophila* o maior deles (BÄCHLI 2008).

WHEELER (1981) menciona que, de uma forma geral, Diptera apresenta uma grande quantidade de espécies, sendo as características de diferenciação entre as famílias pouco marcantes, e a classificação dos exemplares dificultada. Esta dificuldade também se estende para dentro de Drosophilidae, onde é igualmente trabalhosa a identificação de suas espécies. Uma vez que grande parte delas é críptica, são necessários métodos mais refinados do que a observação do aspecto da morfologia externa dos exemplares para sua identificação, como análises de isozimas ou de cromossomos (BRNCIC *et al.* 1971, GARCIA *et al.* 2006), ou a dissecação da genitália, em especial a masculina (STURTEVANT 1921, HSU 1949, BREUER &

ROCHA 1971, VILELA & BÄCHLI 1990). É importante observar que algumas destas espécies crípticas estão em pleno processo de diferenciação, sendo que seu estudo torna-se uma verdadeira observação dos processos evolutivos que as influenciam.

Neste sentido, há exemplos bastante interessantes, como o das espécies pertencentes ao subgrupo *mulleri* (grupo *repleta* de *Drosophila*), cujas larvas e adultos se alimentam em cladódios de cactos em decomposição. Estas moscas vêm sendo bastante estudadas em diferentes regiões áridas de todo o mundo (BARKER & STAMER, 1982). Na região Neotropical, SENE *et al.* (1982) buscam elucidar os processos evolutivos que cercam estas espécies com abordagens que integram a citogenética, a genética molecular, a morfologia e a ecologia. Inicialmente, foi observado que *D. serido* Vilela & Sene 1977 se distribuía por praticamente toda a região nordeste e central do Brasil, alcançando os Andes bolivianos e, ao sul, a Argentina (VILELA & SENE 1977, SENE *et al.* 1982, 1988, RUIZ *et al.* 1982, FONTDEVILA *et al.* 1988). Posteriormente, foi verificado que nesta extensa área em que se distribuía, a espécie apresentava variações populacionais quanto às inversões cromossômicas, à morfologia da genitália masculina e aos haplótipos para o gene mitocondrial COI, evidenciando uma ruptura do fluxo gênico (SENE *et al.* 1982, BAIMAI *et al.* 1983, SILVA & SENE 1991, MANFRIN *et al.* 2001). Em outra abordagem, foram constatadas diferenças populacionais quanto aos cactos hospedeiros utilizados para a oviposição, evidenciando uma diferenciação do nicho das diferentes populações (SENE *et al.* 1982). Assim, durante estes estudos, concluiu-se que *D. serido* se tratava de um complexo de espécies crípticas que, atualmente, está desmembrada em seis espécies (MANFRIN & SENE 2006). Este é apenas um dos diversos estudos realizados com drosofilídeos, em especial do gênero *Drosophila* (POWELL 1997). Apesar de ser bastante estudada quanto aos aspectos genéticos, evolutivos e, mais recentemente, ecológicos, ainda há muito que explorar e ser respondido com a ajuda destes organismos.

NICHO EM ESPÉCIES DE DROSOPHILIDAE

O estudo do nicho ecológico dos organismos pode nos ajudar a compreender como uma determinada comunidade ou assembléia está estruturada, como a diversidade local se mantém e, conseqüentemente, como as diversas espécies estão coexistindo. Isto também é verdadeiro para as assembléias de drosofilídeos. Cabe salientar que para os drosofilídeos, assim como para grande parte dos insetos, a fase larval é crítica, porque pode sofrer forte pressão competitiva. A limitação de recursos durante esta fase, principalmente os tróficos, pode diminuir o valor adaptativo dos indivíduos, refletindo em características do adulto, como fecundidade, longevidade e tamanho, ou mesmo inviabilizar todo o restante do desenvolvimento (ATKINSON 1979a, 1985, GRIMALDI & JAENIKE 1984, JAENIKE & JAMES 1991). Portanto, esta fase é crítica para a exclusão competitiva das espécies, e é onde a maioria dos estudos sobre a interação entre indivíduos se concentra. Seu entendimento é essencial para a identificação das estratégias empregadas, pelas diferentes espécies, para minimizar os efeitos da competição.

Inicialmente, é fácil pensarmos na coexistência das espécies de Drosophilidae pela especialização e diferenciação de seus nichos, principalmente quando se trata do nicho trófico. Em sua maioria, os drosofilídeos utilizam partes de vegetais e fungos em decomposição como locais de criação de suas larvas, onde elas normalmente se alimentam de leveduras que ali se desenvolvem (PAVAN 1959, CARSON 1971, POWELL 1997). Podemos encontrar uma grande variação de substratos utilizados, onde há espécies que ovipositam em frutos fermentados de diferentes famílias de plantas, como Anacardiaceae, Apocynacae, Arecaceae, Campanulaceae, Euphorbiaceae, Guttiferae, Moraceae, Myrtaceae, Passifloraceae, Rosaceae, Sapotaceae e Solanaceae (PAVAN 1959, PIPKIN 1965, HEED 1968, CARSON 1971, ATKINSON & SHORROCKS 1977, KIMURA *et al.* 1977, BRNCIC & VALENTE 1978, ARAÚJO & VALENTE 1981, LACHAISE *et al.* 1982, LACHAISE & TSACAS 1983, PEREIRA *et al.* 1983, VALENTE & ARAÚJO 1986, BONORINO & VALENTE 1989, SAAVEDRA *et al.* 1995, VALIATI & VALENTE 1996, GOÑI *et al.* 1998, VILELA *et al.* 2000, CASTRO & VALENTE 2001, DE TONI *et al.* 2001, VAN KLINKEN & WALTER 2001a, LEÃO & TIDON 2004, BLAUTH & GOTTSCHALK 2007, MARTINS & SANTOS 2007, MAGNACCA *et al.* 2008, GARCIA *et al.* no prelo), em flores de diversas famílias, como Araceae, Aristolochiaceae, Asteraceae, Convolvulaceae, Marantaceae, Malvaceae, Musaceae, Rubiaceae, Solanaceae e Zingiberaceae (FROTA-PESSOA 1952, BRNCIC 1966, 1978, 1983, PIPKIN *et al.* 1966, KIMURA *et al.* 1977, CARSON & OKADA 1980, MONTAGUE & KANESHIRO 1982, OKADA & CARSON 1982a, 1982b, GRIMALDI & JAENIKE 1983, VILELA 1984, 2001, GRIMALDI 1987, HUNTER 1988, 1992, CHASSAGNARD & TSACAS 1992, VILELA & PEREIRA 1992, VILELA & BÄCHLI 2000, VAN KLINKEN & WALTER 2001a, SAKAI 2002, BARKER 2003, GRIMALDI *et al.* 2003, SILVA & MARTINS 2004, SANTOS & VILELA 2005, SCHMITZ & HOFMANN 2005, SCHMITZ *et al.* 2007), em diferentes espécies de fungos das famílias Agaricaceae, Amanitaceae, Coprinaceae, Cortinaceae, Russulaceae, Tricholomataceae, entre outras (BOCK & PARSONS 1978, JAENIKE 1978, HACKMAN & MEINANDER 1979, SHORROCKS & CHARLESWORTH 1980, LACY 1984, ROCHA-PITÉ & BRANDÃO-RIBEIRO 1985, HANSKI 1989, COURTNEY *et al.* 1990, BURLA *et al.* 1991, VAN KLINKEN & WALTER 2001a, YAMASHIDA & HIJII 2003, 2007), ou até mesmo em folhas em decomposição (KIMURA *et al.* 1977, ASHBURNER 1981).

Entretanto, a forma como estes recursos são utilizados pode variar. Muitas espécies podem utilizar somente (ou principalmente) um tipo de substrato para oviposição, com nichos bastante restritos e não amplamente sobrepostos com o de outras espécies. É o exemplo de algumas espécies do grupo *repleta*, que ovipositam em cladódios de cactos em decomposição de diferentes espécies (FANARA *et al.* 1999, 2004). Na Argentina encontramos populações simpátricas de *D. buzzatii* Patterson & Wheeler 1942 e *D. koepferae* Fontdevila & Wasserman *in* Fontdevila *et al.* 1988, onde a primeira oviposita preferencialmente em espécies de cactos do gênero *Opuntia* (Cactaceae) e a segunda em espécies de *Cereus* e *Trichocereus* (Cactaceae). Este mesmo tipo de especialização acontece com as espécies que ocorrem no deserto de Sonora (FOGLEMAN *et al.* 1981, RUIZ & HEED 1988). As espécies do grupo *flavopilosa* também são restritas quanto à utilização de recursos, sendo que ovipositam principalmente em flores do gênero *Cestrum* (Solanaceae) (BRNCIC 1966, 1983, VILELA 1984, HOFMANN 1985, SANTOS & VILELA 2005).

Quanto aos extremos na especialização, podemos citar *D. carcinophila* Wheeler 1960 e *D. endobranchia* Carson & Wheeler 1968, que estão intimamente associadas com caranguejos terrestres, onde as larvas se criam próximo à base de seus olhos, alimentando-se de suas secreções (CARSON 1967, 1971, ASHBURNER 1981). Podemos também observar diversas espécies do gênero *Cladochaeta* parasitando ninfas de Cercopoidae (Homoptera) (GRIMALDI & NGUYEN 1999); espécies de *Rhinoleucophenga* predadoras de Coccidae (Homoptera) (COSTA-LIMA 1950, ASHBURNER 1981); uma espécie predadora de ovos de libélulas – *D. libelulae* Tsacas & Legrand 1979 (TSACAS & LEGRAND 1979); e *D. eleonorae* Tosi *et al.* 1990 ovipositando em guano de morcego em cavernas no interior do Brasil (TOSI *et al.*1990).

ATKINSON & SHORROCKS (1977), em um estudo sobre a preferência na utilização de sítios de oviposição por espécies domésticas de *Drosophila*, em um mercado na Inglaterra, observou a utilização preferencial de "frutas" como sítio de oviposição por *D. simulans* Sturtevant 1919, *D. melanogaster* Meigen 1830 e *D. subobscura* Collin *in* Gordon 1936, e de "legumes" por *D. busckii* Coquillett, 1901. O autor ainda explica a coexistência destas espécies pelo fato de suas populações nunca atingirem um equilíbrio, pois há uma grande migração das larvas das moscas, por parte do transporte dos frutos e legumes para dentro e para fora do mercado. Neste estudo, já podemos notar um menor grau de especialização, onde as espécies conseguem colonizar uma gama maior de recursos. Neste caso, as espécies são ditas generalistas. As espécies cosmopolitas, como *D. busckii*, possuem essa versatilidade e conseguem ovipositar substratos como frutos e flores, além de fungos e uma série de resíduos produzidos pela população humana (CARSON 1971).

Obviamente, encontramos espécies endêmicas do Neotrópico com hábitos generalistas, como as espécies frugívoras pertencentes ao subgrupo *willistoni* de *Drosophila*, que, apesar de não serem tão versáteis quanto *D. busckii*, conseguem utilizar uma ampla gama de frutos de diferentes famílias para oviposição (VALENTE & ARAÚJO 1986; BONORINO & VALENTE 1989, VALIATI & VALENTE 1996). Supõe-se que isso aconteça pelos substratos não possuírem variações muito grandes quanto às qualidades nutricionais, mas sim quanto ao teor de água, por exemplo (JAENIKE & MARKOW 2003). Assim, se algumas espécies são um pouco mais tolerantes às variações nestas últimas características, serão aptas a colonizar uma série de sítios diferentes. As espécies micófagas de Drosophilidae tendem a ser mais generalistas, pois os corpos frutíferos das diferentes espécies de fungos não diferem muito quanto ao seu conteúdo nutricional (COURTNEY *et al.* 1990). Entretanto, observam-se outras formas de segregação do nicho: aparentemente, há uma diferenciação da fauna colonizadora de fungos mais duros, que permanecem por mais tempo em campo, e da colonizadora de fungos mais carnosos, que são mais efêmeros (YAMASHIDA & HIJII 2007). Assim, parece que o acúmulo de toxinas nos corpos de frutificação pouco influencia a colonização das espécies micófagas (COURTNEY *et al.* 1990), mas são limitantes para espécies não adaptadas ao hábito micofágico (JAENIKE *et al.* 1983).

No exemplo anterior, começamos a notar que há outras formas das espécies diferirem quanto a seus nichos, além de uma especialização alimentar acarretando uma mudança no nicho trófico. Em diversos estudos, observa-se que muitas espécies de Drosophilidae apresentam uma distribuição descontínua na natureza. Diversos fatores podem reger a distribuição dos indivíduos e, muitas vezes, podemos observar mudanças graduais nestes fatores, como a formação de gradientes de umidade, por exemplo. Quando mensuramos este tipo de variável, dizemos que abordamos o nicho espacial.

Já foram observadas diferenças na distribuição das espécies de drosofilídeos e, conseqüentemente, na composição de suas comunidades ou assembléias em função de mudanças da fisionomia vegetal (PETERSEN 1960, BURLA & BÄCHLI 2001, VAN KLINKEN & WALTER 2001b, TIDON 2006, MATA *et al.* 2008); da degradação destas fisionomias (AVONDET *et al.* 2003, FERREIRA & TIDON 2005, GOTTSCHALK *et al.* 2007, MATA *et al.* 2008); da distância de corpos de água (MEDEIROS 2000, 2006); da formação de estratos vegetais em florestas (SHORROCKS 1975, TIDON-SKLORZ & SENE 1992, VAN KLINKEN & WALTER 2001b); ou até mesmo de grandes gradientes ambientais, como os latitudinais ou de altitude (BRNCIC & DOBZHANSKY 1957, BÄCHLI & BURLA 1992, BURLA & BÄCHLI 2001, RAFAEL 2007). Assim, mesmo havendo recursos tróficos disponíveis em diversos ambientes, eles não estarão disponíveis se as condições ambientais não forem favoráveis.

Estas diferenças ambientais não precisam necessariamente ocorrer em grande escala, como as mencionadas anteriormente. Mudanças microambientais podem ser o suficiente para promover a coexistência de duas espécies, como as observadas por KANESHIRO *et al.* (1973). Estudando duas espécies simpátricas de *Drosophila* no Hawaii (*D. silvestris* Hardy & Kaneshiro 1968 e *D. heedi* Hardy & Kaneshiro 1971), os autores observaram que ambas se alimentam da seiva de *Myoporum sandwicense* A. Gray (D.C.) (Fabaceae). Entretanto, *D. silvestris* utiliza a seiva ainda no tronco ou nos ramos das árvores, enquanto que *D. heedi* utiliza a seiva que escorre ou goteja no solo.

Outro caso semelhante foi observado nas espécies do grupo *flavopilosa* de *Drosophila*. Como já mencionado anteriormente, todas as espécies deste grupo oviposita em flores do gênero *Cestrum*. Entretanto, podemos encontrar diversas espécies de moscas deste grupo em simpatria em uma determinada área, utilizando as mesmas flores para oviposição

(Brncic 1978, Hofmann 1985, Santos & Vilela 2005). Brncic (1978) observou que algumas espécies, como *D. incompta* Wheeler & Takada *in* Wheeler *et al.* 1962, ovipositam na base da flor fechada, enquanto que outras, como *D. flavopilosa* Frey 1919 e *D. cestri* Brncic 1978, ovipositam somente com a flor aberta.

Assim, já comentamos sobre duas grandes dimensões de variações que podem estar contribuindo com a diferenciação dos nichos entre espécies de Drosophilidae: o trófico e o espacial. Há ainda outra dimensão a ser abordada, a temporal. As condições ambientais, por exemplo, variam durante o ano, ou até mesmo durante um dia. Estas variações podem constituir outro importante componente do nicho (Kronfeld-Schor & Dayan 2003). Assim, caso as espécies tenham flutuações sazonais em seus picos de abundância populacional, como constatado por Dobzhansky & Pavan (1950), Petersen (1960), Brncic *et al.* (1985), Franck & Valente (1985), Benado & Brncic (1994), Burla & Bächli (2001), De Toni *et al.* (2007), Gottschalk *et al.* (2007) e Schmitz *et al.* (2007), ou mesmo terem períodos de atividades diferenciados durante o dia, como observado por Dobzhansky & Pavan (1950) e Bélo & Oliveira-Filho (1978), haveria a possibilidade destas espécies partilharem diferentes recursos, como os tróficos, por exemplo.

Poderíamos também imaginar que, assim como as variáveis ambientais, os recursos utilizados não permaneçam inalterados com o passar do tempo. Um recurso trófico, por exemplo, permanecerá disponível para colonização por determinado período de tempo, antes de se decompor e, quanto mais tempo se passa, menos o recurso estará disponível, a não ser que haja algum tipo de reposição. Estas mudanças no estado dos recursos também proporcionam uma boa oportunidade para a partição dos mesmos. Isso foi constatado com espécies fungívoras de Drosophilidae, onde há uma diferenciação quanto à utilização dos cogumelos dependente do seu grau de decomposição (Courtney *et al.* 1990, Yamashida & Hijii 2003). Já Lachaise et al. (1982) demonstraram que o mesmo ocorre com espécies frugívoras. Estes autores observaram que a seqüência de chegada das espécies de *Drosophila* em figos africanos é característica, sendo a primeira espécie colonizadora *D. yakuba* Burla 1954, seguida por *D. melanogaster* e depois as pertencentes ao grupo *fima*. BURLA (1955) relatou uma variação comparável na colonização de palmeiras recém cortadas (*Raphia* sp.) na Costa do Marfim. Foi observado que as espécies *Scaptodrosophila saba* (Burla 1954) e *Zaprionus seguyi* Tsacas & Chassagnard 1990 são as primeiras a colonizar este recurso. O segundo grupo de espécies que colonizaram é constituído por *Z. inermis* Collart 1937, *S. latifasciaeformis* (Duda 1940) e *D. comoe* Burla 1954, sendo a última, *S. uebe* (Burla 1954).

Segundo SEVENSTER & VAN ALPHEN (1993), o simples fato da disponibilidade de recursos variar temporalmente pode promover a coexistência de espécies com características de história de vida diferenciadas. Estes autores observaram que, em épocas com maior abundância de recursos, espécies de Drosophilidae com ciclo de vida mais curto e, por conseqüência, menor tamanho e longevidade, se sobressaem sobre as populações de espécies com tempo de desenvolvimento maior. Em contrapartida, em épocas onde há escassez de recursos, espécies com ciclos de vida mais longos se sobressaem, uma vez que conseguem alcançar recursos mais distantes, devido sua maior capacidade de vôo, que é relacionado ao seu tamanho, e longevidade. Assim, os autores concluem que a flutuação na disponibilidade de recursos poderia levar estes dois tipos de espécies a sobreviver.

Estes *trade-offs*, variações em uma característica influenciando outras, que foram mencionados anteriormente, podem auxiliar, de outras formas, na manutenção da diversidade local. Foi constatado por BORASH *et al.* (2000a, 2000b) que linhagens diferentes de *D. melanogaster* podem coexistir simplesmente porque uma delas foi selecionada para ter o ciclo de vida mais longo que a outra. Com a seleção dos indivíduos com tempo de desenvolvimento maior, foi alterada, além do tamanho e da longevidade, a resistência às substâncias produzidas pelas larvas, como a uréia. Quanto mais rápido o tempo de desenvolvimento da linhagem, maior sua capacidade de exploração do alimento e sua fecundidade, mas, em contrapartida, há uma diminuição na capacidade de resistência às substâncias excretadas e acumuladas no meio de cultura. Assim, mesmo as fêmeas das duas linhagens ovipositando em um mesmo recurso e ao mesmo tempo, as duas linhagens conseguem coexistir. A linhagem com ciclo de vida curto deposita uma maior quantidade de ovos e explora melhor o meio do que a linhagem com ciclo de vida longo. Entretanto, com o passar do tempo as excretas começam a se acumular e os indivíduos com ciclo de vida curto não sobrevivem bem, diminuindo sua adaptabilidade, e os indivíduos das linhagens com ciclo de vida mais longo conseguem terminar seu desenvolvimento. Esse mecanismo pode estar atuando também na manutenção da coexistência entre diferentes espécies, uma vez que há diferenças marcantes quanto à resistência das mesmas a diferentes compostos e substâncias (KOJIMA & KIMURA 2003), e o *trade-off* das características das moscas tendem a auxiliar esses mecanismos (LACCHAISE 1983, TODA & KIMURA 1997).

Neste ponto já conseguimos ter uma idéia de como pode ser intrincada as relações entre as espécies de Drosophilidae. Mas, há pelo menos mais um agravante: como dito anteriormente, as larvas de Drosophilidae que ovipositam em material em decomposição alimentam-se de leveduras e bactérias que ali se desenvolvem (PAVAN 1959, CARSON 1971, POWELL 1997), e há evidências de que pelo menos algumas espécies de moscas possam ter uma relação íntima com essas espécies de leveduras e bactérias, conseguindo inclusive inocular certas leveduras nos substratos em decomposição (CUNHA *et al.* 1951, 1957, DOBZHANSKY & CUNHA 1955, DOBZHANSKY *et al.* 1956, LACHAISE *et al.* 1979, STARMER 1982, BEGON 1982, MORAIS *et al.* 1994, 1995a, 1995b). Assim, estas moscas, ao ovipositar, poderiam estar proporcionando um ambiente adequado para suas larvas, onde os microorganismos inoculados poderiam ser utilizados como alimento para as larvas. Esta idéia se assemelha a da **construção de nicho**, onde um organismo é capaz de modificar o ambiente em que vive, “co-construindo” e “co-definido” seu nicho ecológico (GRIFFITHS 2005) e, conseqüentemente, facilitando a coexistência entre eles, uma vez que as espécies de Drosophilidae não estariam completamente a mercê da disponibilidade de recursos.

Entretanto, estes mecanismos que promovem a especialização por diferentes recursos, possibilitando a diferenciação do nicho e a coexistência, ocorrem principalmente entre espécies não muito próximas filogeneticamente (TAKAHASHI *et al.* 2005). Assim, comumente, encontram-se relatos de espécies coexistentes que, aparentemente, sobrepõem completamente seus nichos e utilizam os mesmos recursos, como por exemplo, partes vegetais na mesma fase de decomposição. Como explicar a coexistência entre estas espécies? Algumas teorias vêm sendo desenvolvidas para tal, e uma das mais aceitas é o **modelo de agregação**, proposto inicialmente por SHORROCKS *et al.* (1979), ATKINSON & SHORROCKS (1981) e HANSKI (1981).

O modelo pressupõe que se os recursos são efêmeros e discretos, sendo inclusive tratados como ilhas, eles poderiam suportar a coexistência de espécies competidoras, se estas possuírem uma distribuição gregária e aleatória no ambiente. Este modelo prevê que parte do recurso se torne disponível às espécies de pequena capacidade competitiva, pois a probabilidade de ser totalmente colonizado é muito baixa. Além dos estudos que propuseram o modelo, diversos outros foram realizados em comunidades frugívoras e fungívoras do gênero *Drosophila* e deram suporte a ele (HANSKI 1983, GRIMALDI & JAENIKE 1984, ATKINSON & SHORROCKS 1984, ATKINSON 1985, NUNNEY 1990, ROSEWELL *et al.* 1990, SHORROCKS *et al.* 1990, JAENIKE & JAMES 1991, SEVENSTER & VAN ALPHEN 1996, TODA *et al.* 1999, WERTHEIM *et al.* 2000, MITSUI & KIMURA 2000, KRIJGER & SEVENSTER 2001, HARTLEY & SHORROCKS 2002). Nestes trabalhos, os recursos utilizados por estes organismos se enquadram perfeitamente nos pressupostos do modelo: o recurso é discreto e heterogeneamente distribuído pelo ambiente e, na maioria dos casos, não consegue suportar mais de uma geração de moscas, pois este se extingue neste meio-tempo. Entretanto, aparentemente, a aleatoriedade do recurso parece ser o principal fator de coexistência entre as espécies (CHESSON 2000).

Assim, temos um pequeno panorama das possibilidades de relacionamento das espécies de Drosophilidae com o ambiente, espécies de outras taxa e entre si, onde podemos encontrar diversos níveis de divergência do nicho ecológico.

OBJETIVOS

Em Florianópolis, GOTTSCHALK *et al.* (2007) coletaram 106 espécies de Drosophilidae, estudando um gradiente que vai do ambiente Mata Atlântica até o centro da cidade. Destas, 50 foram coletadas exclusivamente em ambientes urbanos e apenas duas exclusivamente no ambiente de mata. No gradiente estudado não foi observada uma diminuição na riqueza e abundância de espécies nativas, mas um aumento desses parâmeros nas espécies exóticas nas áreas mais urbanizadas. Associamos, a princípio, a presença das espécies nativas nas áreas urbanas a pequenos refúgios de vegetação existentes na cidade de Florianópolis.

Entretanto, não sabíamos se as populações de moscas conseguiam se manter na cidade, ou se ela era sempre recolonizada. Somando-se a isso, poucas informações sobre a interação entre espécies neotropicais de Drosophilidae estão disponíveis na literatura corrente, especialmente quando se trata das espécies brasileiras. Grande parte das informações levantadas foi feita de registros esporádicos, sendo que poucos estudos se dedicaram inteiramente a estudar as relações entre as espécies desta família e entre elas e seus substratos de oviposição. Assim, o objetivo geral deste estudo é investigar como as espécies de Drosophilidae se relacionam durante a fase em que as larvas utilizam os recursos tróficos, buscando identificar os principais fatores responsáveis pela manutenção da diversidade de espécies em áreas florestais e urbanas de Florianópolis (SC).

Os objetivos específicos são:

- Investigar os recursos tróficos utilizados pelas espécies de drosofilídeos para oviposição;
- Verificar como as espécies de drosofilídeos utilizam diferentes tipos de recursos tróficos para criação de larvas;

- Verificar se uma possível limitação de recurso para as larvas poderia incrementar a interação competitiva entre as mesmas.

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CAPÍTULO 2

UTILIZAÇÃO DE FRUTOS COMO SÍTIOS DE OVIPOSIÇÃO POR ESPÉCIES NEOTROPICAIS DE DROSOPHILIDAE EM AMBIENTES DE MATA ATLÂNTICA E URBANIZADOS DO SUL DO BRASIL

Este capítulo será reestruturado em dois artigos para futura submissão

Utilização de frutos como sítios de oviposição por espécies Neotropicais de Drosophilidae em ambientes de Mata Atlântica e urbanizados do Sul do Brasil

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ABSTRACT

The present study aims to contribute to the understanding the utilization of fruit as breeding sites for Drosophilidae in areas of Atlantic Rain Forest, through the comparison of the associated fauna and the vegetal host species in areas of native vegetation or urbanized, in the State of Santa Catarina, southern Brazil. Eighty host species belonging to 35 vegetal families were collected, from which 66 species of Drosophilidae emerged. The studied assemblies presented a generalist character of fruit use. In Atlantic Rain Forest were observed the formation of functional ecological groups, where certain species had a higher similarity in the resource utilization. This organization was not observed in the urban assemblies, which have a high niche overlap and lower species diversity. The areas of Atlantic Rain Forest and urbanized were characteristic in their resource composition, with a decrease in breeding sites diversity in areas with higher antropic degree. This decrease seems to be a restriction factor in studied assemblies, since this loss of breeding sites diversity could be associated with a reduction in the environmental heterogeneity and, consequently, to the higher niche overlap of the drosophilids species.

KEY WORDS: Coexistence, Environmental variation, Niche, Richness

RESUMO

O presente estudo visa contribuir para o entendimento da utilização de frutos como sítios de oviposição por Drosophilidae em áreas de Mata Atlântica, pela comparação da fauna associada aos frutos de espécies vegetais em regiões com vegetação nativa ou urbanizadas, no Estado de Santa Catarina, sul do Brasil. Foram coletadas 80 espécies vegetais pertencentes 35 famílias, de onde emergiram 66 espécies de Drosophilidae. As assembléias estudadas apresentaram um caráter generalista quanto à utilização dos frutos. Na Mata Atlântica verificou-se a formação de grupos ecológicos funcionais, onde certas espécies possuem uma maior similaridade na utilização dos recursos. Este tipo de organização não foi observado nas assembléias urbanas, as quais têm grande sobreposição de nichos e uma menor diversidade de espécies. As áreas de Mata Atlântica e urbanizadas são características quanto sua composição de recursos, havendo uma diminuição na diversidade de sítios de oviposição com o aumento do grau de antropização. Este parece ser um fator limitante nas assembléias estudadas, já que esta perda de diversidade de sítios de oviposição parece estar associada a uma diminuição na heterogeneidade ambiental e, conseqüentemente, a uma maior sobreposição do nicho das espécies de drosofilídeos.

PALAVRAS-CHAVE: Coexistência, Nicho, Riqueza, Variação ambiental

INTRODUÇÃO

A região de Florianópolis, no Estado de Santa Catarina, sul do Brasil, vem sendo alvo de intensos estudos quanto à diversidade da fauna de Drosophilidae (Diptera), focando sua resposta a diferentes fatores ambientais como, por exemplo, o tipo de vegetação, o grau de perturbação ambiental e as variações climáticas sazonais (DE TONI & HOFMANN 1995, DÖGE *et al.* 2004, 2006, 2007, DE TONI *et al.* 2007, GOTTSCHALK *et al.* 2006, 2007, SCHMITZ *et al.* 2004, 2007). Atualmente, já foram registradas 125 espécies da família no estado (CAPÍTULO 5), sendo que este número tende a aumentar ainda mais com o relato de novos registros e descrição de novas espécies. Com esses estudos sistemáticos foi possível saber que as espécies de drosofilídeos não se distribuem igualmente nos diversos ambientes do litoral catarinense, e que há uma forte variação sazonal na abundância das espécies. Entretanto, a maioria dos estudos que vinham sendo realizados enfocava a fauna de Drosophilidae atraída por iscas de banana em fermentação. Apesar destas iscas terem se mostrado bastante apropriadas para a coleta, uma vez que possibilitam estudos comparativos, pouco se sabe das relações entre as espécies de Drosophilidae e seus substratos de oviposição, e quais fatores que afetam a utilização destes recursos na região. Em estudos preliminares, realizados por DE TONI *et al.* (2001), SCHMITZ & HOFMANN (2005) e SCHMITZ *et al.* (2007), há relatos da emergência de espécies de Drosophilidae de frutos e flores de algumas espécies vegetais da região.

Os fatores que podem afetar a utilização dos recursos tróficos por espécies de Drosophilidae vêm despertando o interesse de estudiosos, pois esta influência está diretamente relacionada com a manutenção da diversidade de espécies e, conseqüentemente, os mecanismos que evitam a exclusão competitiva (PIPKIN 1965, BRNCIC & VALENTE 1978, ATKINSON 1985, NUNNEY 1990, SHORROCKS & SEVENSTER 1995, SEVENSTER & VAN ALPHEN 1993, 1996). Neste sentido, há evidências de que a partição de recursos pode ser a principal força motriz da manutenção da diversidade em assembléias de drosofilídeos (Atkinson & Shorrocks 1977, Yamashida & Hijii 2003, 2007). Já outros estudos atribuem a coexistência a efeitos estocásticos e ao padrão de distribuição gregário das populações (Sevenster & Van Alphen 1996a, Wertheim *et al.* 2000).

O levantamento de informações sobre a utilização de recursos como sítio de oviposição por Drosophilidae foi destacado por Carson (1971), que apontou sua necessidade para o entendimento dos processos evolutivos que regem estas populações. Por conta disso, alguns estudos foram conduzidos em diversas partes do mundo (Carson & Stalker 1951, Heed 1968, Carson 1971, Kimura *et al.* 1977, Atkinson 1985, van Klinken & Walter 2001, Magnacca *et al.* 2008). Na região Neotropical, foram conduzidos estudos no Panamá (Pipkin 1965, Sevenster 1992, Sevenster & van Alphen 1993, 1996), na região Amazônica (Martins 2001, Martins & Santos 2007) e no Cerrado (Leão & Tidon 2004, Blauth & Gottschalk 2007). Na Mata Atlântica, informações sobre sítios de oviposição das espécies de Drosophilidae são encontradas espalhadas pela literatura (Araújo & Valente 1981, Pereira *et al.* 1983, Valente & Araújo 1986, Bonorino & Valente 1989, Saavedra *et al.* 1995, Valiati & Valente 1996, Garcia *et al.* no prelo), mas nenhum estudo reúne um grande volume de informações.

Este estudo visa contribuir com o entendimento da colonização de frutos por espécies de Drosophilidae em áreas de Mata Atlântica, através da análise e comparação da fauna associada às diferentes espécies vegetais em áreas com vegetação nativa ou urbanizada, no litoral do Estado de Santa Catarina, sul do Brasil. Buscamos esclarecer alguns pontos sobre a biologia das diferentes espécies de moscas coletadas, assim como dos fatores que podem estruturar suas assembléias, entre eles, seu grau de especialização, a riqueza de Drosophilidae que as espécies hospedeiras abrigam, a influência da composição de plantas hospedeiras sobre a composição dos drosofilídeos, e a manutenção das populações de espécies nativas de Drosophilidae em áreas urbanas.

MATERIAL E MÉTODOS

COLETA DO MATERIAL BIOLÓGICO

As coletas foram realizadas em onze pontos do litoral do Estado de Santa Catarina, no sul do Brasil, na cidade de Florianópolis ou em seus arredores (Tabela 1). Os pontos amostrados consistem em oito áreas insulares ou continentais de Mata Atlântica *sensu stricto* e em três áreas urbanizadas insulares, que foram descritos anteriormente por DE TONI *et al.* (2007) e GOTTSCHALK *et al.* (2007). As coletas realizadas em áreas de Mata Atlântica se concentraram entre os anos de 1999 e 2000 (com exceção do ponto **F4**, onde foram realizadas coletas posteriormente), enquanto que nos pontos localizados nas áreas urbanizadas, as coletas foram realizadas mais recentemente, a partir de 2002 (Tabela 2).

Para as coletas dos frutos foram realizadas buscas visuais por aproximadamente duas horas em cada ponto de coleta, em cada amostragem. Nas áreas de Mata Atlântica, as buscas foram feitas em trilhas em meio à vegetação, sendo percorrida aproximadamente 1 km de sua extensão e adentrando na mata adjacente em vários pontos, totalizando aproximadamente 10.000 m^2 amostrados. Nas áreas urbanas (jardins e áreas verdes, pontos **C1** e **C2**), foi percorrido uma área de extensão semelhante em cada amostragem. Apenas no ponto **C3** a coleta se concentrou na área de descarte dos frutos do mercado onde a amostragem ocorreu, sendo recolhidas amostras que representassem os frutos disponíveis no local. Quando a disponibilidade de frutos foi muito alta e não foi possível recolher todos os frutos presentes no local, foram escolhidos até 100 frutos, de preferência aqueles que tinham algum indício de colonização, como rachaduras e machucados. Assumimos que os frutos coletados no mercado foram colonizados no próprio ponto de coleta, indicado pelo tempo de emergência dos drosofilídeos e pela abundância dos mesmos sobrevoando o depósito.

Os frutos recolhidos foram transportados para o laboratório em sacos de papel, onde foram colocados em recipientes de vidro ou plástico de diferentes tamanhos com o fundo coberto com vermiculita ou areia autoclavada, e fechados com rolhas de espuma ou com tecido. Os frutos que não couberam nos recipientes foram cortados no menor número de partes possível e então armazenados. Eles foram mantidos em câmara climatizada a 25±1°C por aproximadamente 30 dias, e os adultos emergentes foram aspirados e identificados. Nestes mesmos dias o aspecto do fruto foi observado e, se necessário, foram acrescentadas algumas gotas de água para hidratá-los.

Para este estudo, a unidade amostral foi definida como o conjunto de frutos originados de uma única árvore, e que atuavam como uma unidade de atração para as moscas no campo. No mercado, a unidade amostral foi definida como os frutos da uma mesma espécie recolhidos numa mesma amostragem.

IDENTIFICAÇÃO DO MATERIAL BIOLÓGICO

A identificação dos drosofilídeos foi realizada através da morfologia externa dos mesmos e da genitália masculina, preparada de acordo com a técnica proposta por WHEELER & KAMBYSELLIS (1966) e modificada por KANESHIRO (1969). Espécimes representativos das coletas foram depositados no Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN-FZB). As espécies vegetais foram determinadas com o ajuda do Prof. Dr. Daniel Falkenberg, do Departamento de Botânica da Universidade Federal de Santa Catarina (UFSC).

ANÁLISE DOS DADOS

ESPECIFICIDADE NA UTILIZAÇÃO DOS FRUTOS

A especificidade dos drosofilídeos foi avaliada de duas formas. A primeira foi sugerida por MAGNACCA *et al.* (2008), onde foram consideradas espécies monófagas as que possuiam mais de 2/3 dos indivíduos registrados em apenas uma espécie ou família de planta hospedeira, dependendo do nível de especificidade abordado, e não mais que 1/4 deles registrados em outro recurso. Todas as espécies que não possuíram estas características foram consideradas polífagas. Os autores que propuseram a metodologia realizaram este cálculo somente ao nível das famílias hospedeiras. Em nosso estudo, também optamos por realizar a classificação ao nível das espécies hospedeiras, onde foram excluídas aquelas com menos de três amostras coletadas.

Foi calculado o índice de especialização (**Ds**) (SEVENSTER 1992) para o banco de dados completos e considerando somente as espécies hospedeiras coletadas em três amostras ou mais, em ambientes de Mata Atlântica ou urbanizados. Seu cálculo é similar ao índice de diversidade de Simpson (MAGURRAN 2003), mas aplicado para as diferentes espécies de plantas hospedeiras que cada espécie de drosofilídeo utiliza. Assim, este índice indica o inverso da probabilidade de dois indivíduos de uma mesma espécie de mosca emergir de uma única espécie de fruto.

Foi realizada uma análise de correlação de Pearson entre o número de amostras e o número de espécies de plantas hospedeiras em que cada espécie de Drosophilidae foi registrada, onde ambos os valores sofreram transformações logarítmicas para se ajustarem aos pressupostos do teste (ZAR 1999). Este teste foi realizado a fim de verificarmos se um crescimento na amostragem das espécies de Drosophilidae está relacionado com o aumento na riqueza de espécies hospedeiras.

RIQUEZA DE DROSOPHILIDAE NAS ESPÉCIES HOSPEDEIRAS

Foram construídas curvas de acumulação de espécies para os recursos com cinco amostras ou mais, visando avaliar o esforço amostral para cada espécie de planta hospedeira e medir a taxa de adição de espécies de drosofilídeos que utilizam os recursos (MAGURRAN

2003). Para a construção das curvas foi utilizado o software EstimateS 8.00 (COLWELL 2000), usando a média e o desvio padrão de 500 reamostragens sucessivas dentro do banco de dados.

Foram realizadas análises de correlação de Pearson entre o número de amostras coletadas de cada espécie de planta hospedeira e a abundância dos drosofilídeos emergentes, e entre o número de amostras coletadas de cada planta hospedeira e o número de espécies emergentes de Drosophilidae, em ambos os tipos de ambientes amostrados. Foi feita uma transformação logarítmica dos dados a fim de adequá-los ao teste (ZAR 1999).

VARIAÇÃO ESPACIAL NA DISPONIBILIDADE DAS ESPÉCIES HOSPEDEIRAS

Uma análise de correspondência destendenciada (DCA – *Detrended Correspondence Analysis*) foi realizada buscando evidenciar as diferenças na composição das amostras de frutos obtidas em cada ponto de coleta (HILL & GAUCH 1980), com os pontos de coleta como variável independente e a composição de espécies hospedeiras como variável dependente. Para tal, foi utilizado como valores de abundância o número de vezes que cada espécie hospedeira foi coletada em cada ponto. Este tipo de análise foi conduzida no programa R 2.5.0 (R DEVELOPMENT CORE TEAM 2007), com o pacote VEGAN 1.8-8 (OKSANEN *et al.* 2007).

ESTRUTURA DAS ASSEMBLÉIAS E MANUTENÇÃO DAS POPULAÇÕES DE DROSOPHILIDAE

Para a comparação das comunidades emergentes dos frutos de cada ponto de coleta foram construídos gráficos de *Whittaker* com a somatória dos drosofilídeos emergentes de todos os frutos em cada ponto de coleta (KREBS 1999). Estes gráficos também foram comparados àqueles construídos com os dados das amostragens com iscas de banana, que foram realizadas nos mesmos pontos de coleta por DE TONI *et al.* (2007) e GOTTSCHALK *et al.* (2007).

Adicionalmente, foi realizada uma DCA a fim de compararmos a composição das faunas amostradas nos diferentes pontos, tanto para as amostras obtidas através da emergência dos drosofilídeos dos frutos, como para a fauna de drosofilídeos atraídos por iscas de banana (DE TONI *et al.* 2007, GOTTSCHALK *et al.* 2007). Nesta análise, a variável independente foi os pontos de coleta e a variável dependente a composição de espécies de Drosophilidae.

RELAÇÃO ENTRE ESPÉCIES DE DROSOPHILIDAE E ESPÉCIES HOSPEDEIRAS

Para a comparação das assembléias de drosofilídeos emergentes de cada espécie de fruto foi realizada outra DCA, agora com as espécies hospedeiras como variável independente e as espécies de Drosophilidae como variável dependente. Além disso, foram calculados os índices de amplitude de nicho de Morisita e de sobreposição de nicho de Pianka (KREBS 1999). A unidade de análise utilizada foi a amostra de fruto, sendo considerada toda a variação espacial, temporal e de espécies hospedeiras. Para ambos os índices, foram calculadas as médias e variâncias dos valores obtidos em cada um dos ambientes estudados (áreas de Mata Atlântica e urbanizadas).

RELAÇÃO ENTRE A UTILIZAÇÃO DAS ESPÉCIES HOSPEDEIRAS POR DROSOPHILIDAE E AS VARIÁVEIS AMBIENTAIS

Para verificarmos a influência das variáveis ambientais, como o tipo de ambiente, as distâncias entre os pontos de coletas (obtidas através das coordenadas geográficas de cada ponto) e a época do ano que foram realizadas as coletas (variação sazonal), sobre a composição das espécies de Drosophilidae e de plantas hospedeiras em cada coleta, foram realizados testes de Mantel (DINIZ-FILHO 2000). O índice de Jaccard foi calculado para obter a similaridade entre as amostras de Drosophilidae emergentes e entre as amostras de espécies vegetais (KREBS 1999). As distâncias entre os pontos foram obtidas com auxílio de um GPS e os tipos de ambientes foram classificados como Mata Atlântica ou áreas urbanizadas, sendo consideradas as quatro estações oficiais do ano na variação sazonal, onde para coletas em uma mesma estação atribuiu-se similaridade 1,0, para coletas em estações adjacentes atribuiu-se valor de similaridade de 0,5 e para coletas em estações não adjacentes atribuiu-se similaridade zero.

Também foram realizados testes de Mantel parcial entre a similaridade das assembléias de Drosophilidae e de frutos nas diferentes coletas eliminando as variações espacial, sazonal e ambiental (DINIZ-FILHO 2000). Estes testes também foram realizados no programa R 2.5.0, com o pacote VEGAN 1.8-8, com 10.000 aleatorizações. Estas análises foram realizadas em dois níveis de classificação das plantas hospedeiras, ao nível de espécie e de família.

RESULTADOS

Em nossas amostragens foram observados sítios de oviposição para 66 espécies de Drosophilidae (Tabela 3), com um total de 38.771 indivíduos emergidos dos frutos coletados. Nos pontos de Mata Atlântica, 26.665 drosofilídeos pertencentes a 57 espécies foram amostrados, sendo sete espécies exóticas (Tabela 4). Já, dos frutos coletados nas áreas urbanizadas emergiram 12.106 indivíduos de 32 espécies, dez delas exóticas (Tabela 5). Frutos de 80 espécies vegetais foram coletados, pertencentes a 34 famílias. Entretanto, não emergiram drosofilídeos dos frutos de *Schinus terebintifolius* (Anacardiaceae), *Ilex* sp. (Aquifoliaceae), *Didymopanax morottotoni* (Araliaceae), *Euterpe edulis* (Arecaceae), *Cecropia adenopus* (Cecropiaceae), *Clusia criuva* (Clusiaceae), *Cucurbita pepo* (Cucurbitaceae), *Alchornea triplinervea* (Euphorbiaceae), *Leandra* sp. (Melastomataceae), *Lafoensia pacari* (Lythraceae), *Trichilia* sp. (Meliaceae), *Rappanea umbellata* (Myrsinaceae), *Eugenia stigmatosa, Gomidesia palustres* (Myrtaceae), *Passiflora* sp. (Passifloraceae), *Peperomia* sp. (Piperaceae), *Cupania vernalis*, *Paullinia* sp. (Sapindaceae) e *Solanum* sp. (Solanaceae).

ESPECIFICIDADE NA UTILIZAÇÃO DOS FRUTOS

As espécies de Drosophilidae coletadas em áreas de Mata Atlântica e urbanizadas foram submetidas à classificação quanto ao grau de polifagia, que está apresentada nas Tabelas 6 e 7, respectivamente. Também estão apresentados os valores do índice de especialização, **Ds**, para os dados completos e excluindo as espécies hospedeiras com menos de três amostras coletadas, o número de espécies hospedeiras e o número total de amostras das quais as espécies de Drosophilidae emergiram.

O número de espécies polífagas é elevado nos dois ambientes amostrados e, além disso, algumas espécies classificadas como monófagas em ambiente de Mata Atlântica são polífagas em áreas urbanas, como *D. neocardini*, *D. repleta* e *S. latifasciaeformis* (autoria das espécies na Tabela 3). A classificação efetuada com a exclusão das espécies de hospedeiros com menos de três amostras muda este panorama, onde muitas das espécies ora classificada como polífagas com os dados completos agora foram classificadas como monófagas. Além disso, quando realizamos a classificação ao nível das famílias de plantas hospedeiras, não há a mudança da classificação dos drosofilídeos de polífagas para monófagas, o que caracterizaria que as espécies poderiam ser especializadas ao nível das famílias hospedeiras.

A maioria das espécies consideradas monófagas são unicatas, isto é, foram amostradas uma única vez, sendo muitas delas representadas por apenas um indivíduo (*singletons*). Das coletas realizadas em Mata Atlântica, a única espécie considerada monófaga na classificação ao nível de espécie e que não foi coletada em apenas uma ocasião foi *D. neocardini*, que nas amostras na cidade foi classificada como polífaga. Portanto, o panorama observado é o de uma comunidade onde a maioria das espécies são polífagas, e os poucos registros de espécies monófagas foram atribuídos devido a uma pequena representatividade destas espécies nas amostragens. Este mesmo padrão foi observado nos valores calculados para o índice de especialização (**Ds**), onde as espécies com menores valores são aquelas coletadas uma única vez, e não necessariamente em uma espécie de fruto pouco amostrada.

Este padrão é claro na Figura 1, onde está apresentado o número de espécies de Drosophilidae em função do número de espécies hospedeiras utilizadas por elas, tanto em áreas de floresta como urbanizadas, com e sem as espécies unicatas e *singletons*. As espécies de drosofilídeos coletadas em apenas uma espécie de planta hospedeira são, em sua maioria, aquelas coletadas em uma única ocasião. Entretanto, quando observamos as outras amostras destes mesmos frutos, estas espécies de drosofilídeos não foram amostradas uma segunda vez. Em contrapartida, as espécies hospedeiras que abrigaram espécies de drosofilídeos que emergiram de uma pequena variedade de recursos não pertenciam a uma mesma família de plantas. Um padrão similar é observado na Figura 2, onde está apresentado o número de espécies de drosofilídeos dentro das faixas de valores de **Ds** nos dois ambientes amostrados. A maioria das espécies de drosofilídeos com valores de **Ds** entre 1,0 e 1,9 são *singletons* ou unicatas.

Ainda, observamos uma correlação significativa entre o número de amostras em que cada espécie de Drosophilidae foi coletada e o número de plantas hospedeiras registradas para ela (para as áreas de Mata Atlântica: $r = 0.97$ e $p < 0,0001$, e para áreas de cidade: $r = 0.96$ e $p < 0,0001$). Portanto, há uma tendência de que quanto mais coletarmos um recurso, mais espécies de drosofilídeos podemos encontrar associadas e ele.

RIQUEZA DE DROSOPHILIDAE NAS DIFERENTES ESPÉCIES HOSPEDEIRAS

Nas Tabelas 8 e 9 estão apresentados o número de indivíduos e de espécies de drosofilídeos emergentes das espécies de plantas hospedeiras amostradas, além do número de amostras coletadas de cada espécie de planta nos pontos de Mata Atlântica e urbanizados, respectivamente. Em ambos ambientes, a maioria das espécies hospedeiras abrigou um número elevado de espécies de drosofilídeos (média de aproximadamente sete espécies por recurso em cada ambiente), mesmo quando coletadas apenas uma ou poucas amostras das mesmas. Entretanto, este número tendeu a aumentar conforme mais amostras das espécies hospedeiras foram obtidas, assim como observado nas curvas de acumulação de espécies construídas para os recursos que possuíram mais de cinco amostras em um mesmo ambiente (Figura 3). Estas curvas não se estabilizaram e, na maioria dos casos, sequer alcançaram o ponto de inflexão (ponto onde há uma redução na taxa de acréscimo de espécies em função do número de amostras), mesmo no caso de *S. romanzoffiana*, que possui 20 amostras na Mata Atlântica.

Outra evidência de que a riqueza de drosofilídeos tende a aumentar com o esforço amostral é a forte correlação positiva entre o número de amostras coletadas e o número de espécies de drosofilídeos registradas para cada recurso (Mata Atlântica: $r = 0,78$, $p < 0,0001$; áreas urbanizadas: $r = 0,73$, $p = 0,00005$) (Figura 4). O mesmo acontece se comparamos o número de indivíduos e de espécies emergentes de drosofilídeos em cada espécie de planta hospedeira (Mata Atlântica: $r = 0,82$, $p < 0,0001$; áreas urbanizadas: $r = 0,65$, $p = 0,0006$) (Figura 5).

VARIAÇÃO ESPACIAL NA DISPONIBILIDADE DAS ESPÉCIES HOSPEDEIRAS

Na Tabela 10 estão apresentados os números de coletas realizadas em cada ponto e o número de coletas em que foram amostrados frutos, o número total de amostras obtidas por ponto e o número de coletas com amostras colonizadas por Drosophilidae, e o número de espécies de plantas hospedeiras coletadas e o número de espécies de plantas que houve emergência de moscas dos frutos. Cabe ressaltar que, apesar de não quantificarmos precisamente os frutos em campo, nossas amostragens refletem o número de árvores com frutos e o número de espécies que frutificaram em cada ponto. A disponibilidade dos frutos, refletida pelo número de coletas em que foram encontrados frutos, pelo número de amostras coletadas por ponto e pelas espécies hospedeiras as quais elas pertenciam, variou entre os pontos de coleta, inclusive dentro de um mesmo ambiente. Este padrão é evidenciado na DCA das espécies vegetais coletadas em cada ponto, na qual utilizamos como abundância o número de amostras coletadas das espécies hospedeiras, e onde observamos uma mudança gradual na composição específica dos frutos coletados em cada ponto (Figura 6). Os valores de explicação dos eixos utilizados somam 35,19% da variação total dos dados.

De uma maneira geral, observa-se uma maior disponibilidade de recursos em áreas de Mata Atlântica, traduzida pelo número de amostras obtidas por coleta nestas áreas, quando comparadas aos jardins e áreas verdes nas áreas urbanizadas (Tabela 11). O mesmo acontece em relação ao número de espécies vegetais encontradas por coleta. O ponto **C3,** o mercado, é uma exceção dentro da cidade, devido à grande disponibilidade de frutos. Nele, foram obtidas 16 amostras colonizadas em apenas uma das coletas. Entretanto, nas áreas de mata há uma taxa menor de colonização das amostras onde, no total, somente de 56% delas emergiu algum drosofilídeo. Nos jardins e áreas verdes, esta taxa sobe para 76% e no mercado é de 88%.

ESTRUTURA DAS ASSEMBLÉIAS E MANUTENÇÃO DAS POPULAÇÕES DE DROSOPHILIDAE

Nos estudos de DE TONI *et al.* (2007) e GOTTSCHALK *et al.* (2007) foram realizados levantamentos de espécies de Drosophilidae ao longo de alguns anos nos mesmos pontos de coleta apresentados no presente trabalho, mas as coletas foram realizadas com a utilização de iscas de bananas fermentadas. Lançando mão destes resultados, é possível compará-los com a estrutura das diferentes assembléias que emergiram dos frutos e avaliarmos se são condizentes. Cabe ressaltar que, normalmente, as amostragens com iscas de bananas atraem uma grande riqueza de espécies de Drosophilidae e, raramente, amostras tão ricas quanto estas são obtidas por outros meios. Assim, foram construídos gráficos de *Whittaker* com os dados de DE TONI *et al.* (2007) e de GOTTSCHALK *et al.* (2007), com iscas de bananas, e com o resultado de nossas coletas, avaliando a fauna emergente dos frutos coletados em cada ponto de coleta (Figura 7).

Na Figura 7A estão as curvas obtidas para as espécies atraídas por iscas de banana nos oito pontos de coleta de Mata Atlântica. O ponto **F4** foi amostrado nos estudos de DE TONI *et al.* (2007) e GOTTSCHALK *et al.* (2007) independentemente, portanto aparece duas vezes no gráfico. Observa-se que as curvas de abundância obtidas são similares entre si e com as construídas para as comunidades obtidas em áreas urbanas, coletadas com iscas de banana

(Figura 7B). Em todos os pontos, há um grande número de espécies raras, indicado pelo alongamento da curva no eixo *x*.

Este mesmo padrão foi observado nas comunidades emergentes dos frutos nas áreas de Mata Atlântica (Figura 7C). Entretanto, observa-se uma maior heterogeneidade entre os pontos devido a diferenças no número de amostras de frutos obtidas e da composição das espécies vegetais de onde as moscas emergiram. Os pontos de coleta de onde foi obtido um menor número de amostras possuem curvas mais curtas neste gráfico. Esta relação também foi observada nos frutos coletados em áreas urbanizadas (Figura 7D), onde o ponto **C1**, onde foi coletado o menor número de amostras, possui a menor curva. Entretanto, as curvas construídas com as espécies emergentes em frutos coletados nas áreas urbanizadas não indicam a ausência de espécies raras, com um encurtamento da cauda da curva (indicado pelas setas).

A composição das amostras nas áreas de Mata Atlântica e urbanizadas são características, independente da forma como foi realizada a amostragem (com iscas ou com a coleta de frutos para a análise da fauna emergente), como evidenciado na DCA apresentada na Figura 8A. Entretanto, as amostras em mata foram mais heterogêneas. Observa-se que as espécies exóticas são mais abundantes em áreas de cidade, assim como várias espécies nativas, dentre elas *D. cardinoides* e *D. mercatorum* (Figura 8B). Já, as espécies do grupo *tripunctata* são mais abundantes nos pontos de Mata Atlântica. Os valores de explicação dos eixos utilizados somam 50,6% da variação total dos dados.

RELAÇÃO ENTRE ESPÉCIES DE DROSOPHILIDAE E ESPÉCIES HOSPEDEIRAS

Foi realizada uma DCA para avaliar a relação entre as espécies de plantas hospedeiras e de Drosophilidae nos pontos de coleta urbanizados (Figura 9) e com vegetação de Mata Atlântica (Figura 10). Nas coletas realizadas na cidade, observa-se que *Cecropia glaziovii*, *Aleurites moluccana*, *Chorisia* sp. e *Maclura* sp. foram as espécies hospedeiras com a fauna emergente mais diferenciada (Figura 9A), sendo colonizadas principalmente por espécies de moscas nativas (Figura 9B). Aparentemente, as espécies de uma mesma família de plantas hospedeiras não são similares quanto a suas espécies colonizadoras, onde a maioria delas possui uma fauna pouco fiel. As espécies exóticas de drosofilídeos são bastante generalistas, estando presentes em uma ampla gama de espécies hospedeiras, e utilizam esses recursos em conjunto com espécies nativas. Nota-se que nem todas as espécies utilizam os mesmos recursos, onde é possível observar uma maior similaridade na utilização dos recursos por certas espécies de Drosophilidae (cada espécie indicadas por um vetor) apontados na mesma direção (Figura 9B). Os valores de explicação dos eixos utilizados nos gráficos desta DCA somam 42,9% da variação total dos dados.

As espécies de drosofilídeos coletadas nas áreas de Mata Atlântica apresentaram padrão semelhante, onde não houve a formação de grupos de espécies hospedeiras mais homogêneos quanto à colonização dos drosofilídeos. Entretanto, as espécies *A. moluccana*, *Cabralea* sp., *Lichia* sp., *Ocotea* sp., *Posoqueria* sp. e Fruto 4 apresentaram faunas características (Figura 10A). Neste caso, as espécies exóticas de Drosophilidae colonizaram uma mesma gama de recursos, e apesar de serem bastante generalistas, apresentaram-se agrupadas sobrepondo mais seus nichos entre si do que com as espécies nativas. A exceção foi *D. busckii*, que sobrepõe seu nicho com espécies nativas ao invés das outras espécies exóticas (Figura 10B). Assim, como observado em ambientes urbanos, há certa diferenciação das espécies de Drosophilidae quanto à utilização dos frutos, mas com a formação de grandes grupos de espécies utilizando uma mesma gama de recursos. Os eixos da DCA apresentados explicam 33,0% da variação total dos dados.

Quanto à análise de sobreposição de nicho entre as espécies de Drosophilidae, na cidade elas apresentaram uma sobreposição média maior do que na Mata Atlântica.

Entretanto a variância foi ligeiramente menor, o que reflete que na mata há uma compartimentalização maior dos recursos e a formação de grupos funcionais de drosofilídeos na utilização dos mesmos, o que não estaria acontecendo na cidade (Tabela 12). Já, quanto à amplitude de nicho, a média e variância apresentada em ambos os ambientes é praticamente a mesma, indicando que as espécies de drosofilídeos utilizam aproximadamente uma mesma riqueza de recursos independentemente do ambiente em que se encontram, o que reforça a similaridade entre as assembléias.

RELAÇÃO ENTRE A UTILIZAÇÃO DAS ESPÉCIES HOSPEDEIRAS POR DROSOPHILIDAE E AS VARIÁVEIS AMBIENTAIS

Buscamos relacionar a influência das espécies ou famílias de plantas hospedeiras na composição das espécies emergentes de Drosophilidae, assim como a influência da variação espacial, sazonal e dos tipos de ambiente na composição tanto da fauna de Drosophilidae quanto na flora frutífera com uma análise de Mantel (Figuras 11 e 12). Na análise ao nível das espécies hospedeiras, observamos que a composição das plantas hospedeiras foi a variável mais fortemente correlacionada com a composição da fauna de Drosophilidae, seguida da variação espacial. A variação sazonal não influenciou significativamente a fauna de Drosophilidae, mas pode ter influência sobre a composição dos frutos disponíveis para as mesmas (Figura 11). Entretanto, a variação no tipo de ambiente influenciou significativamente a composição dos recursos coletados, mas não a composição das espécies de Drosophilidae emergentes. Ao retirarmos a influência de uma das variáveis ambientais de cada vez com uma análise de Mantel parcial, observamos que continuamos a ter significância na correlação entre a composição das espécies de Drosophilidae e espécies hospedeiras (r=0,18, p=0,0001 ao retirarmos a influência da variação espacial; r=0,20, p=0,0001 ao retiramos a influência da variação sazonal e r=0,19, p=0,0001 ao tirarmos a influência da variação ambiental). Cabe salientar que a significância destes testes (α = 0,05) foi corrigida com a correção de Bonferroni para testes univariados (ZAR 1999).

Estas mesmas análises foram realizadas utilizando as famílias de plantas hospedeiras como unidade de análise, ao invés das espécies hospedeiras (Figura 12). O padrão geral de respostas às variáveis ambientais é praticamente o mesmo, onde apenas a variação sazonal não influencia a composição das famílias dos frutos coletados. Entretanto observa-se uma diminuição na correspondência entre as espécies de Drosophilidae e de plantas hospedeiras. Esta diminuição persiste mesmo ao retirarmos o efeito das variáveis ambientais com o teste de Mantel parcial (r=0,14, p=0,0001 ao retirarmos a influência da variação espacial; r=0,15, p=0,0002 ao retiramos a influência da variação sazonal e r=0,14, p=0,0002 ao tirarmos a influência da variação ambiental). Apesar de significantes, a correlação não é forte em nenhuma das comparações realizadas.

DISCUSSÃO

Das 108 espécies registradas nos pontos de Mata Atlântica de Florianópolis (listadas em DE TONI *et al.*, 2007 e GOTTSCHALK *et al.*, 2007), coletadas primeiramente com iscas de bananas, observamos sítios de oviposição para 53 delas, totalizando 51,0% das espécies. Três espécies foram registradas somente emergindo dos frutos, e não sendo registradas em iscas anteriormente, dentre elas: *D. ananassae*, uma espécie exótica e cosmopolita bastante coletada em áreas antropizadas (Tabela 5, PARSONS & STANLEY 1981, GOTTSCHALK *et al.* 2007), *D. frotapessoai*, uma espécie do grupo *tripunctata* que em nossas amostragens foi coletada somente em frutos do gênero *Psidium*, e *D. zottii* (aff.), uma espécie ainda não descrita, coletada em apenas uma ocasião, no ponto **F4**, emergindo de *Campomanesia* sp. (Tabela 4). Nos estudos de VAN KLINKEN & WALTER (2001) e MAGNACCA *et al.* (2008) foi observado sítios de oviposição para uma porcentagem pequena das espécies conhecidas nas localidades estudadas, apesar de, nestes estudos, os autores não se restringiram aos frutos como sítios de criação das larvas, sendo levantados também fungos, flores, folhas e seiva de árvores.

Nas áreas antropizadas de Florianópolis, por outro lado, o número de espécies com sítios de oviposição registrados cai para 28, dentre as 105 espécies coletadas (GOTTSCHALK *et al.*, 2007). Portanto, apenas 27,7% das espécies registradas nestas localidades possuem também registros de sítios de oviposição. Ainda, quatro espécies foram registradas somente em nossas amostragens de frutos, *C. pectinifemur* e *Scaptomyza* sp. – coletadas no mercado em quatro e uma ocasião, respectivamente (ponto **C3**), e *D. pellewae* (grupo *tripunctata*) e *D. polymorpha* (aff.) (grupo *cardini*) no *Campus* da UFSC, a primeira espécie sendo representada por apenas um único indivíduo (ponto **C2**) (Tabela 5). Cabe ressaltar que *D. pellewae* foi registrada pela primeira vez no Brasil, tendo sido coletada somente no Panamá e na Colombia (PIPKIN & HEED 1964). Como já mencionado, dez das espécies registradas nas cidades são exóticas e, com exceção de *D. atrata*, *D. capricorni*, *D. pallidipennis*, *D. paramediostriata*, *D. setula* e *D. zottii*, as espécies nativas emergentes dos frutos coletados em áreas urbanizadas foram também comuns nas amostragens com iscas de banana, sendo que *D. cardinoides* é considerada característica áreas de urbanas na região central do Brasil (MATA *et al.* 2008a). Portanto, a maioria das espécies raras coletadas por GOTTSCHALK *et al.* (2007) continuam sem registros de sítios de oviposição na cidade.

As espécies que não tiveram registros de sítios de oviposição em nosso estudo podem não ser preferencialmente frugívoras, ou então possuem como sítios de oviposição espécies vegetais que não foram amostradas no presente trabalho. Normalmente, estas espécies são raras em outras amostragens realizadas no Neotrópico (VILELA & MORI 1999, MEDEIROS & KLACZKO 2004, MATA *et al.* 2008b). Por exemplo, os sítios de oviposição das espécies do subgrupo *fasciola* (grupo *repleta* de *Drosophila*) são cactos epifíticos (PEREIRA *et al.* 1983). Já as pertencentes ao grupo *tripunctata* de *Drosophila* são fungívoras facultativas (CAPÍTULO 4), e as pertencentes aos gêneros *Hirtodrosophila* fungívoras obrigatórias. As espécies de *Zygothrica* podem utilizar, além de alguns fungos, flores de diversas famílias como sítio de oviposição (GRIMALDI 1987, SEPEL *et al.* 2000, SANTOS & VILELA 2005). Este fato evidencia a eficiência das amostragens com iscas de banana para trabalhos de levantamentos taxonômicos, provavelmente relacionada à maior amplitude dos sítios de alimentação dos adultos, quando comparados com os sítios de oviposição, sendo que eles nem sempre são coincidentes (GRIMALDI 1987, SAAVEDRA *et al.* 1995, SILVA *et al.* 2005).

Mesmo com estas diferenças quanto aos sítios de oviposição e de alimentação, há uma grande correspondência entre as amostras de moscas emergentes dos frutos e das atraídas por iscas de banana, tanto quanto à estrutura das assembléias (Figura 7) e quanto à composição de espécies (Figura 8). Este fato, associado a ausência das espécies raras, sugere que os recursos disponíveis dentro da cidade de Florianópolis não são suficientes para suportar toda diversidade encontrada nas primeiras amostragens realizadas por GOTTSCHALK *et al.* (2007), caracterizada por uma grande quantidade de espécies raras, assim como a maioria das assembléias de Drosophilidae amostradas nos biomas brasileiros (VILELA & MORI 1999, MARTINS 2001, TIDON 2006, SCHMITZ *et al.* 2007). Provavelmente, as espécies raras coletadas por GOTTSCHALK *et al.* (2007) são provenientes de ambientes fonte próximos às áreas urbanas. Estes ambientes possuiriam capacidade de sustentar uma alta diversidade de recursos e os indivíduos das diferentes espécies emigrariam dos mesmos para as áreas urbanizadas. Assim, a cidade de Florianópolis estaria funcionando como um ambiente escoadouro, como também sugerido para as assembléias amostradas em áreas de manguezal ao lado da cidade (SCHMITZ *et al.* 2007).

Quanto ao comportamento das diferentes espécies na escolha dos sítios de oviposição, a maioria apresentou hábito polifágico, evidenciado pelos critérios sugeridos por MAGNACCA *et al.* (2008), pelo índice de especificidade (**Ds**), pelas DCAs e pela amplitude média dos nichos. Este mesmo padrão, com muitas espécies com comportamento de oviposição generalista, já foi detectado em assembléias de Drosophilidae neotropicais (SEVENSTER 1992, SAAVEDRA *et al.* 1995, SILVA *et al.* 2005). Além disso, em nossas amostragens as espécies com hábito monofágico geralmente são raras, possivelmente devido a um artefato do tamanho amostral destas populações, ou seja, estas espécies estão sendo consideradas monofágas porque ainda não foram suficientemente amostradas. Este cenário não muda em função dos ambientes estudados, pois tanto na Mata Atlântica quanto na cidade as espécies apresentam o mesmo grau de especialização pelos recursos.

Entretanto, há uma diferença na utilização dos recursos por essas espécies: na mata há uma sobreposição menor do nicho, com a formação de grupos funcionais de espécies que co-ocorrem com maior freqüência em certos tipos de recursos (WINEMILLER & PIANKA 1990). SEVENSTER (1992) observou este mesmo comportamento em assembléias coletadas em florestas do Panamá. Entretanto, em nossas amostras nas áreas de cidade há uma maior sobreposição do nicho das diferentes espécies, o que caracterizaria uma assembléia com competição difusa ou partição de recursos (WINEMILLER & PIANKA 1990). Acreditamos não ser o caso, uma vez que há uma forte pressão competitiva entre espécies de Drosophilidae (BARKER 1983, POWELL 1997) e as evidências da partição de recursos, apesar de terem sido demonstradas em algumas assembléias (ATKINSON 1979), parecem ser fracas para a maioria das assembléias estudadas (SEVENSTER 1992, TODA *et al.* 1999, WERTHEIM *et al.* 2000, TAKAHASHI *et al.* 2005). É possível que, na escala estudada, um dos mecanismos para a manutenção da diversidade de Drosophilidae na cidade de Florianópolis esteja associado à instabilidade ambiental e dos recursos tróficos existentes, como constatado por SHORROCKS (1974) e ATKINSON & SHORROCKS (1977) em assembléias urbanas de *Drosophila* em Londres.

A formação dos grupos funcionais de espécies que utilizam os mesmos recursos também foi observada por SEVENSTER (1992) e SAAVEDRA *et al.* (1995) em áreas de vegetação natural. Nas cidades, apesar de evidenciarmos uma maior similaridade de algumas espécies quanto ao uso dos frutos disponíveis (Figura 10), esta divisão não se refletiu nos índices de sobreposição calculados (Tabela 12). Assim, estes grupos não devem ser tão eficientes na utilização dos recursos quanto os formados nos ambientes amostrados de Mata Atlântica.

As espécies classificadas nos mesmos grupos funcionais tendem a ser mais próximas filogeneticamente, como, por exemplo, a maioria das espécies do grupo *tripunctata*, que utilizam as mesmas espécies hospedeiras. Este padrão de autocorrelação filogenética na distribuição das espécies foi observado por PIPKIN (1965) e, posteriormente, por SEVENSTER (1992), em drosofilídeos emergentes de frutos em florestas tropicais do Panamá. MEDEIROS (2006) também constatou essa correlação na distribuição dos drosofilídeos em um gradiente ambiental provocado por um córrego. A autocorrelação filogenética na utilização de recursos parece ser comum para diversos grupos de organismos (DINIZ-FILHO 2000) e pode estar associada simplesmente a maior similaridade genética entre as espécies, acarretando em respostas similares às variações ambientais, ou a conservação evolutiva dos nichos (WIENS & GRAHAM 2005).

Contrastando com o exposto para os drosofilídeos, as espécies hospedeiras utilizadas pelos grupos funcionais destas mescas não são relacionadas filogeneticamente, como evidenciado pelas relações entre a composição de espécies de Drosophilidae e a de plantas hospedeiras quando tratadas ao nível de família (Figura 12), ao invés de espécies (Figura 11). Relações entre grupos monofiléticos de drosofilídeos e de plantas hospedeiras são observadas nas comunidades havaianas (MAGNACCA *et al.* 2008), mas estas não são tão fortes quanto a especialização ao tipo de substrato, como frutos, fungos, folhas ou seiva de árvores.

As diferenças entre a sobreposição de nicho nos dois tipos de ambientes estudados sugerem que a partição dos recursos é possível somente em áreas de mata, onde a diversidade de recursos é maior. Entretanto, esta partição parece relacionada a uma preferência das espécies por certos recursos, mas não a uma obrigatoriedade em seu uso. Assim, conforme a diversidade de recursos diminui e os sítios preferenciais das espécies nativas podem vir a se esgotar, elas podem acabar ovipositando em recursos alternativos, onde sua habilidade competitiva ficaria prejudicada (FANARA *et al.* 1999, 2004). A facilidade em explorar recursos diferenciados fica evidenciada pela grande importância de determinados sítios de oviposição raros na dieta das espécies de drosofilídeos.

Algumas espécies de plantas hospedeiras parecem abrigar uma grande diversidade de espécies de Drosophilidae. O melhor exemplo disso é *Syagrus romanzoffiana*, de onde emergiram 41 espécies em nosso estudo e, se desejássemos tentar levantar toda a riqueza de espécies capaz de se criar em seus frutos, seriam necessárias ainda várias coletas (Figura 3).

A sugestão de que Arecaceae é uma das famílias mais exploradas por Drosophilidae em florestas neotropicais, onde suas espécies sustentam grande parte da diversidade destas moscas (MARTINS & SANTOS 2007), é condizente com nossos resultados.

A diversidade de frutos, que variou no tempo e no espaço, pode contribuir para a manutenção da diversidade de drosofilídeos mediante a formação de grupos funcionais. A diversidade de recursos é considerada um fator importante na definição das forças competitivas entre espécies coexistentes, como, por exemplo, a densidade de indivíduos nos frutos, que depende, dentre outras coisas, do tamanho e da qualidade nutricional dos mesmos (SEVENSTER 1992). Além disso, alguns substratos podem ser mais propensos ao crescimento de diferentes espécies de levedos ou bactérias, o que também pode auxiliar na coexistência, aumentando a heterogeneidade local (LACHAISE *et al.* 1979, MORAIS *et al.* 1994, 1995a, 1995b).

Nos pontos de Mata Atlântica foram encontrados mais recursos, o que leva a uma menor probabilidade das espécies de Drosophilidae se encontrarem, o que pode estar proporcionando a manutenção dos grupos funcionais. Isto também está refletido na menor taxa de colonização dos frutos, significando um maior "espaço" para a flutuação da ocorrência das espécies. SEVENSTER & VAN ALPHEN (1993) desenvolveram um modelo que atribui a manutenção de espécies com histórias de vida diferentes à flutuação sazonal da abundância de recursos num mesmo local. Os pressupostos para este modelo são preenchidos nas áreas de Mata Atlântica estudadas, com a flutuação temporal e espacial da disponibilidade de frutos, e espécies com diferentes histórias de vida (MARKOW & O'GRADY 2006).

É clara a influência da degradação dos ambientes na disponibilidade de recursos, o que pode acarretar, como já mencionado, em um aumento da sobreposição de nicho entre os drosofilídeos. A perda de espécies raras nos frutos da cidade é um importante indicador desta perda de diversidade, principalmente por muitas delas serem espécies naturalmente mais raras e podem sofrer uma pressão maior quanto à competição com outras espécies devido a suas pequenas populações.

Ainda, as espécies de Drosophilidae parecem estar associadas aos diferentes ambientes coletados, independendo da forma de coleta e dependendo do grau de degradação ambiental ou urbanização. Isto é, em muitos aspectos, muito favorável para seu uso como bioindicadores, como sugerido por MATA *et al.* (2008a). Além disso, corrobora a idéia de que as iscas de banana são capazes de capturar uma parcela representativa da fauna de Drosophilidae, principalmente frugívora, e espelham as flutuações que ocorrem na mesma, nos diferentes ambientes. Mas, aparentemente, não indica se as populações amostradas, principalmente das espécies raras, são viáveis nos pontos coletados.

CONCLUSÕES

Foram identificados os sítios de oviposição de 66 espécies de Drosophilidae em áreas de Mata Atlântica e urbanizadas no litoral do Estado de Santa Catarina, Brasil. As espécies de moscas amostradas mostraram-se generalistas, com excessão das espécies raras que apresentaram uma menor amplitude de variação na utilização das espécies hospedeiras. Entretanto, este fato pode ser um artefato causado pelo pequeno tamanho das amostras das populações destas moscas.

Foi observada uma mudança na composição das espécies hospedeiras com o aumento da urbanização, além de uma diminuição em sua diversidade. De uma forma geral, as assembléias de Drosophilidae de floresta e de cidade são características e, relacionada à mudança no ambiente. Foram observadas diferenças na dominância das espécies emergentes dos frutos e na sobreposição dos nichos das mesmas. Evidencia-se, pela baixa sobreposição de nicho, a formação de grupos funcionais de espécies de drosofilídeos nas áreas de mata, enquanto que as assembléias de áreas urbanas caracterizam-se por uma alta sobreposição de nicho, o que pode evidenciar um quadro de partição dos recursos.

Aparentemente, as populações da maioria das espécies de Drosophilidae não conseguem persistir em áreas de cidade, uma vez que não foram observados indivíduos emergindo dos frutos coletados neste ambiente. Além disso, as assembléias urbanas emergentes dos frutos coletados apresentavam-se desprovidas de espécies raras. Entretanto, algumas espécies nativas aparentemente possuem aptidão para colonizar com sucesso ambientes antrópicos, como é o caso de *D. mercatorum* e *D. cardinoides*, por exemplo.

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LEGENDAS

Tabela 1 – Pontos de coleta estudados, com suas coordenadas geográficas, tipo de ambiente e grau de preservação (de acordo com Döge *et al.*, 2004; 2006; 2007; Gottschalk *et al.*, 2006).

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Figura 9 – Análise de correspondência destendenciada (DCA) relacionando as espécies de Drosophilidae e as espécies de plantas hospedeiras das quais emergiram, para frutos coletados em áreas urbanizadas. A) Gráfico comparando a similaridade das faunas emergentes de cada espécie hospedeira. B) Influência das espécies na segregação dos pontos relativos às espécies hospedeiras (vetores). Nomes em negrito sinalizam espécies exóticas.

Figura 10 – Análise de correspondência destendenciada (DCA) relacionando as espécies de Drosophilidae e as espécies de plantas hospedeiras das quais emergiram, para frutos coletados em Mata Atlântica. A) Gráfico comparando a similaridade das faunas emergentes de cada espécie hospedeira. B) Influência das espécies na segregação dos pontos relativos às espécies hospedeiras (vetores). Nomes em negrito sinalizam espécies exóticas.

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Figura 12 – Resultados das análises de Mantel, comparando a similaridade na composição das espécies de Drosophilidae em cada coleta (espécies de Drosophilidae), com a similaridade da composição de frutos amostrados, ao nível das famílias hospedeiras (famílias hospedeiras), com a distância entre os pontos de coleta amostrados (variação espacial), com a época do ano amostrada (variação sazonal) e com o tipo de ambiente amostrado, Mata Atlântica ou áreas urbanizadas (variação no ambiente). *Correlações significativas para $\alpha = 0,05$, aplicando-se a correção de Bonferroni.

Tabela 1

Pontos de coleta	**Código**	**Coordenadas geográficas**	**Tipo de ambiente**	**Grau de preservação***
Parque Estadual da Serra do Tabuleiro I – Ponto **E** de De Toni *et al.*(2007)	F1	27º44’48”S; 48º48’44”W	Mata Atlântica, continente	a
Parque Estadual da Serra do Tabuleiro II – Ponto **F** de De Toni *et al.*(2007)	F2	27º44’55”S; 48º48’72”W	Mata Atlântica, continente	a
Parque Municipal da Lagoa do Peri, Ilha de Santa Catarina - Ponto **D** de De Toni *et al.*(2007)	F3	27º45’23”S; 48º32’58”W	Mata Atlântica, insular	b
Morro da Lagoa da Conceição, Ilha de Santa Catarina – ponto **A** de De Toni *et al.*(2007); ponto **NU** de Gottschalk *et al.* (2007)	F4	27°35’27”S; 48°28’33”W	Mata Atlântica, insular	c
Ratones Grande Island - site **B** of De Toni *et al.*(2007)	F5	27º28’58”S; 48º33’71”W	Mata Atlântica, insular	d
Ilha de Ratones Pequeno – ponto **C** de De Toni *et al.*(2007)	F6	27º29’69”S; 48º33’97”W	Mata Atlântica, insular	d
Ilha do Arvoredo – ponto **G** de	F7	27º17’57”S;	Mata Atlântica,	e

De Toni *et al.*(2007)		48º21’23”W	insular	
Ilha do Campeche – ponto **H** de De Toni *et al.*(2007)	F8	27º41’81”S; 48º28’88”W	Mata Atlântica, insular	e
Morro da Cruz, Ilha de Santa Catarina – ponto **LU** de Gottschalk *et al.* (2007)	C1	27°35’04”S; 48°31’04”W	Área urbanizada (jardins e áreas verdes), insular	f
Campus da Universidade Federal de Santa Catarina, Ilha de Santa Catarina – ponto **MU** de Gottschalk *et al.* (2007)	C2	27°36’13”S; 48°31’22”W	Área urbanizada (jardins e áreas verdes), insular	f
Mercado, Ilha de Santa Catarina – próximo ao ponto **HU** de Gottschalk *et al.* (2007)	C3	27°34’24”S; 48°32’15”W	Área urbanizada (dentro de um prédio), insular	f

* a – área bem preservada, em avançado estado de regeneração, com muito pouca influência humana; b – área bem preservada, em avançado estado de regeneração, com pouca influência humana; c – área moderadamente preservada, em avançado estado de regeneração, com influência humana razoável; d – área em estado de regeneração intermediário, com moderada influência humana; e – áreas em estado de regeneração intermediário, com alta influência humana; f – áreas urbanas. Essa classificação leva em consideração o estado de conservação da vegetação e a acessibilidade e o fluxo de pessoas na área.

Tabela 2

Data da coleta	**Estação**	**Pontos de coleta**
Março de 1999	Outono	F1, F2, F3, F4, F5, F6, F7, F8
Junho de 1999	Inverno	F1, F2, F3, F4, F5, F6, F7, F8
Setembro de 1999	Primavera	F1, F2, F3, F4, F5, F6, F7, F8
Dezembro de 1999	Verão	F1, F2*, F3*, F4, F5, F6, F7, F8
Março de 2000	Outono	F1, F2, F3, F4, F5, F6, F7, F8
Junho de 2000	Inverno	F1, F2, F3, F4, F5, F6, F7, F8
Setembro de 2000	Primavera	F1, F2, F3, F4, F5, F6, F7, F8
Dezembro de 2000	Verão	F1, F2, F3*, F4, F5, F6, F7, F8
Agosto de 2002	Inverno	F4, C1, C2
Novembro de 2002	Primavera	F4*, C1*, C2*
Fevereiro de 2003	Verão	F4*, C1*, C2
Maio de 2003	Outono	F4, C1*, C2
Agosto de 2003	Inverno	F4*, C1*, C2
Fevereiro de 2005	Verão	C1*, C2, C3
Março de 2005	Verão	F4, C1, C2, C3
Abril de 2005	Outono	F4*, C1, C2, C3
Maio de 2005	Outono	C1, C2, C3
Julho de 2005	Inverno	C1*, C2, C3
Setembro de 2005	Primavera	C1*, C2, C3

* Coletas sem registros de frutos.

Tabela 3

Grupo	**Espécies**	**Código**
Gênero *Chymomyza*		
procnemis	*C. pectinifemur* Duda, 1927	CPECT
Gênero *Diathoneura*		
Subgênero *Diathoneura*		
	D. smithi Vilela & Bächli, 1990	DSMIT
	Diathoneura sp.1	DIATH
Gênero *Drosophila*		
Subgênero *Dorsilopha*		
busckii	*D. busckii* Coquillett, 1901*	DBUSC
Subgênero *Drosophila*		
annulimana	*D. annulimana* Duda, 1927	DANNU
bromeliae	*D. bromelioides* Pavan & Cunha, 1947	DBROM
calloptera	*D. atrata* Burla & Pavan, 1953	DATRA
	D. quadrum (Wiedemann, 1830)	DQUAD
cardini	*D. cardini* Sturtevant, 1916	DCDNI
	D. cardinoides Dobzhansky & Pavan, 1943	DCDNO
	D. neocardini Streisinger, 1946	DNEOC
	D. polymorpha Dobzhansky & Pavan, 1943	DPOLY
	D. polymorpha (aff.)	DPOLA
dreyfusi	*D. dreyfusi* Dobzhansky & Pavan, 1943	DDREY
	D. briegeri Pavan & Breuer, 1954	DBRIE
guarani	*D. griseolineata* Duda, 1927	DGRIS

	D. guaru Dobzhansky & Pavan, 1943	DGUAR
	D. maculifrons Duda, 1927	DMACU
	D. ornatifrons Duda, 1927	DORNA
immigrans	*D. immigrans* Sturtevant, 1921*	DIMMI
pallidipennis	*D. pallidipennis* Dobzhansky & Pavan, 1943	DPALL
repleta	*D. hydei* Sturtevant, 1921	DHYDE
	D. mercatorum Patterson & Wheeler, 1942	DMERC
	D. onca Dobzhansky & Pavan, 1943	DONCA
	D. repleta Wollaston, 1858	DREPL
	D. senei Vilela, 1983	DSENE
	D. zottii Vilela, 1983	DZOTT
	D. zottii (aff.)	DZOTA
tripunctata	*D. bandeirantorum* Dobzhansky & Pavan, 1943	DBAND
	D. bodemannae Pipkin & Heed, 1964	DBODE
	D. frotapessoai Vilela & Bächli, 1990	DFROT
	D. medioimpressa Frota-Pessoa, 1954	DMIMP
	D. mediopicta Frota-Pessoa, 1954	DPICT
	D. mediopictoides Heed & Wheeler, 1957	DPICO
	D. mediopunctata Dobzhansky & Pavan, 1943	DPUNC
	D. mediosignata Dobzhansky & Pavan, 1943	DSIGN
	D. mediostriata Duda, 1925	DSTRI
	D. nappae Vilela, Valente & Basso-da-Silva, 2004	DNAPP
	D. neoguaramunu Frydenberg, 1956	DNGUA
	D. paraguayensis Duda, 1927 / *D. cuaso* Bächli,	DPGUA

	Vilela & Ratcov, 2000	
	D. paramediostriata Townsend & Wheeler, 1955	DPSTR
	D. pellewae Pipkin & Heed, 1964	DPELL
	D. setula Heed & Wheeler, 1957	DSETU
	D. tristriata Heed & Wheeler, 1957	DTRIS
virilis	*D. virilis* Sturtevant, 1916*	DVIRI
Subgênero *Sophophora*		
melanogaster	*D. ananassae* Doleschall, 1858*	DANAN
	D. kikkawai Burla, 1954*	DKIKK
	D. malerkotliana Parshad & Paika, 1964*	DMALE
	D. melanogaster Meigen, 1830*	DMELA
	D. simulans Sturtevant, 1919*	DSIMU
saltans	*D. prosaltans* Duda, 1927	DPROS
	D. saltans Sturtevant, 1916	DSALT
	D. sturtevanti Duda, 1927	DSTUR
willistoni	*D. bocainensis* Pavan & Cunha, 1947	DBCNE
	D. bocainoides Carson, 1954	DBCNO
	D. capricorni Dobzhansky & Pavan, 1943	DCAPR
	D. fumipennis Duda, 1925	DFUMI
	D. nebulosa Sturtevant, 1916	DNEBU
	D. willistoni Sturtevant, 1916 / *D. paulistorum* Dobzhansky & Pavan, in Burla et al., 1949	DWILL
não determinadas	*Drosophila* sp.1	DSP1
	Drosophila sp.3	DSP3

Gênero *Rhinoleucophenga*	*Rhinoleucophenga* spp.	RHINO
Gênero *Scaptodrosophila*		
latifasciaeformis	*S. latifasciaeformis* (Duda, 1940)*	SLATI
Gênero *Scaptomyza*	*Scaptomyza* sp.	SCAPT
Gênero *Zaprionus*		
armatus	*Z. indianus* Gupta, 1970*	ZINDI
Gênero *Zygothrica*	*Zygothrica* spp.	ZYGOT

*Espécies exóticas do Neotrópico.

Tabela 4

Famílias Hospedeiras	**Annonaceae**	**Araliaceae**	**Arecaceae**	**Bombacaceae**	**Combretaceae**	**Euphorbiaceae**	**Fabaceae**	**Lauraceae**	
Espécies Hospedeiras	***Xylopia* sp. (XYLO) (4)**	***Schefflera* sp. (SCHE) (1)**	***Syagrus romanzoffiana* (SROM) (24)**	***Pseudobombax* sp. (PSEU) (1)**	***Terminalia catappa* (TCAT) (1)**	***Aleurites moluccana* (AMOL) (2)**	***Inga* sp. (INGA) (1)**	***Cinamomum* sp. (CINA) (4)**	***Ocotea* sp. (OCOT) (2)**
DSMIT									
DIATH			1 (1)						
DBUSC*			33 (3)		1 (1)				
DANNU			1 (1)						
DBROM			8 (2)					3 (1)	
DATRA	2 (1)	4 (1)	30 (7)						
DQUAD			4 (1)						
DCDNO						52 (2)			
DNEOC			14 (4)						
DPOLY			371 (13)		2 (1)	17 (1)			
DDREY			1 (1)						
DBRIE									1 (1)

DGRIS	2 (1)		693 (13)			3 (1)	3 (1)	1 (1)	
DGUAR									
DMACU									
DORNA			1 (1)						
DIMMI*			28 (2)						
DPALL									
DMERC			20 (1)						
DONCA			14 (2)						
DREPL									
DSENE			1 (1)						
DZOTT			6 (2)						
DZOTA									
DBAND			4 (2)						
DBODE			3 (1)						
DFROT									
DMIMP									3 (1)
DPICT			9 (5)						
DPICO									
DPUNC	3 (1)		220 (11)			3 (1)			3 (1)
DSIGN			76 (7)			3 (1)			
DSTRI			44 (1)			8 (1)			
DNAPP			11 (1)						
DNGUA									
DPGUA	6 (1)		1 (1)						

DTRIS									
DANAN*									
DKIKK*						3 (1)			
DMALE*			284 (5)						
DMELA*			969 (6)			41 (1)			
DSIMU*	1 (1)		9.957 (16)		2 (1)			144 (1)	
DPROS			1 (1)						
DSALT			1 (1)						
DSTUR			8 (4)			3 (1)			
DBCNE	7 (1)		7 (2)						
DBCNO			5 (1)						
DCAPR	5 (1)		412 (9)						
DFUMI			10 (5)						
DNEBU			1 (1)						
DWILL	1 (1)		4.974 (19)				2 (1)	2 (1)	
DSP1			1 (1)						
DSP3									
RHINO			16 (5)			4 (1)			
SLATI*			1 (1)						
ZINDI*			207 (5)	3 (1)					
ZYGOT			3 (3)						
TOTAL	**27 (1)**	**4 (1)**	**18.451 (20)**	**3 (1)**	**5 (1)**	**137 (2)**	**5 (1)**	**150 (2)**	**7 (2)**

*Espécies exóticas do Neotrópico.

Tabela 4 (cont.)

Famílias Hospedeiras	**Magnoliaceae**	**Malpighiaceae**			**Meliaceae**		**Moraceae**		
Espécies Hospedeiras	***Talauma* sp. (TALA) (4)**	***Byrsonima legustifolia* (BLEG) (1)**	***Byrsonima* sp. (BYRS) (9)**	**Malpighiaceae (MALP) (1)**	***Cabralea* sp. (CABR) (5)**	***Guarea* sp. (GUAR) (7)**	***Coussapoa* sp. (CAUS) (1)**	***Ficus* sp. (FICU) (7)**	***Helicostylis* sp. (HELI) (1)**
DSMIT									
DIATH									
DBUSC*					118 (1)				
DANNU									
DBROM								1 (1)	
DATRA	2 (1)		3 (1)			16 (1)		2 (1)	
DQUAD									
DCDNO	4 (1)							3 (1)	
DNEOC			30 (1)						
DPOLY				3 (1)				1 (1)	
DDREY				1 (1)					
DBRIE									

DGRIS	34 (1)	1 (1)	6 (2)	1 (1)	7 (1)	3 (1)	1 (1)
DGUAR							
DMACU	1 (1)						
DORNA						2 (1)	
DIMMI*							
DPALL							
DMERC			1 (1)				
DONCA							
DREPL					8 (1)		
DSENE							
DZOTT			2 (1)		50 (5)	1 (1)	
DZOTA							
DBAND			1 (1)				
DBODE							
DFROT							
DMIMP							
DPICT							
DPICO					7 (1)		
DPUNC			6 (2)			1 (1)	8 (1)
DSIGN						5 (2)	5 (1)
DSTRI							
DNAPP							
DNGUA			22 (1)			1 (1)	
DPGUA	27 (2)	2 (1)	50 (3)		26 (1)	1 (1)	

DTRIS					16 (1)				
DANAN*			1 (1)						
DKIKK*									
DMALE*		4 (1)					10 (1)	99 (1)	
DMELA*	16 (1)		180 (1)	260 (1)				196 (1)	13 (1)
DSIMU*	4 (1)	1 (1)	4 (2)		4 (2)		134 (1)	134 (1)	28 (1)
DPROS									
DSALT									
DSTUR				1 (1)					
DBCNE			77 (2)						
DBCNO			22 (1)						
DCAPR	3 (1)		101 (4)	5 (1)					
DFUMI		5 (1)	15 (1)						
DNEBU									
DWILL	1 (1)	349 (1)	111 (2)		1 (1)	1 (1)	23 (1)	10 (2)	
DSP1			1 (1)						
DSP3			43 (2)						
RHINO			1 (1)					1 (1)	
SLATI*									
ZINDI*			3 (1)					12 (1)	
ZYGOT						3 (1)			
TOTAL	**92 (3)**	**362 (1)**	**680 (5)**	**271 (1)**	**237 (5)**	**34 (4)**	**167 (1)**	**473 (3)**	**41 (1)**

*Espécies exóticas do Neotrópico.

Tabela 4 (cont.)

Famílias Hospedeiras	**Myrtaceae**								
Espécies Hospedeiras	***Campomanesia* sp. (CAMP) (5)**	***Chrysophyllum* sp. (CHRY) (1)**	***Eugenia brasiliensis* (EBRA) (1)**	***Eugenia uniflora* (EUNI) (5)**	***Gomidesia spectabilis* (GSPE) (7)**	***Myrcia* sp. (MYRC) (2)**	***Psidium cattleyanum* (PCAT) (13)**	***Psidium guayava* (PGUA) (9)**	***Sygygium cumini* (SCUM) (2)**
DSMIT									
DIATH									
DBUSC*		1 (1)		1 (1)					
DANNU									
DBROM			9 (1)	4 (1)			5 (1)		
DATRA	13 (1)						1 (1)		
DQUAD									
DCDNO			4 (1)						
DNEOC								4 (1)	
DPOLY				7 (2)				2 (1)	
DDREY									
DBRIE									

DGRIS			5 (1)	10 (1)				
DGUAR						1 (1)		
DMACU								
DORNA								
DIMMI*	1 (1)			3 (1)				
DPALL	1 (1)							
DMERC								
DONCA								
DREPL								
DSENE								
DZOTT								
DZOTA	17 (1)							
DBAND								
DBODE								
DFROT							42 (1)	70 (1)
DMIMP								
DPICT								
DPICO								
DPUNC		1 (1)	16 (1)	85 (2)	9 (2)		4 (1)	
DSIGN					1 (1)			
DSTRI			6 (1)					
DNAPP								
DNGUA	2 (1)							
DPGUA	3 (1)							

DTRIS									
DANAN*									
DKIKK*							1 (1)	7 (1)	
DMALE*							10 (2)	15 (2)	
DMELA*	1 (1)			165 (3)	1 (1)		5 (1)	34 (1)	
DSIMU*	98 (2)		1 (1)	139 (3)	5 (1)	3 (1)	295 (3)	320 (4)	
DPROS									
DSALT									
DSTUR	1 (1)								
DBCNE		2 (1)			14 (2)				
DBCNO					4 (1)				
DCAPR		85 (1)			11 (2)				
DFUMI					29 (2)				
DNEBU									
DWILL	4 (1)		4 (1)	69 (2)	241 (5)	276 (2)	429 (4)	12 (3)	2 (1)
DSP1									
DSP3									
RHINO									
SLATI*									
ZINDI*				14 (1)			10 (2)	107 (3)	
ZYGOT		1 (1)				7 (1)			
TOTAL	**141 (4)**	**90 (1)**	**45 (1)**	**497 (3)**	**315 (5)**	**287 (2)**	**802 (8)**	**571 (5)**	**2 (1)**

*Espécies exóticas do Neotrópico.

Tabela 4 (cont.)

Famílias Hospedeiras	**Olacaceae**	**Oxalidaceae**	**Rosaceae**	**Rubiaceae**				**Rutaceae**	**Sapotaceae**
Espécies Hospedeiras	***Heisteria* sp. (HEIS) (1)**	***Averrhoa carambola* (ACAR) (1)**	***Prunus* sp.2 (PRU2) (2)**	***Lichia* sp. (LICH) (1)**	***Posoqueria latifolia* (PLAT) (4)**	***Posoqueria* sp. (POSO) (2)**	***Psychotria* sp. (PSYC) (8)**	***Citrus sinensis* (CSIN) (3)**	***Crysophyllum* sp. (CHRY) (1)**
DSMIT									
DIATH									
DBUSC*									
DANNU									
DBROM									
DATRA	4 (1)				6 (1)	1 (1)			
DQUAD									
DCDNO		1 (1)		6 (1)		10 (1)			
DNEOC									
DPOLY						4 (1)			
DDREY									
DBRIE									

DGRIS							
DGUAR							
DMACU							
DORNA							
DIMMI*							
DPALL		1(1)				2 (1)	
DMERC							
DONCA		2(1)				2 (1)	
DREPL							
DSENE							
DZOTT							
DZOTA							
DBAND							
DBODE							
DFROT							
DMIMP							
DPICT		8 (1)		1 (1)			
DPICO							
DPUNC				1 (1)	4 (2)		
DSIGN		2 (2)					
DSTRI		12 (2)					
DNAPP							
DNGUA							
DPGUA			2 (1)	2 (1)			

DTRIS									
DANAN*		10 (1)						1 (1)	
DKIKK*		2 (1)							
DMALE*		12 (2)							
DMELA*		12 (1)			82 (1)		119 (2)		
DSIMU*		349 (2)			4 (1)		48 (3)	6 (1)	28 (1)
DPROS									
DSALT									
DSTUR									
DBCNE									
DBCNO									
DCAPR			1 (1)						
DFUMI							1 (1)		
DNEBU									
DWILL		65 (2)	9 (1)				30 (3)		
DSP1							1 (1)		
DSP3									
RHINO					3 (1)				
SLATI*									
ZINDI*								3 (1)	
ZYGOT						1 (1)	10 (2)		
TOTAL	**4 (1)**	**487 (2)**	**12 (1)**	**6 (1)**	**99 (2)**	**16 (1)**	**213 (6)**	**14 (2)**	**28 (1)**

*Espécies exóticas do Neotrópico.

Tabela 4 (cont.)

Famílias Hospedeiras	**Solanaceae**	**Thymelaeaceae**	**Não identificado**				
Espécies Hospedeiras	***Solanum inaequale* (SINE) (11)**	***Daphnopsis* sp. (DAPH) (1)**	**Fruit 1 (FRU1) (15)**	**Fruit 2 (FRU2) (6)**	**Fruit 3 (FRU3) (2)**	**Fruit 4 (FRU4) (2)**	**TOTAL (214)**
DSMIT						1 (1)	**1 (1)**
DIATH							**1 (1)**
DBUSC*			11 (1)			56 (1)	**221 (9)**
DANNU							**1 (1)**
DBROM							**30 (7)**
DATRA	11 (1)		5 (1)		5 (1)		**105 (21)**
DQUAD							**4 (1)**
DCDNO	25 (1)						**105 (9)**
DNEOC							**48 (6)**
DPOLY	1 (1)						**408 (22)**
DDREY							**2 (2)**
DBRIE							**1 (1)**
DGRIS	52 (2)		132 (1)	1 (1)			**955 (31)**

DGUAR							**1 (1)**
DMACU							**1 (1)**
DORNA							**3 (2)**
DIMMI*							**32 (4)**
DPALL	4 (1)						**8 (4)**
DMERC							**21 (2)**
DONCA							**18 (4)**
DREPL							**8 (1)**
DSENE							**1 (1)**
DZOTT	19 (1)						**78 (10)**
DZOTA							**17 (1)**
DBAND	1 (1)						**6 (4)**
DBODE							**3 (1)**
DFROT							**112 (2)**
DMIMP							**3 (1)**
DPICT							**18 (7)**
DPICO							**7 (1)**
DPUNC	30 (4)	3 (1)	14 (3)		8 (1)	17 (1)	**436 (38)**
DSIGN	7 (3)	35 (1)	12 (2)		8 (1)		**154 (21)**
DSTRI							**70 (5)**
DNAPP		1 (1)	1 (1)				**13 (3)**
DNGUA							**25 (3)**
DPGUA	1 (1)	6 (1)	10 (3)				**137 (18)**
DTRIS							**16 (1)**

DANAN*							**12 (3)**
DKIKK*							**13 (4)**
DMALE*	1 (1)						**435 (15)**
DMELA*			2 (1)			1 (1)	**2.097 (25)**
DSIMU*	258 (3)						**11.967 (54)**
DPROS							**1 (1)**
DSALT							**1 (1)**
DSTUR							**13 (7)**
DBCNE					27 (1)		**134 (9)**
DBCNO					2 (1)		**33 (4)**
DCAPR	202 (4)		2 (1)		42 (1)		**869 (26)**
DFUMI					42 (1)		**102 (11)**
DNEBU							**1 (1)**
DWILL	731 (3)				98 (1)	2 (1)	**7.447 (61)**
DSP1							**3 (3)**
DSP3							**43 (2)**
RHINO							**25 (9)**
SLATI*							**1 (1)**
ZINDI*	3 (1)						**373 (16)**
ZYGOT							**25 (9)**
TOTAL	**1.346 (7)**	**45 (1)**	**189 (5)**	**1 (1)**	**232 (1)**	**77 (2)**	**26.665 (119)**

*Espécies exóticas do Neotrópico.

Tabela 5

Famílias Hospedeiras	**Arecaceae**		**Cecropiaceae**	**Combretaceae**	**Ebenaceae**	**Euphorbiaceae**	**Fabaceae**	**Malvaceae**	**Meliaceae**
Espécies Hospedeiras	***Syagrus romanzoffiana* (SROM) (2)**	**COCO (3)**	***Cecropia glaziovii* (CGLA) (3)**	***Terminalia catappa* (TCAT) (2)**	***Diospyros kaki* (DKAK) (3)**	***Aleurites moluccana* (AMOL) (3)**	***Phaseolus vulgaris* (PVUL) (1)**	***Chorisia* sp. (CHOR) (2)**	***Melia azedarach* (MAZE) (5)**
CPECT									
DBUSC*							6 (1)		
DATRA			3 (1)						
DCDNI									
DCDNO				4 (1)		383 (3)	1 (1)		
DNEOC				3 (1)		11 (2)			
DPOLY				4 (1)					
DPOLA				16 (1)					
DGRIS								1 (1)	2 (1)
DIMMI*									1 (1)
DPALL									
DHYDE									

DMERC	1 (1)					1 (1)				
DREPL							13 (1)			
DZOTT										
DPUNC										
DPGUA			11 (1)	14 (1)		45 (3)				
DPSTR				8 (1)			3 (1)			
DPELL										
DSETU										
DVIRI*										
DANAN*					3 (1)					
DKIKK*		4 (1)		6 (1)	21 (1)		1 (1)			
DMALE*	35 (1)			530 (1)	44 (3)	3 (1)				47 (1)
DMELA*										1 (1)
DSIMU*	279 (1)			122 (1)	180 (2)					187 (1)
DPROS										
DCAPR										
DWILL	1 (1)			203 (1)	3 (1)	5 (1)				1 (1)
SLATI*				6 (1)						
SCAPT										
ZINDI*	1 (1)			612 (2)	4 (1)					56 (2)
TOTAL	**317 (1)**	**4 (1)**	**14 (1)**	**1.528 (2)**	**255 (3)**	**448 (3)**	**24 (1)**		**1 (1)**	**295 (2)**

*Espécies exóticas do Neotrópico.

Tabela 5 (cont.)

Famílias Hospedeiras	**Moraceae**		**Musaceae**	**Myrtaceae**		**Passifloraceae**	**Rosaceae**		
Espécies Hospedeiras	***Ficus carica* (FCAR) (1)**	***Maclura* sp. (MACL) (1)**	***Musa* sp. (MUSA) (6)**	***Psidium guayava* (PGUA) (8)**	***Sygygium cumini* (SCUM) (2)**	***Passiflora edulis* (PEDU) (3)**	***Eriobotrya japonica* (EJAP) (4)**	***Malus* sp. (MALU) (3)**	***Prunus* sp.1 (PRUN) (1)**
CPECT			3 (1)			19 (2)			
DBUSC*						800 (1)			
DATRA									
DCDNI						3 (1)			
DCDNO			55 (1)	11 (1)		9 (2)	11 (1)		
DNEOC			1 (1)				3 (1)		
DPOLY			2 (1)	2 (1)					
DPOLA				3 (2)					
DGRIS							1 (1)		
DIMMI*			19 (1)			4 (2)	1 (1)		
DPALL									
DHYDE			23 (1)						
DMERC			125 (1)	2 (1)			6 (1)		31 (1)

DREPL			22 (1)			32 (1)			
DZOTT							4 (2)		
DPUNC		2 (1)					6 (1)		
DPGUA				16 (1)					
DPSTR			10 (1)			23 (2)			
DPELL									
DSETU									
DVIRI*									
DANAN*			432 (4)	58 (3)		305 (1)		1 (1)	7 (1)
DKIKK*	1 (1)		36 (1)	50 (4)	1 (1)	3 (1)	13 (1)	4 (1)	
DMALE*	1 (1)		113 (3)	1,070 (6)	8 (1)	103 (2)	51 (4)	6 (1)	17 (1)
DMELA*			111 (4)	105 (3)		78 (1)	3 (1)	4 (2)	46 (1)
DSIMU*	3 (1)		1.049 (4)	868 (7)	17 (2)	424 (2)	38 (3)	16 (2)	84 (1)
DPROS							3 (1)		
DCAPR							4 (1)		
DWILL			25 (4)	158 (5)	1 (1)	10 (1)	49 (2)	37 (1)	1 (1)
SLATI*									
SCAPT						3 (1)			
ZINDI*			26 (2)	902 (8)	20 (1)	1 (1)	168 (4)	18 (1)	13 (1)
TOTAL	**5 (1)**	**2 (1)**	**2.052 (4)**	**3.245 (8)**	**47 (2)**	**1.817 (2)**	**361 (4)**	**86 (3)**	**199 (1)**

*Espécies exóticas do Neotrópico.

Tabela 5 (cont.)

Famílias Hospedeiras	**Rosaceae**	**Rutaceae**			**Solanaceae**		
Espécies Hospedeiras	***Pyrus* sp. (PYRU) (1)**	***Citrus* x *limon* (CLIM) (1)**	***Citrus reticulata* (CRET) (3)**	***Citrus* x *sinensis* (CSIN) (7)**	***Capsicum cordiforme* (CCOR) (3)**	***Solanum lycopersicum* (SLYC) (4)**	**TOTAL (72)**
CPECT				8 (1)			**30 (4)**
DBUSC*					216 (2)	19 (2)	**1.041 (6)**
DATRA							**3 (1)**
DCDNI				4 (1)	12 (2)	1 (1)	**20 (5)**
DCDNO			9 (1)	17 (1)			**500 (12)**
DNEOC				67 (1)			**85 (6)**
DPOLY							**8 (3)**
DPOLA							**19 (3)**
DGRIS			4 (1)	2 (1)			**10 (5)**
DIMMI*		1 (1)		1 (1)	134 (1)		**161 (8)**
DPALL					12 (1)		**12 (1)**
DHYDE						1 (1)	**24 (2)**

DMERC				16 (2)	17 (1)		**199 (8)**
DREPL							**67 (3)**
DZOTT				12 (1)			**16 (3)**
DPUNC			11 (1)				**19 (3)**
DPGUA			13 (1)				**99 (7)**
DPSTR				42 (1)			**86 (6)**
DPELL				1 (1)			**1 (1)**
DSETU				6 (1)			**6 (1)**
DVIRI*				6 (1)			**6 (1)**
DANAN*	2 (1)			21 (4)		10 (2)	**839 (18)**
DKIKK*				1 (1)		1 (1)	**142 (16)**
DMALE*	1 (1)			44 (3)		4 (1)	**2.077 (31)**
DMELA*			4 (1)	7 (3)			**359 (17)**
DSIMU*	20 (1)	5 (1)	77 (2)	55 (6)	43 (1)	39 (3)	**3.506 (41)**
DPROS							**3 (1)**
DCAPR							**4 (1)**
DWILL			18 (3)	223 (1)	1 (1)	1 (1)	**737 (26)**
SLATI*				106 (1)			**112 (2)**
SCAPT							**3 (1)**
ZINDI*	36 (1)			55 (4)			**1.912 (29)**
TOTAL	**59 (1)**	**6 (1)**	**136 (3)**	**694 (7)**	**435 (2)**	**76 (4)**	**12.106 (59)**

*Espécies exóticas do Neotrópico.

Tabela 6

	Especificidade			Ds	Ds‡	Número de espécies hospedeiras	Número de amostras
	Espécies	Família	Espécies ‡				
DSMIT†	M	M	-	1,00	-	1	1
DIAT1†	M	M	M	1,00	1,00	1	1
DBUSC	P	P	M	2,47	1,37	7	9
DANNU†	M	M	M	1,00	1,00	1	1
DBROM	P	P	P	2,03	2,97	6	7
DATRA	P	P	P	10,03	5,34	15	21
DQUAD†	M	M	M	1,00	1,00	1	1
DCDNO	P	P	M	3,25	2,24	8	9
DNEOC	M	M	P	1,51	1,51	3	6
DPOLY	P	P	M	3,42	1,35	9	22
DDREY	P	P	M	1,10	1,00	2	2
DBRIE†	M	M	-	1,00	-	1	1
DGRIS	P	P	M	4,85	3,60	17	31
DGUAR†	M	M	-	1,00	-	1	1
DMACU†	M	M	M	1,00	1,00	1	1
DORNA	P	P	P	1,20	1,20	2	2
DIMMI	P	P	M	2,32	2,32	3	4
DPALL	P	P	M	3,29	1,73	4	4
DMERC	P	P	M	1,38	1,38	2	2
DONCA	P	P	M	2,93	1,00	3	4

DREPL†	M	M	M	1,00	1,00	1	1
DSENE†	M	M	M	1,00	1,00	1	1
DZOTT	P	P	P	1,73	1,73	5	10
DZOTA†	M	M	M	1,00	1,00	1	1
DBAND	P	P	M	2,93	2,93	3	4
DBODE†	M	M	M	1,00	1,00	1	1
DFROT	P	M	P	1,66	1,66	2	2
DMIMP†	M	M	-	1,00	-	1	1
DPICT	P	M	M	1,49	1,00	3	7
DPICO†	M	M	M	1,00	1,00	1	1
DPUNC	P	P	P	6,76	2,97	19	38
DSIGN	P	P	P	2,36	4,16	10	21
DSTRI	P	P	M	3,57	1,00	4	5
DNAPP	P	P	M	2,28	1,64	3	3
DNGUA	P	P	M	1,35	1,35	3	3
DPGUA	P	P	P	6,71	3,53	13	18
DTRIS†	M	M	M	1,00	1,00	1	1
DANAN	P	P	M	1,28	1,00	3	3
DKIKK	P	P	M	3,10	1,18	4	4
DMALE	P	P	M	3,53	2,05	8	15
DMELA	P	P	P	4,13	4,98	17	25
DSIMU	P	P	M	4,66	2,24	24	54
DPROS†	M	M	M	1,00	1,00	1	1
DSALT†	M	M	M	1,00	1,00	1	1

DSTUR	P	P	M	2,86	1,90	4	7
DBCNE	P	P	M	2,90	1,40	6	9
DBCNO	P	P	M	2,31	1,48	4	4
DCAPR	P	P	P	4,17	3,21	11	26
DFUMI	P	P	P	1,74	2,09	6	11
DNEBU†	M	M	M	1,00	1,00	1	1
DWILL	P	P	M	5,95	3,33	25	61
DROS1	P	P	P	2,47	2,47	3	3
DROS3	M	M	M	1,00	1,00	1	2
RHINO	P	P	M	3,32	2,25	5	9
SCAPT†	M	M	M	1,00	1,00	1	1
ZINDI	P	P	P	4,30	3,01	10	16
ZYGOT	P	P	P	3,69	1,96	6	9

Tabela 7

	Especificidade			Ds	Ds‡	Número de espécies hospedeiras	Número de amostras
	Espécies	Família	Espécies ‡				
CPECT	P	P	P	1,41	1,92	3	4
DBUSC	P	M	M	1,57	1,00	4	6
DATRA†	M	M	-	1,00	-	1	1
DCDNI	P	M	M	1,79	1,73	4	5
DCDNO	P	P	M	1,52	1,38	9	12
DNEOC	P	P	M	2,29	1,92	5	6
DPOLY	P	P	P	1,75	1,80	3	3
DPOLA	P	M	M	1,09	1,00	2	3
DGRIS	P	P	P	3,82	1,82	5	5
DIMMI	P	P	M	1,27	1,17	7	8
DPALL†	M	M	-	1,00	-	1	1
DHYDE	P	P	M	1,09	1,09	2	2
DMERC	P	P	M	2,87	1,29	8	8
DREPL	P	P	M	2,61	1,00	3	3
DZOTT	P	P	M	1,87	1,87	2	3
DPUNC	P	P	P	2,61	1,70	3	3
DPGUA	P	P	P	3,70	1,84	5	7
DPSTR	P	P	M	3,65	1,71	5	6
DPELL*†	M	M	M	1,00	1,00	1	1
DSETU†	M	M	M	1,00	1,00	1	1

DVIRI†	M	M	M	1,00	1,00	1	1
DANAN	P	P	M	2,29	1,27	9	18
DKIKK	P	P	P	6,93	4,08	13	16
DMALE	P	P	M	3,80	2,09	16	31
DMELA	P	P	P	3,73	2,17	9	17
DSIMU	P	P	P	7,13	2,81	18	41
DPROS†	M	M	M	1,00	1,00	1	1
DCAPR†	M	M	M	1,00	1,00	1	1
DWILL	P	P	P	3,35	4,67	16	26
SLATI	P	P	M	1,38	1,00	2	2
SCAPT†	M	M	-	1,00	-	1	1
ZINDI	P	P	M	2,95	2,13	13	29

Tabela 8

Espécies de plantas hospedeiras	Abundância dos drosofilídeos	Número de amostras	Riqueza de drosofilídeos coletados
ACAR	487	2	13
AMOL	137	2	10
BLEG	362	1	6
BYRS	680	5	21
CABR	237	5	9
CAMP	141	4	10
CHRY	90	1	5
CINA	150	2	4
COUS	167	1	3
CRYS	28	1	1
CSIN	14	2	5
DAPH	45	1	4
EBRA	45	1	7
EUNI	497	3	10
FICU	473	3	13
FRU1	189	5	9
FRU2	1	1	1
FRU3	232	1	8
FRU4	77	2	5
GSPE	315	5	9
GUAR	34	4	10

HEIS	4	1	1
HELI	41	1	2
INGA	5	1	2
LICH	6	1	1
MALP	271	1	6
MYRC	287	2	4
OCOT	7	2	3
PCAT	802	8	10
PGUA	571	5	9
PLAT	99	2	7
POSO	16	1	4
PRU2	12	1	3
PSEU	3	1	1
PSYC	213	6	7
SCHE	4	1	1
SCUM	2	1	1
SINE	1.346	7	15
SROM	18.451	20	41
TALA	92	3	9
TCAT	5	1	3
XYLO	27	1	8

Tabela 9

Espécies de plantas hospedeiras	Abundância dos drosofilídeos	Número de amostras	Riqueza de drosofilídeos coletados
AMOL	448	3	6
CCOR	435	2	7
CGLA	14	1	2
CHOR	1	1	1
CLIM	6	1	2
COCO	4	1	1
CRET	136	3	7
CSIN	694	7	20
DKAK	255	3	6
EJAP	361	4	15
FCAR	5	1	3
MACL	2	1	1
MALU	86	3	7
MAZE	295	2	7
MUSA	2.052	4	16
PEDU	1.817	2	15
PGUA	3.245	8	12
PRU1	199	1	7
PVUL	24	1	5
PYRU	59	1	4
SCUM	47	2	5

SLIC	76	4	8
SROM	317	1	5
TCAT	1.528	2	12

Tabela 10

Pontos de coleta	Coletas		Amostras		Número de espécies hospedeiras		Drosophilidae	
	Realizadas	**Com frutos**	**Coletadas**	**Colonizadas**	**Coletadas**	**Colonizadas**	**S**	**N**
Mata Atlântica								
F1	8	8	26	11	12	7	15	291
F2	8	7	19	10	12	8	14	933
F3	8	7	25	9	19	8	13	619
F4	15	11	50	36	28	21	27	3.359
F5	8	8	25	13	15	8	28	6.753
F6	8	7	12	7	4	2	15	4.257
F7	8	8	19	9	13	7	10	2.304
F8	8	8	38	24	18	13	25	8.149
Total	**71**	**64**	**214**	**119**	**64***	**57***	**57***	**26.665**
Áreas urbanizadas								
C1	11	4	5	5	5	5	10	770

C2	11	10	33	24	12	11	25	6.284
C3	5	5	34	30	15	14	22	5.052
Total	**27**	**19**	**72**	**59**	**26***	**24***	**32***	**12.106**
TOTAL	**99**	**83**	**286**	**178**	**80***	**61***	**66***	**38.771**

* Os valores totais não representam a somatória do número de espécies coletadas em cada ponto de coleta.

Tabela 11

Pontos de coleta	**Amostras/Coleta**	**Espécies de plantas/Coleta**	**Freqüência de amostras colonizadas**
Mata Atlântica			
F1	3,25	1,50	0,42
F2	2,38	1,50	0,53
F3	3,13	2,38	0,36
F4	3,33	1,87	0,72
F5	3,13	1,88	0,52
F6	1,50	0,50	0,58
F7	2,38	1,63	0,47
F8	4,75	2,25	0,63
Total	**3,01**	**0,90**	**0,56**
Áreas urbanizadas			
C1	0,45	0,45	1,00
C2	3,00	1,09	0,73
C3	6,80	3,00	0,88
Total	**2,67**	**0,96**	**0,82**

Tabela 12

	Mata Atlântica	Áreas urbanizadas
Sobreposição de nicho	0,07 ± 0,031	0,79 ± 0,016
Amplitude de nicho	0,44 ± 0,354	0,46 ± 0,341

Figura 1

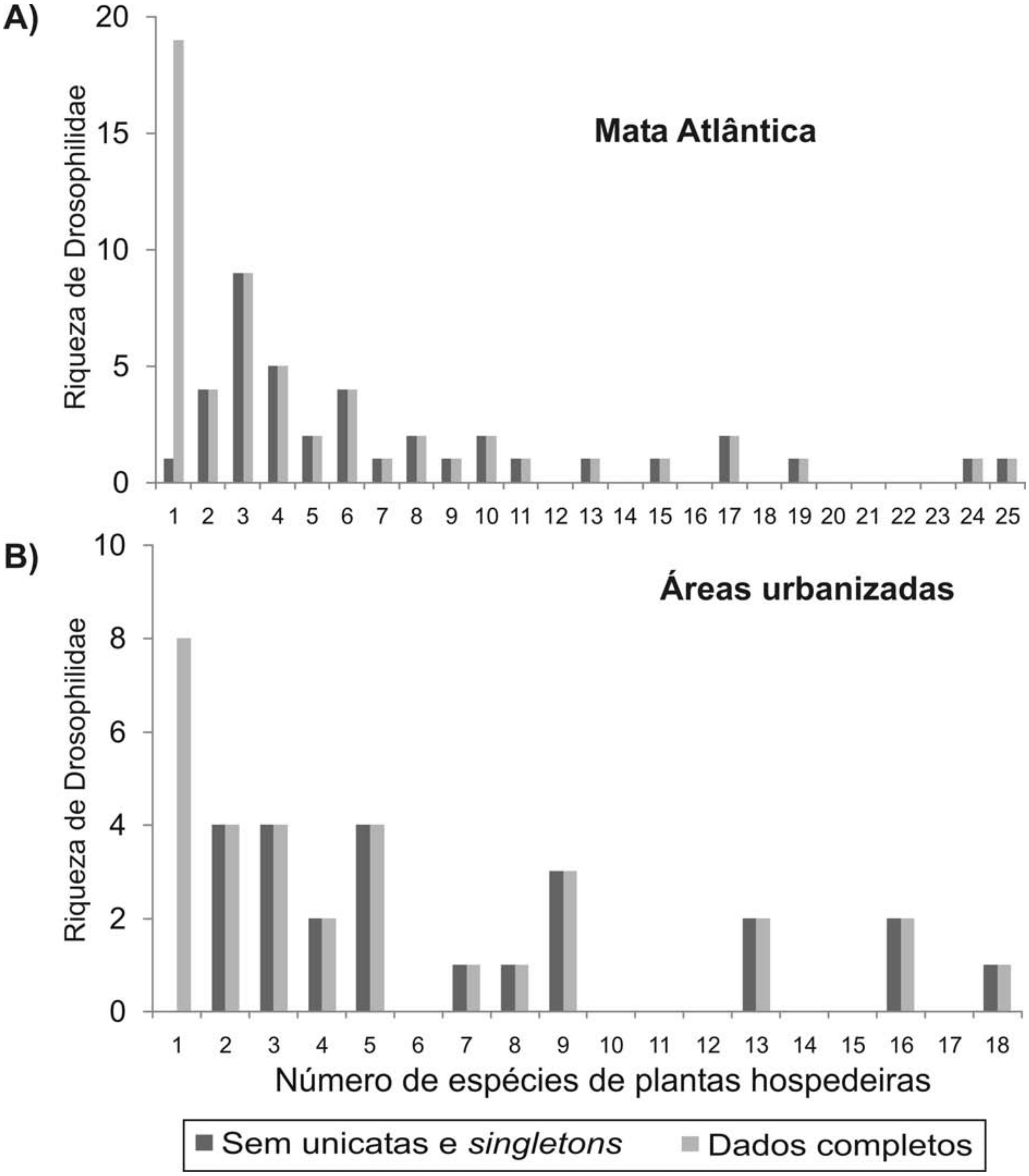

A)
Mata Atlântica
Riqueza de Drosophilidae
0
5
10
15
20
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
B)
Áreas urbanizadas
Riqueza de Drosophilidae
0
2
4
6
8
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Número de espécies de plantas hospedeiras
Sem unicatas e singletons
Dados completos

Figura 2

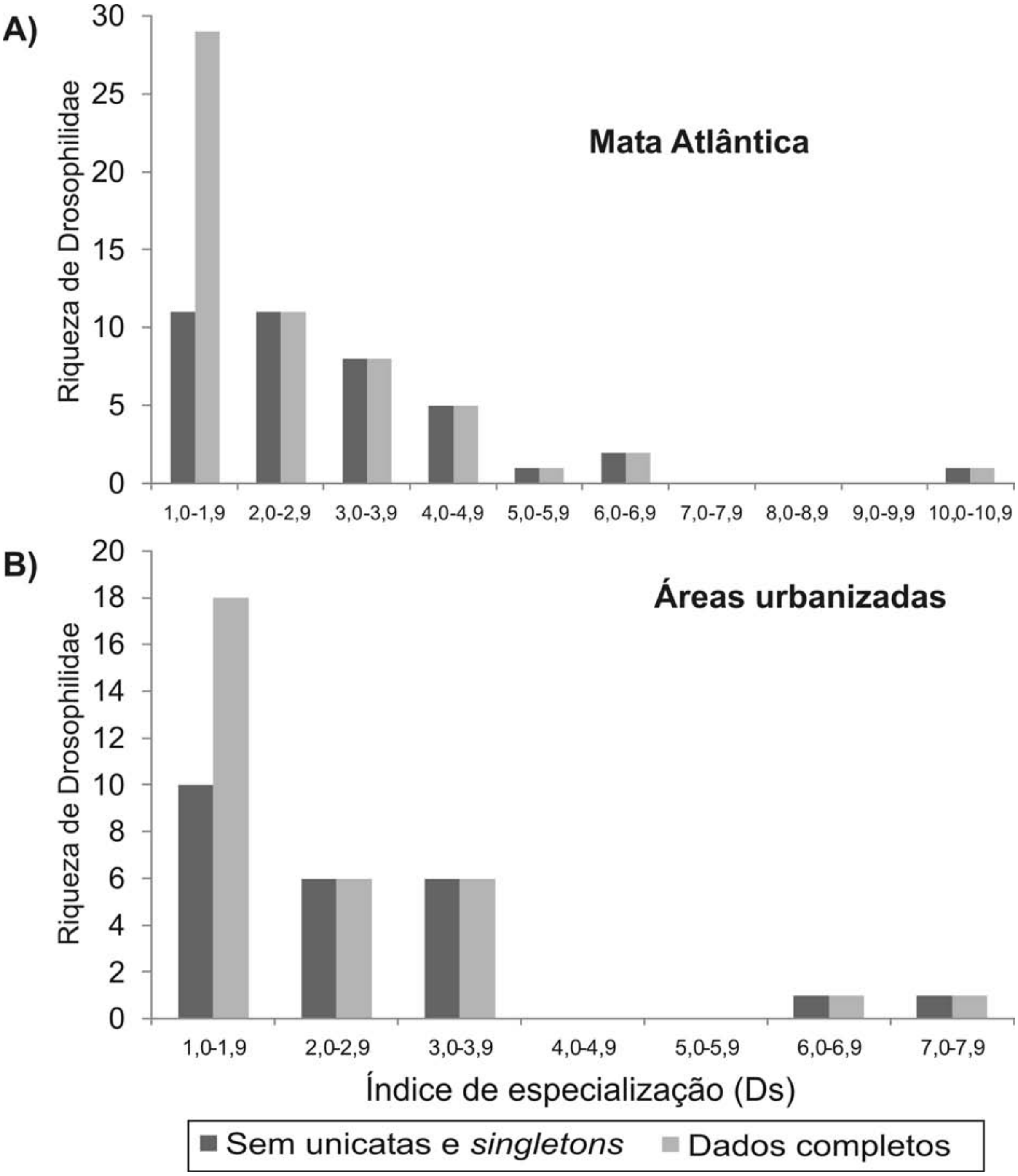

A)
Mata Atlântica
Riqueza de Drosophilidae
0
5
10
15
20
25
30
1,0-1,9
2,0-2,9
3,0-3,9
4,0-4,9
5,0-5,9
6,0-6,9
7,0-7,9
8,0-8,9
9,0-9,9
10,0-10,9
B)
Áreas urbanizadas
Riqueza de Drosophilidae
0
2
4
6
8
10
12
14
16
18
20
1,0-1,9
2,0-2,9
3,0-3,9
4,0-4,9
5,0-5,9
6,0-6,9
7,0-7,9
Índice de especialização (Ds)
Sem unicatas e *singletons*
Dados completos

Figura 3

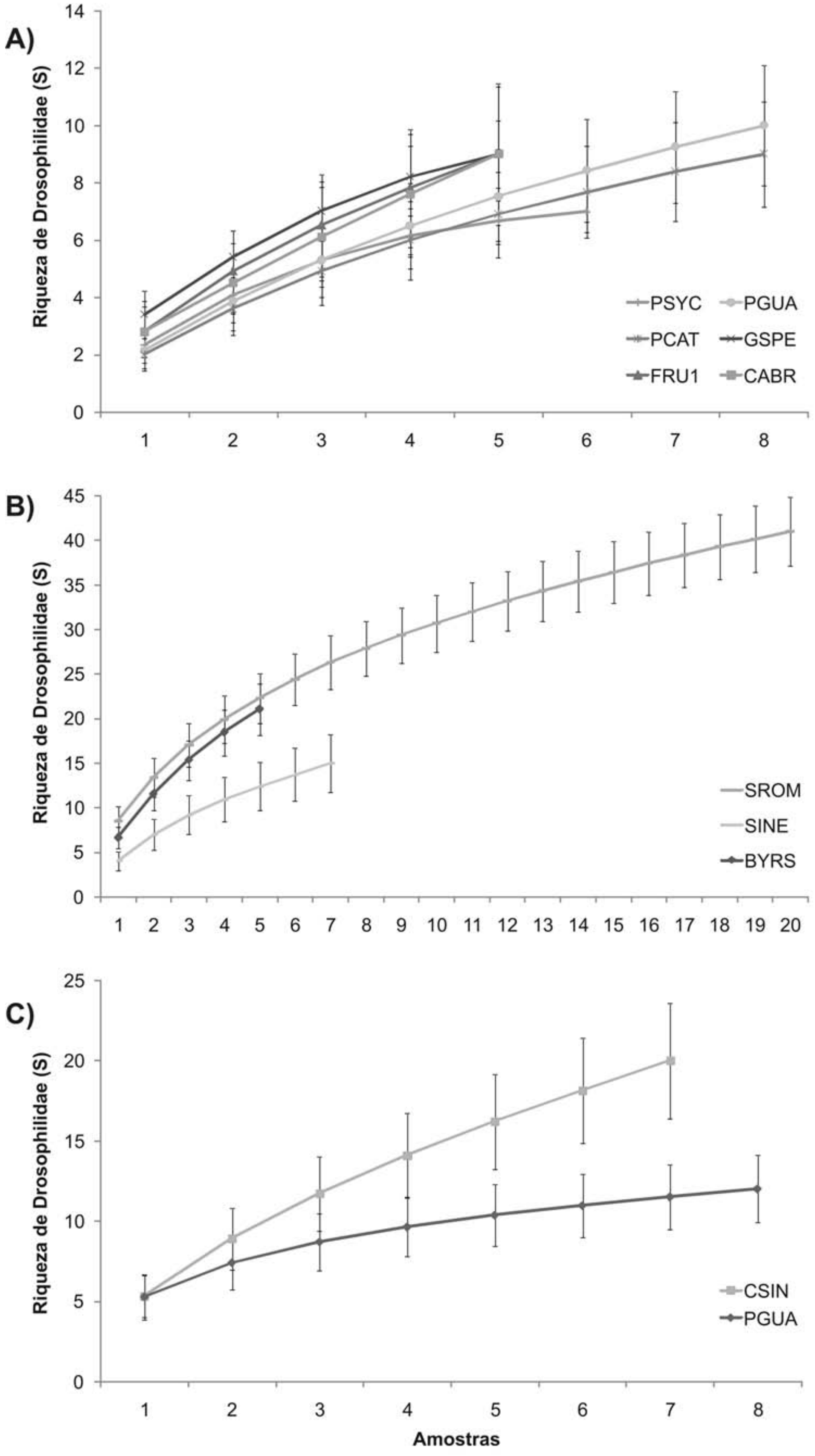

A)
Riqueza de Drosophilidae (S)
0
2
4
6
8
10
12
14
1
2
3
4
5
6
7
8
PSYC
PGUA
PCAT
GSPE
FRU1
CABR
B)
Riqueza de Drosophilidae (S)
0
5
10
15
20
25
30
35
40
45
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
SROM
SINE
BYRS
C)
Riqueza de Drosophilidae (S)
0
5
10
15
20
25
1
2
3
4
5
6
7
8
Amostras
CSIN
PGUA

Figura 4

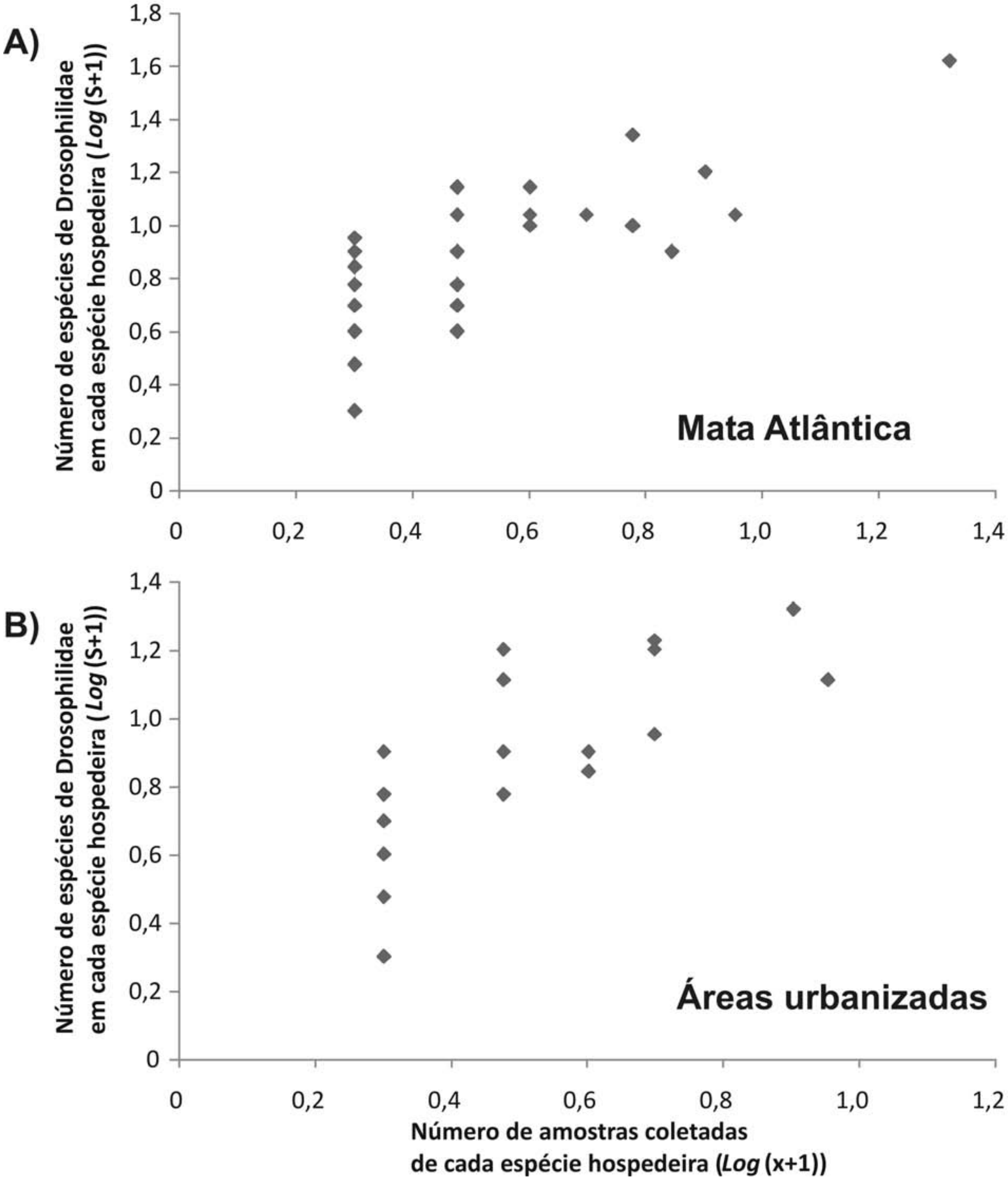

A)
1,8
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
Número de espécies de Drosophilidae
em cada espécie hospedeira (*Log* (S+1))
Mata Atlântica
0
0,2
0,4
0,6
0,8
1,0
1,2
1,4
B)
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
Número de espécies de Drosophilidae
em cada espécie hospedeira (*Log* (S+1))
Áreas urbanizadas
0
0,2
0,4
0,6
0,8
1,0
1,2
Número de amostras coletadas
de cada espécie hospedeira (*Log* (x+1))

Figura 5

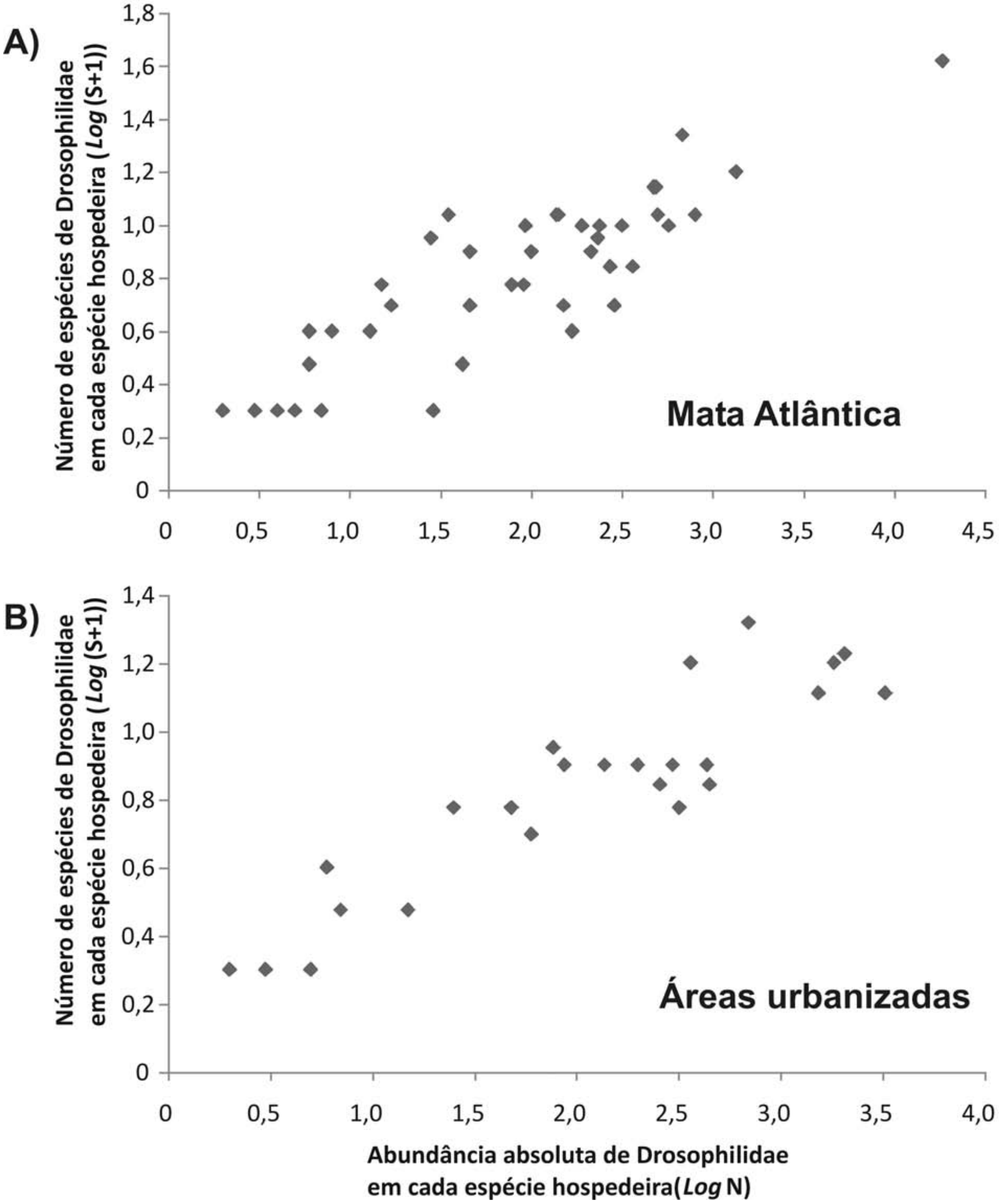

A)
Número de espécies de Drosophilidae em cada espécie hospedeira (*Log* (S+1))
1,8
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
0
0,5
1,0
1,5
2,0
2,5
3,0
3,5
4,0
4,5
Mata Atlântica
B)
Número de espécies de Drosophilidae em cada espécie hospedeira (*Log* (S+1))
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
0
0,5
1,0
1,5
2,0
2,5
3,0
3,5
4,0
Áreas urbanizadas
Abundância absoluta de Drosophilidae em cada espécie hospedeira(*Log* N)

Figura 6

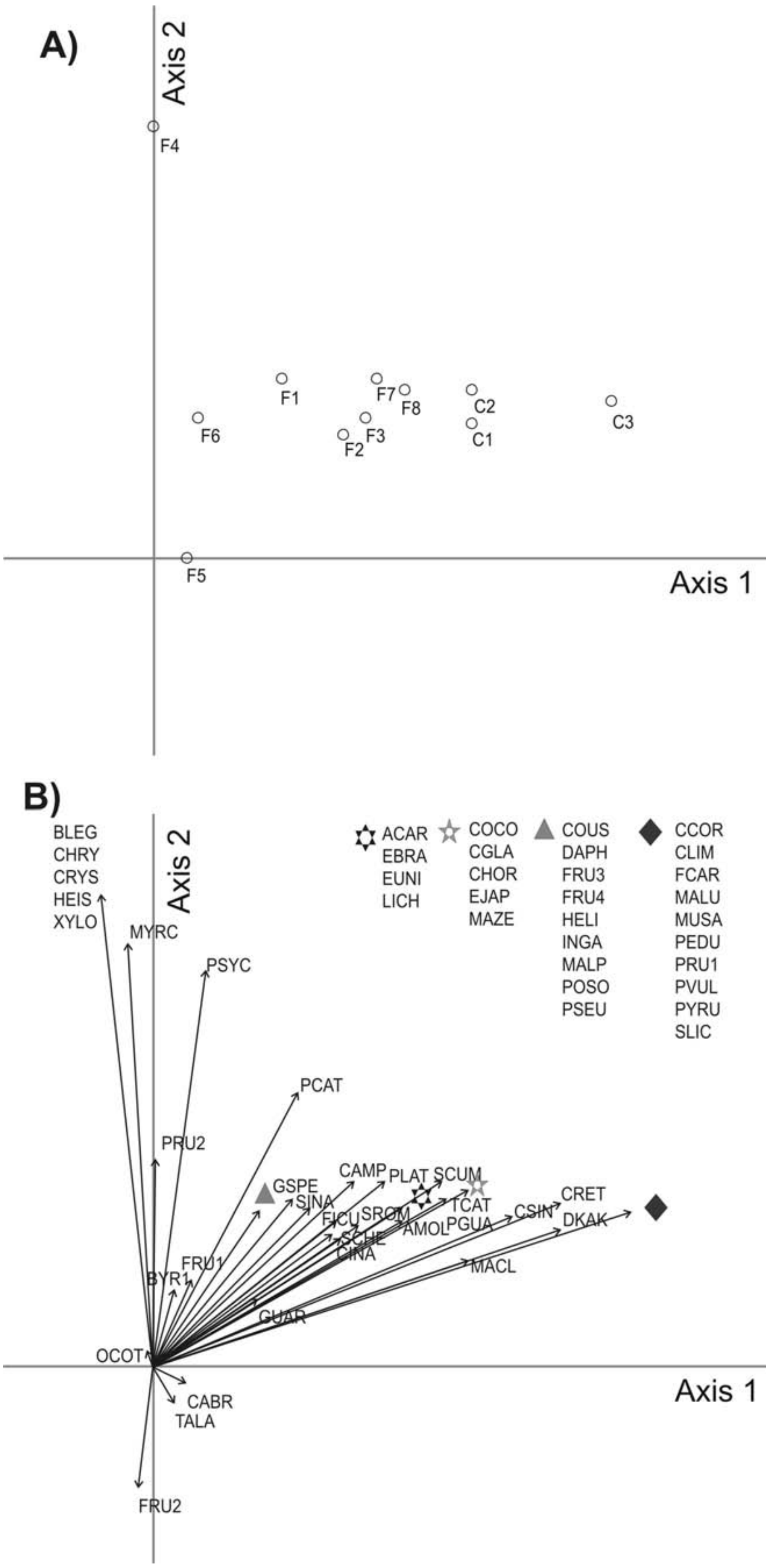

A)
Axis 2
Axis 1
F4
F1
F7
F8
C2
C3
F6
F3
F2
C1
F5
B)
Axis 2
Axis 1
ACAR
EBRA
EUNI
LICH
COCO
CGLA
CHOR
EJAP
MAZE
COUS
DAPH
FRU3
FRU4
HELI
INGA
MALP
POSO
PSEU
CCOR
CLIM
FCAR
MALU
MUSA
PEDU
PRU1
PVUL
PYRU
SLIC
BLEG
CHRY
CRYS
HEIS
XYLO
MYRC
PSYC
PCAT
PRU2
CAMP
PLAT
SCUM
GSPE
SINA
FICU
SROM
TCAT
PGUA
AMOL
SCHE
CINA
CSIN
CRET
DKAK
MACL
FRU1
BYR1
GUAR
OCOT
CABR
TALA
FRU2

Figura 7

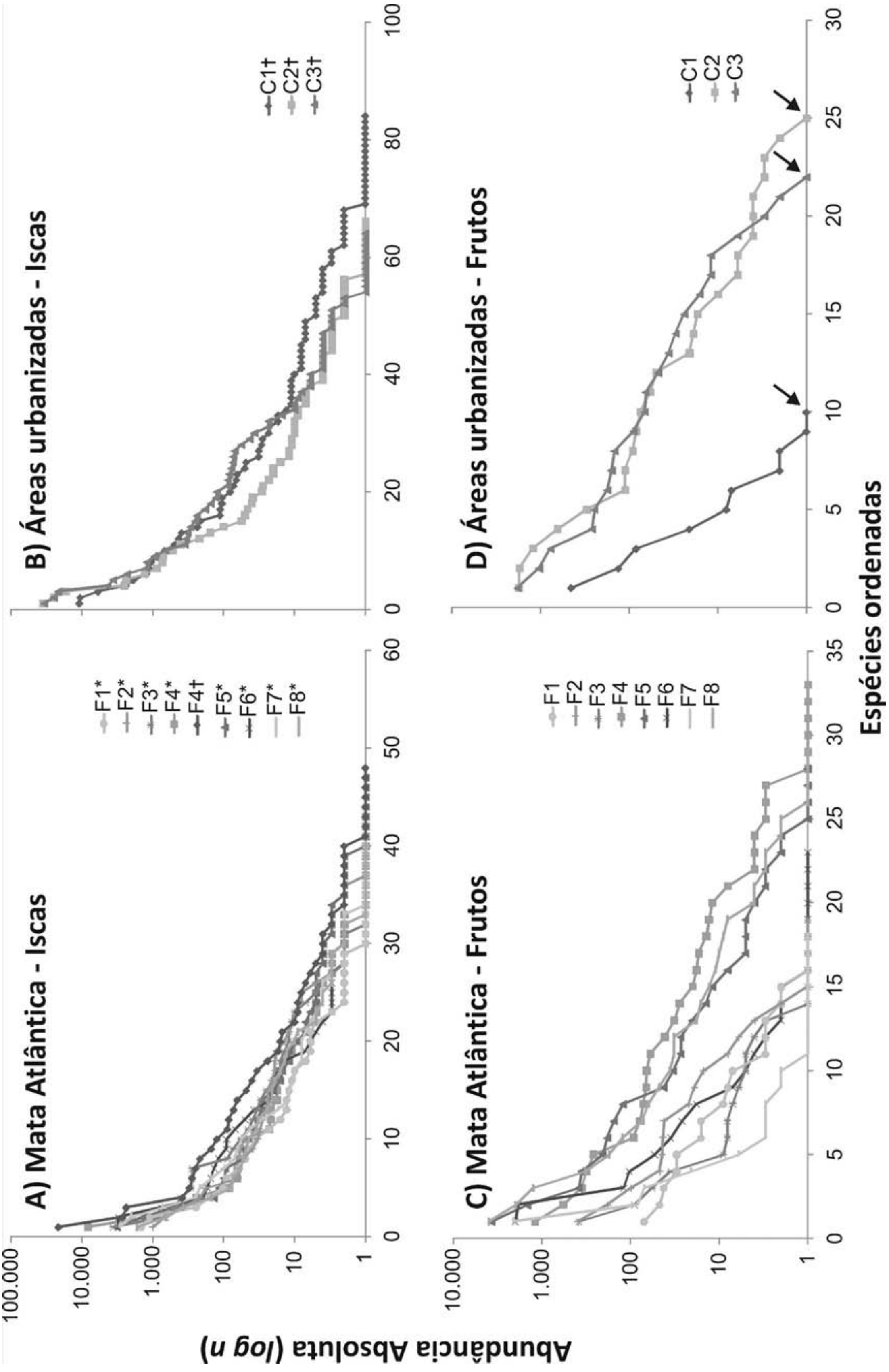

A) Mata Atlântica - Iscas
B) Áreas urbanizadas - Iscas
C) Mata Atlântica - Frutos
D) Áreas urbanizadas - Frutos
Abundância Absoluta (log n)
Espécies ordenadas
100.000
10.000
1.000
100
10
1
0
10
20
30
40
50
60
80
100
5
15
25
35
F1*
F2*
F3*
F4*
F4†
F5*
F6*
F7*
F8*
C1†
C2†
C3†
F1
F2
F3
F4
F5
F6
F7
F8
C1
C2
C3

Figura 8

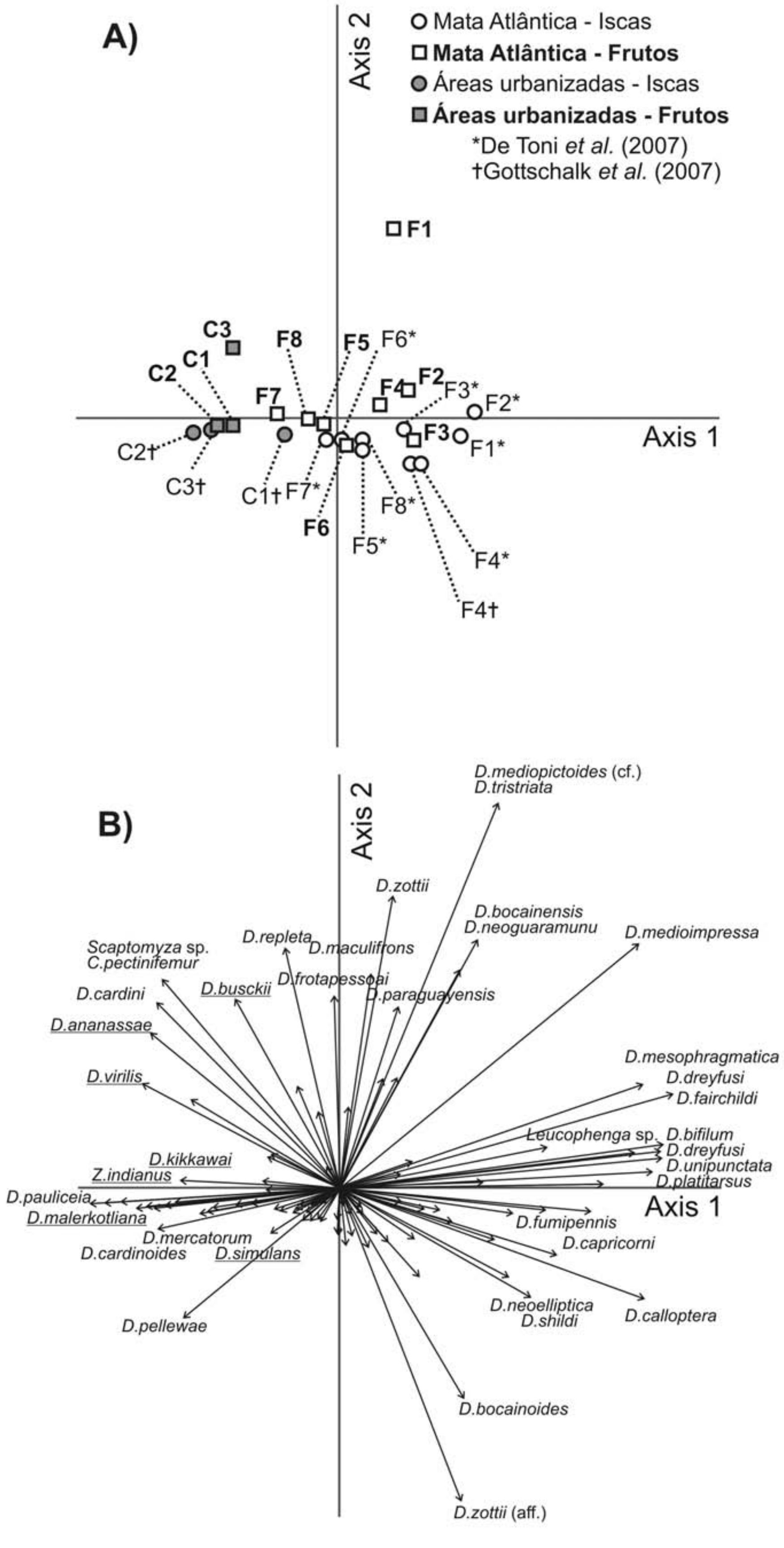

A)
Axis 2
Axis 1
○ Mata Atlântica - Iscas
□ **Mata Atlântica - Frutos**
● Áreas urbanizadas - Iscas
■ **Áreas urbanizadas - Frutos**
*De Toni *et al.* (2007)
†Gottschalk *et al.* (2007)
F1
C3
C1
C2
F8
F7
F5
F6*
F4
F2
F3*
F2*
F3
F1*
C2†
C3†
C1†
F7*
F6
F8*
F5*
F4*
F4†
B)
Axis 2
Axis 1
D.mediopictoides (cf.)
D.tristriata
D.zottii
D.bocainensis
D.neoguaramunu
D.medioimpressa
D.repleta
D.maculifrons
Scaptomyza sp.
C.pectinifemur
D.frotapessoai
D.cardini
D.busckii
D.paraguayensis
D.ananassae
D.mesophragmatica
D.virilis
D.dreyfusi
D.fairchildi
Leucophenga sp.
D.bifilum
D.dreyfusi
D.kikkawai
D.unipunctata
Z.indianus
D.platitarsus
D.pauliceia
D.malerkotliana
D.fumipennis
D.mercatorum
D.capricorni
D.cardinoides
D.simulans
D.neoelliptica
D.shildi
D.calloptera
D.pellewae
D.bocainoides
D.zottii (aff.)

Figura 9

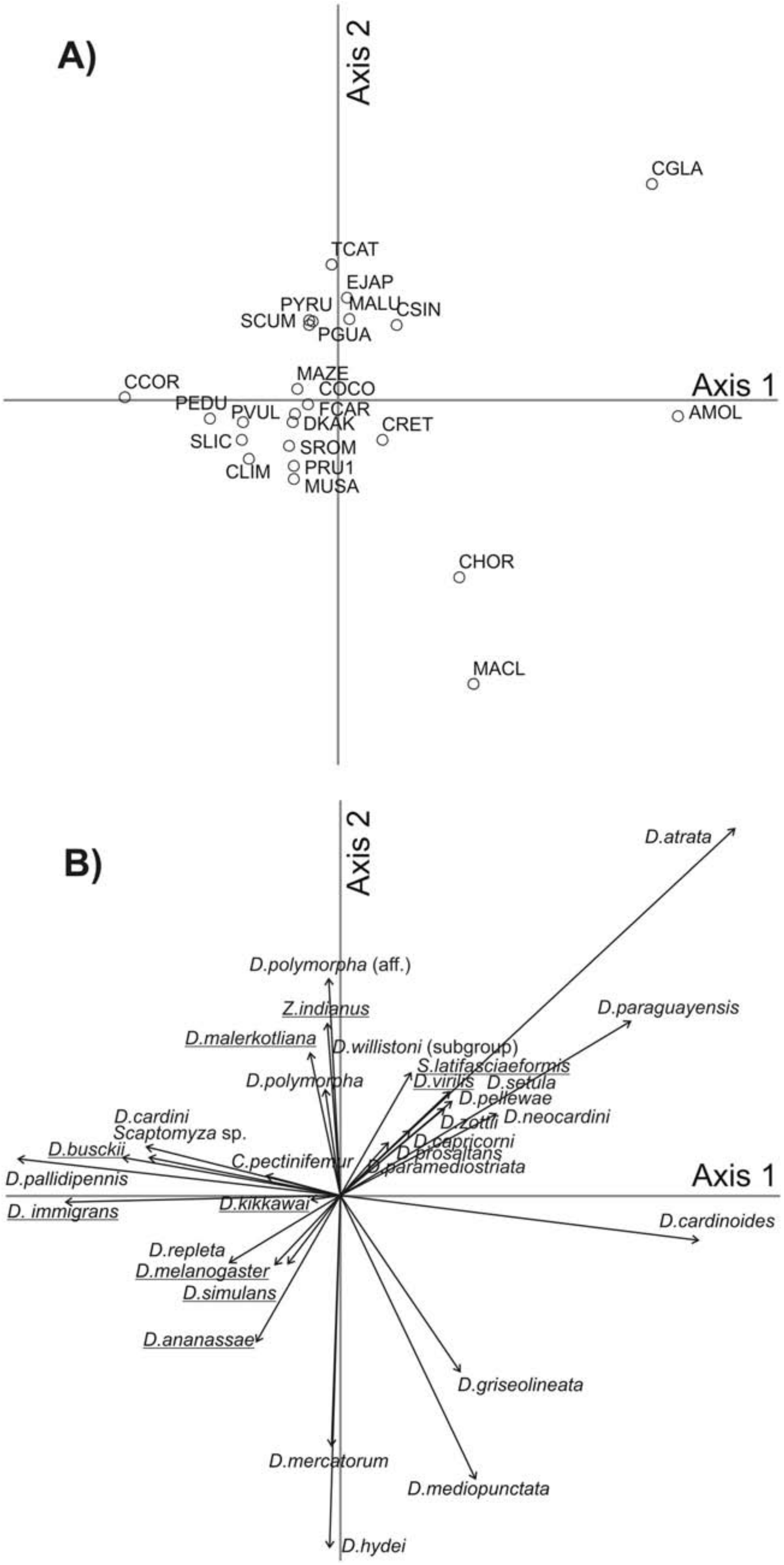

A)
Axis 2
Axis 1
CGLA
TCAT
EJAP
PYRU
MALU
CSIN
SCUM
PGUA
MAZE
CCOR
COCO
PEDU
PVUL
FCAR
DKAK
CRET
AMOL
SLIC
SROM
CLIM
PRU1
MUSA
CHOR
MACL
B)
Axis 2
D.atrata
D.polymorpha (aff.)
Z.indianus
D.paraguayensis
D.malerkotliana
D.willistoni (subgroup)
S.latifasciaeformis
D.polymorpha
D.virilis
D.setula
D.pellewae
D.zottii
D.neocardini
D.cardini
Scaptomyza sp.
D.capricorni
D.busckii
C.pectinifemur
D.prosaltans
D.paramediostriata
D.pallidipennis
Axis 1
D.kikkawai
D. immigrans
D.cardinoides
D.repleta
D.melanogaster
D.simulans
D.ananassae
D.griseolineata
D.mercatorum
D.mediopunctata
D.hydei

Figura 10

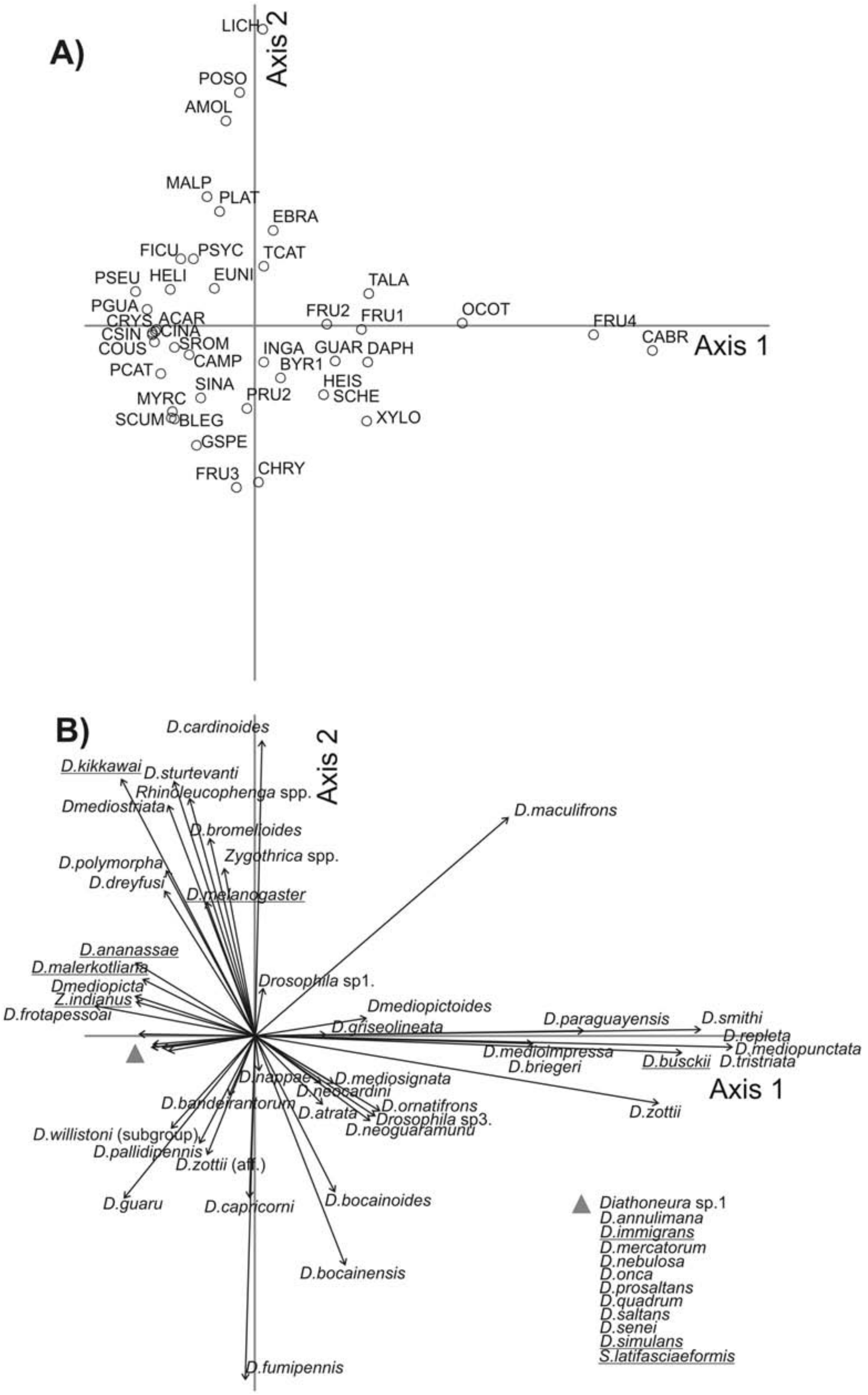

A)
Axis 2
Axis 1
LICH
POSO
AMOL
MALP
PLAT
EBRA
FICU
PSYC
TCAT
PSEU
HELI
EUNI
TALA
PGUA
CRYS
ACAR
CSIN
CINA
COUS
SROM
CAMP
PCAT
FRU2
FRU1
OCOT
FRU4
CABR
INGA
GUAR
DAPH
BYR1
HEIS
SCHE
SINA
MYRC
PRU2
SCUM
BLEG
XYLO
GSPE
FRU3
CHRY
B)
Axis 2
Axis 1
D.cardinoides
D.kikkawai
D.sturtevanti
Rhinoleucophenga spp.
Dmediostriata
D.bromelioides
D.maculifrons
Zygothrica spp.
D.polymorpha
D.dreyfusi
D.melanogaster
D.ananassae
D.malerkotliana
Dmediopicta
Z.indianus
D.frotapessoai
Drosophila sp1.
Dmediopictoides
D.griseolineata
D.paraguayensis
D.smithi
D.repleta
D.mediopunctata
D.medioimpressa
D.briegeri
D.busckii
D.tristriata
D.zottii
D.nappae
D.mediosignata
D.neocardini
D.bandeirantorum
D.ornatifrons
D.atrata
Drosophila sp3.
D.neoguaramunu
D.willistoni (subgroup)
D.pallidipennis
D.zottii (aff.)
D.guaru
D.capricorni
D.bocainoides
D.bocainensis
D.fumipennis
▲ Diathoneura sp.1
D.annulimana
D.immigrans
D.mercatorum
D.nebulosa
D.onca
D.prosaltans
D.quadrum
D.saltans
D.senei
D.simulans
S.latifasciaeformis

Figura 11

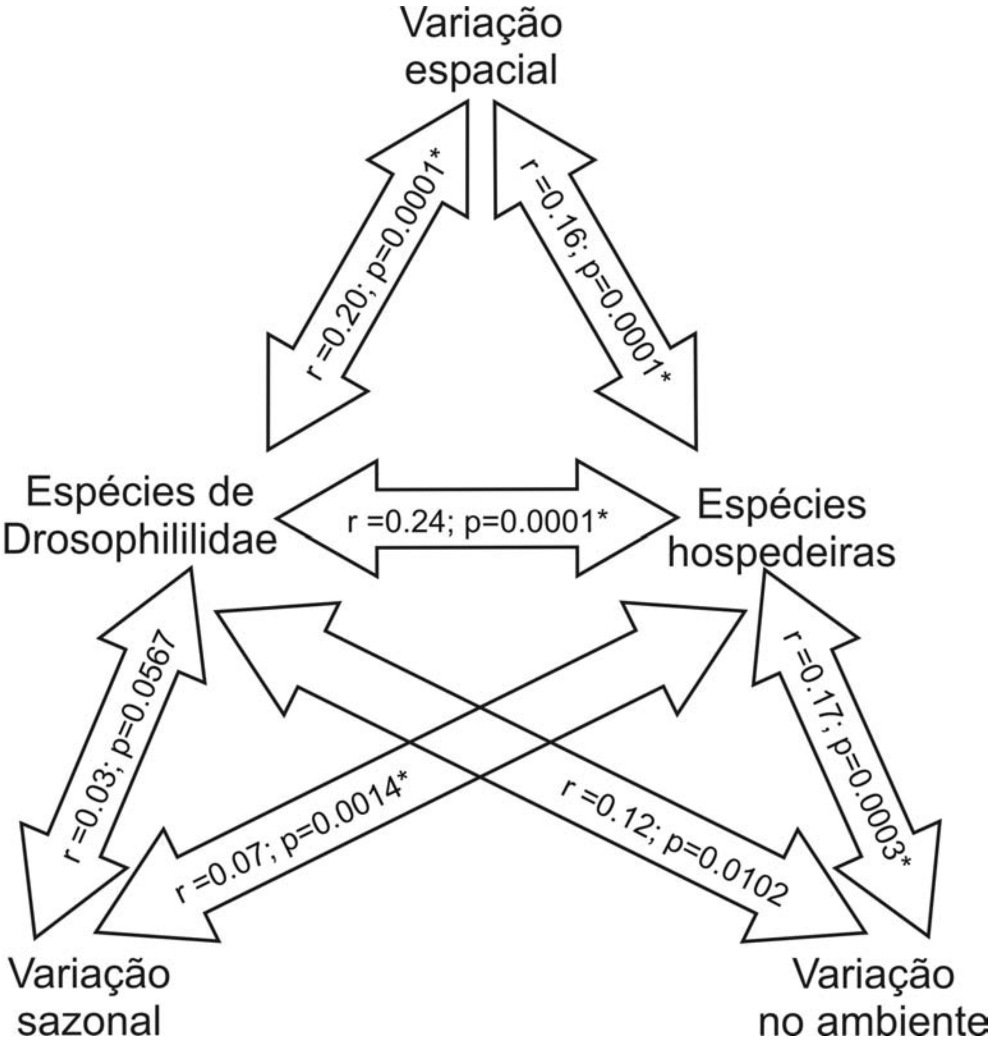
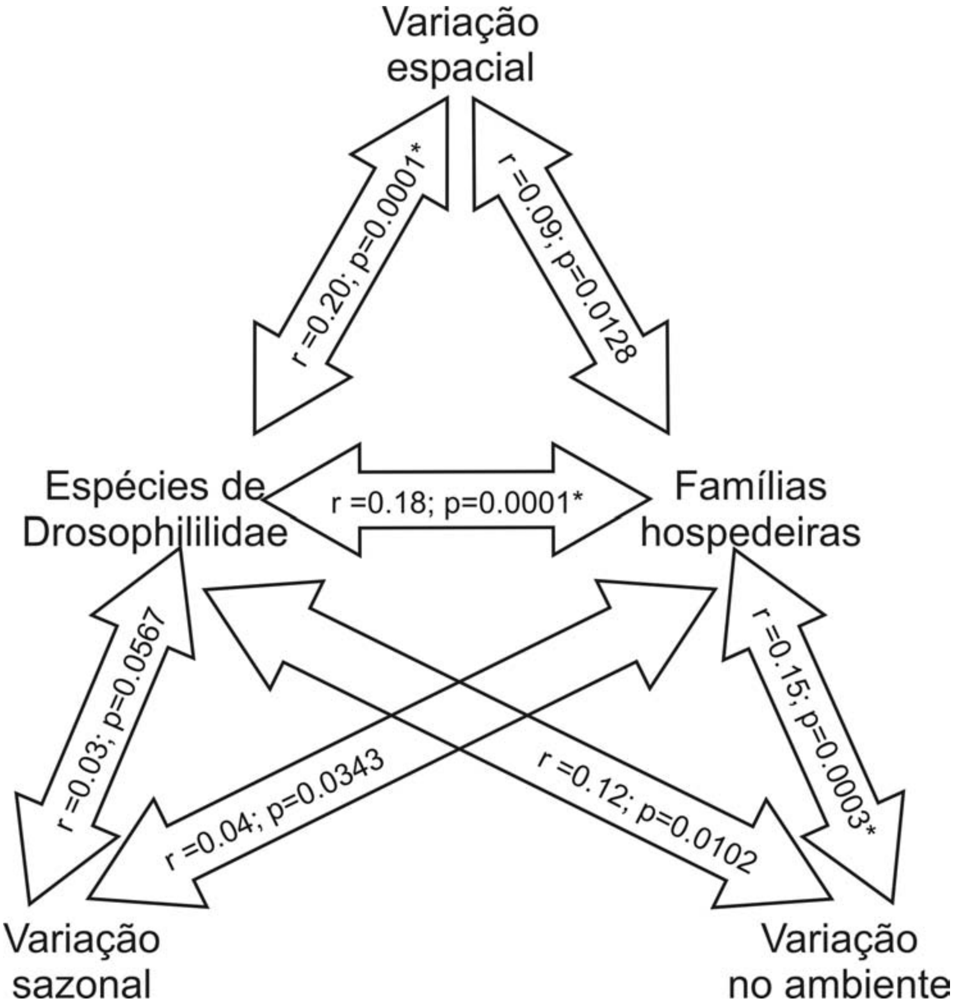

Variação espacial
r =0.20; p=0.0001*
r =0.16; p=0.0001*
Espécies de Drosophililidae
r =0.24; p=0.0001*
Espécies hospedeiras
r =0.03; p=0.0567
r =0.17; p=0.0003*
r =0.07; p=0.0014*
r =0.12; p=0.0102
Variação sazonal
Variação no ambiente

Figura 12


Variação espacial
r =0.20; p=0.0001*
r =0.09; p=0.0128
Espécies de Drosophililidae
r =0.18; p=0.0001*
Famílias hospedeiras
r =0.03; p=0.0567
r =0.04; p=0.0343
r =0.12; p=0.0102
r =0.15; p=0.0003*
Variação sazonal
Variação no ambiente

CAPÍTULO 3

INFLUENCE OF RESOURCE LIMITATION ON THE INTERACTION BETWEEN SPECIES OF DROSOPHILIDAE (DIPTERA): A LABORATORY EXPERIMENT WITH A NATURAL FRUGIVOROUS COMMUNITY

Artigo submetido à revista *Oecologia*

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Influence of resource limitation on the interaction between species of Drosophilidae (Diptera): a laboratory experiment with a natural frugivorous community

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Abstract

The competition between species of the family Drosophilidae is essentially of exploratory character and depends on resource availability. Yet, little is known about the way these interactions affect the populations in the natural environment. This study is an attempt to identify the influence of resource availability variables in the competitive interactions between populations of a natural drosophilid community that colonizes *Buchenavia tomentosa* fruits, a Neotropical Combretaceae. *Buchenavia tomentosa* fruits were observed to offer a nutritional restriction to the larvae of the flies studied, specially under high population density, which suggests the increased competition between individuals. The wing size analysis of individuals of the species *Drosophila nebulosa* and *Zaprionus indianus* revealed that these species present distinct responses to resource constraints. The first species did not show wing size variation across the different treatments of resource availability offered or size variation dependent on population density. On the other hand, *Z. indianus* was more sensitive to the decreased resource availability, which was demonstrated by the size reduction observed under more restrictive conditions. Moreover, size of individuals and density of individuals per fruit are correlated aspects for this species. It was also possible to conclude that the intraspecific competition is less intense than interspecific competition, as larger wing size correlates directly with species dominance of a fruit.

Keywords: Competition, *Drosophila*, Natural populations, Resources, *Zaprionus*.

Introduction

In nature, the interaction between individuals of two different species may be positive or negative. When the populations use the same resources, this interaction could be negative, and one population inhibits the growth or the maintenance of the other by means of competition for resources available in the environment (Odum and Barret, 2005; Begon et al., 2006). This competition may be direct, when there is interference in distribution and/or response of one individual over the other, or indirect, when there is no such response and the individuals of different populations compete by means of resource exploitation, and are thus indirectly affected (Case and Gilpin, 1974).

Competition between *Drosophila* species is mostly of exploratory nature, specially in the larva stage (Barker, 1983; Powel, 1997). The intensity of this competition bears a direct correlation with the number of individuals involved therein, i.e, competition is density-dependent. This interaction has a direct effect on the fitness of individuals, which in turn is related to the characteristics of the life history like viability, development period, fecundity and body size (Sevenster and van Alphen, 1993a; Baldal et al., 2005).

It is possible to measure these characteristics in a laboratory, and thus establish their link with competition, since the laboratory is the site where it is possible to control the environmental variables that affect populations (Diamond, 1986). Nevertheless, in natural communities these measurements may not reflect just the effect of competition between organisms, since these are also under the results of other kinds of pressure, like predation and parasitism (Schoener, 1983; van der Linde, 2005). In order to understand the dynamic of these communities, more field studies or investigations that combine field and laboratory approaches are necessary, like the methodology chosen in the present study.

With a view to clarifying some aspects of the competition between individuals of natural drosophilid populations, the present study investigates how constraints in food resources affect the intensity of competition between larvae that colonize the fruit of *Buchenavia tomentosa* Eichler (Combretaceae).

Materials and methods

Samplings were conducted in June 2007, in the woods administered by the county of Tangará da Serra, State of Mato Grosso, Brazil, where the fruits of *B. tomentosa* were collected. The area under one tree was cleared and on the next day the fruits that had fallen were labeled. After three days, the fruits were taken to the laboratory, where they were randomly allocated to form treatment groups, as follows: 30 fruits were individually placed in vials containing autoclaved sand, where the larvae had only the fruit itself as food resource (**Sand**); 30 fruits were individually placed in culture medium, where, apart from the fruit itself, the larvae had access to supplementary feeding (**Culture**); and 30 fruits were placed in three vials (10 fruits per vial) containing autoclaved sand, in which the larvae could migrate from one fruit to another during development (**Ten Fruits**). All vials were kept under controlled temperature (21 ± 1°C) for one month, for which period the emerged flies were collected daily. The culture medium described by Marques et al. (1966) was chosen due to its efficiency in supplying the rearing requirements of the frugivorous Drosophilidae species that had been previously recorded in the region (Blauth and Gottschalk, 2007).

Also, one week after the collection and transportation of the fruits to the laboratory, the flies that were flying over the fruits remained in the collection site were collected with an entomological net (**Field**), for comparison with the flies reared in the laboratory.

In order to assess the influence of resource treatments in the structure of emerging flies assemblies, the drosophilid fauna that emerged from each treatment was compared in terms of species abundance, species richness, by the Shannon-Wiener diversity index and by the Morisita-Horn similarity index, followed by the construction of an UPGMA dendrogram

(Magurran, 2003). Dendrogram construction was carried out using the software Past version 1.72 (Hammer et al., 2001).

Wing size was also compared for treatments using two analysis of variance (ANOVA) of the distance between the r-m vein and the tip of the R_{4+5} vein of wings (Figure 1) of the most abundant species in the samples: *Drosophila nebulosa* Sturtevant, 1916 and *Zaprionus indianus* Gupta, 1970. The Tukey test for differently samples of different sizes was used to reveal how the treatments differed as to the results produced (Zar, 1999).

Wing measurements of the same species were compared by an analysis of covariance (ANCOVA) for sex and **Sand** and **Culture** treatments, for which the co-variable was either the number of flies that emerged from each fruit (density of individuals in each fruit), or the relative abundance of the species used in the analysis. The correlation between co-variables, density of individuals in each fruit and relative abundance of *D. nebulosa* or of *Z. indianus*, was tested by means of a Pearson test (Zar, 1999).

The number of flies that emerged from each fruit was used to represent the density of individuals per fruit, considering the observations previously made by Sevenster and van Alphen (1996). The authors demonstrated that the eggs of drosophilids laid on fruits of *Spondias mombin* L. (Anacardiaceae) and the adult flies that emerged therefrom exhibit the same distribution pattern.

Although some other families of insects emerge from the fruits studied, those were not analyzed due to their low abundance, and because some of them were not frugivorous, like the coleopteran of the family Bruchidae, which feed on seeds. Apart from this, these families probably do not interfere seriously with the development of Drosophilidae as compared to the family’s own species, since niche overlapping is more intense the more related the species involved in the competition are (Odum and Barrett, 2005).

All statistical analyses were conducted using the R. software version 2.5.0 (R Development Core Team, 2007).

Results

Of the 90 *B. tomentosa* fruits collected in the field, 2,847 drosophilids from eight species emerged, with only six species collected flying over the fruits in the field (Table 1). Apart from Drosophilidae, individuals from other species of seven insect families emerged from the fruits: Lonchaeidae, Sepsidae and Sciaridae (Diptera); Bruchidae, Curculionidae and Nitidulidae (Coleoptera); and Figitidae (Hymenoptera).

The total drosophilid abundance was greater in the fruits kept in the culture medium (**Culture**), followed by the abundance of specimens maintained separately in sand (**Sand**) and by the occurrence of flies that emerged from the ten fruits maintained in sand (**Ten fruits**) (Table 2). In turn, the Shannon-Wiener index and species richness were higher in **Ten fruits**. As for the diversity index, **Sand** exhibited the second highest value, followed by **Culture**. Nevertheless, the **Culture** treatment was richer than the **Sand** treatment. The difference in the Morisita-Horn similarity index between the treatments was very small (Figure 2).

Means and standard deviations for the wing measurements of *D. nebulosa* and *Z. indianus*, the two most abundant species in this experiment, are shown in Table 3. Based on these measurements, an ANOVA was conducted to compare all the treatments and the characteristics of the flies according to sex (Table 4). The test indicated that the males are significantly smaller than the females, in both species. As regards the treatments, wing length of *D. nebulosa* was shorter in **Field** than in other treatments, which in turn did not differ from one another (Figure 3). As for *Z. indianus*, the individuals were larger in the **Culture** treatment than in the **Sand** and **Field** treatments, which did not differ from each other (Figure

4). In the **Ten Fruits** treatment, intermediary values of wing length were observed. The probabilities were under 0.00001 in all significant comparisons made using the Tukey test.

The results of the ANCOVA differed from those of the ANOVA (Tables 5 and 6, Figures 4 to 7). When wing length of *D. nebulosa* was compared across treatments and sexes, and the densities of individuals being defined as co-variable, no significant differences were observed in the comparisons, and likewise no statistically significant relationship was observed between wing size and density of individuals (Table 5, Figure 4). Yet, in the ANCOVA with *Z. indianus* measurements, we observed that wing size does in fact correlated negatively with density of individuals per fruit, and that this correlation is significantly different in each treatment (Table 5, Figure 5).

In the ANCOVA which compared wing length of *D. nebulosa* in sexes and treatments, with its relative abundance as co-variable (Table 6, Figure 6), the wing length showed significant differences in all variables compared, which also exhibited a significant association between them. In the ANCOVA that compared wing length of *Z. indianus* in sexes and treatments, with its relative abundance as co-variable (Table 6, Figure 7), wing size responds significantly to the treatments and to the relative abundance, and the association between these two variables was also statistically significant.

We carried out a Pearson correlation test between the two co-variables used in the ANCOVAs to verify the whether one co-variable influenced the other. No significant test results were observed for the any of species or treatments. The values for *D. nebulosa* were $r = 0.19$ and $p = 0.32$ for **Culture** and $r = 0.23$ and $p = 0.32$ for **Sand**, while for *Z. indianus* these values were $r = -0.19$ and $p = 0.32$ for **Culture** and $r = -0.05$ and $p = 0.83$ for **Sand**.

Discussion

Direct evidences of competition in natural communities are seldom found, since environmental variables are not easy to control or measure (Schoener, 1983). In turn, laboratory experiments on the subject have clearly shown the existence of competition under different circumstances (Barker, 1983). In an attempt to associate these two methodologies, as suggested by Diamond (1986), we transferred to the laboratory part of the system that forms the structure of the community studied: the resource (*B. tomentosa* fruits) and the consumers (drosophilids). By investigating these consumers, we collected evidence that the resource may elicit competition in the light of resource constraints. More specifically, we observed that the competition between *D. nebulosa* and *Z. indianus* does not influence these species to the same extent.

By comparing wing size of *D. nebulosa* that emerged from the fruits brought to laboratory, it becomes clear that this species undergoes little competitive pressure under the experimental conditions adopted, since the wing size did not differ between treatments, even in **Sand**, the most restrictive configuration. Nevertheless, the flies that emerged in **Field** are smaller than those that emerged in the laboratory, which constitutes indication of greater pressure in the natural environment. Possibly, this difference in size between flies reared in the laboratory and flies collected in the field is not a consequence of competition, but of other variables that may have influenced the development of individuals, like variations in temperature or predation, or even a more considerable trophic resource depletion due to the faster deterioration of fruit.

In turn, *Z. indianus* presented a higher variation in wing size for the different treatments. This species showed greater sensitivity to resource constraints as compared to *D. nebulosa*. The fruits do not seem to be enough for all individuals to develop properly, at least when drosophilid density is high. The fact that the treatment **Ten fruits** has led to individuals whose size laid between that of **Culture** and **Sand** is symptom of some degree of migration of *Z. indianus* larvae from one fruit to another, at least under the conditions defined in the present study. Nevertheless, it is probable that the pressures suffered by *Z. indianus* in the field were similar to those that this species experienced in the **Sand** treatment, in which larvae were isolated from the fruit on which eggs were laid and ecloded, since the flies collected (**Field**) were similar in size as compared to the **Sand** flies.

Drosophila nebulosa and *Z. indianus* were dissimilar also in response to the increase in density of individuals per fruit. While in *Z. indianus* this variation greatly influenced size of flies, in *D. nebulosa* no significant response to this variation was observed. This suggests that the last species is free from the effect of density, at least at the levels studied. In turn, when the relative abundance values for both species are related with size measurements, we observe changes in the response to the different treatments. Both species expressed significant differences for the treatments and, more importantly, a positive influence of relative abundance was observed in wing size for *D. nebulosa* and *Z. indianus*. This may be a result of less intense competitive pressure when these are the prevailing species in the fruit, i.e., the intraspecific competition seems to be less marked than interspecific competition. For instance, in fruits in which the proportion of *Z. indianus* is higher, the flies of this species are larger, independently of the number of individuals that emerged from the fruit, since the correlation between density of individuals and relative abundance of *Z. indianus* is not significant. We observed the same pattern for *D. nebulosa*, since this species is influenced by the composition of emerging species from each fruit, even though it does not suffer any influence of density of individuals.

The model for the r and K reproduction strategies of parental investment in offspring, previously proposed by MacArthur and Wilson (1967), may assist in gaining a better understanding of the patterns observed. Within Drosophilidae, a trade-off between the characteristics of life history that fit in this model has been observed (Atkinson, 1979; Gilpin et al., 1986; Sevenster and van Alphen, 1993a). The species that fit in the r-strategy exhibit a lesser investment per egg and a greater investment in the number of eggs, which reflects, for example, a short life cycle, a greater ability to exploit resources and shorter longevity. The opposite pattern is expected for species that fit in the K-strategy, in which a greater investment per egg and a lesser investment in number of eggs is observed. Apart from this, there are models of coexistence of drosophilid species based on the r and K model and on the availability of resources in nature, which also apply to other species that utilize short-lived resources whose availability oscillates with time (Sevenster and van Alphen, 1993b).

Drosophila nebulosa life characteristics place the species more properly in the r-strategy of investment in offspring, with short life cycle (approximately 13 days for the individual to go from the egg stage to the adult stage, at 25°C), high fecundity and competitive ability (Wallace, 1974; Gilpin et al., 1986; Markow and O'Grady, 2006; D. D. Lopes, unpublished data). These characteristics may help understand the lack of a response to the increase in density of individuals in our experiments. On the other hand, *Z. indianus* exhibits a longer life cycle — around 18 days at 25°C (de Setta and Carareto, 2005; D. D. Lopes, unpublished data) — and, in spite of the limited knowledge of fecundity and competitive ability of individuals of the Neotropical species, it is possible to fit the species in the K-strategy (Krijger et al., 2001), which could also explain the greater sensitivity to density of individuals.

Nevertheless, one question remains to be answered. What is the reason behind the fact that *D. nebulosa* is not the dominant species in the community studied, since *Z. indianus* does not outdo *D. nebulosa* in terms of response to competition, in theory, and since species that fit in the r-strategy eliminate those that fit in the K-strategy, in similar situations (Gilpin et al., 1986)? This question rouses further interest if we take into account the fact that several of the *Z. indianus* strains recently collected in different Brazilian localities exhibit low viability, notwithstanding their high fecundity (M. S. Gottschalk, unpublished data). In spite of this, what we observed in the present and in other collections is that *Z. indianus* is often the most abundant species, which underlines its competitive supremacy under the conditions of the natural environment. Much of the influence of *Z. indianus* over Neotropical drosophilid has yet to be addressed in further studies.

Despite this remarkable intra- and interspecific variation in the species studied, apparently the structure of the community does not seem to vary with availability of resources for the species, since the Morisita-Horn index revealed high similarity between the specimens that emerged from the different treatments. By looking at the results of the biometry analysis and of abundance of individuals, it seems that **Culture,** the treatment with the largest food resource, is the one that best affords fly development. Yet, if we take into account the diversity and the richness of each treatment, it appears that the ideal condition for the survival of the largest number of species is the presence of fruits one next to the other (**Ten fruits**). In this treatment configuration, larvae are able to migrate from one fruit to the other, which may also have led to the more modest dominance of the emerging community. However, this hypothesis needs confirmation, since little is known as to the migration ability of larvae in the field, specially under starvation conditions.

Laboratory experiments allow to limit the number of variables, which facilitates the analysis. This approach has proved its usefulness, in spite of the fact that extrapolations are restricted (Diamond, 1986). In this sense, natural experiments, in which observations are conducted in natural communities without bringing in any extraneous effect, lend more consistency to extrapolations, since the elements being studied are all natural, and thus the observations are confined to what actually happens in nature only. A transition design is the field experiment, in which the researcher artificially introduces one community in the field, which will be influenced by the environmental variables. Our proposal, which does not fit in any of these classes, comprises the transference of communities to the laboratory and measures the effects of some predefined conditions imposed on these communities, while the consequences of other conditions are minimized.

The methodology adopted in the present study afforded the nutritional constraint of *B. tomentosa* fruit, specially in a setting of high drosophilid density, which led to an increase in the competition between individuals on each fruit. Therefore, it was possible to observe that interspecific competition in general promotes a decrease in the number of emerging species and affects the size of individuals. Yet, the behavior of *D. nebulosa* and of *Z. indianus* revealed that the species react differently to this competition imposed by resource constraints.

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Table 1 – Abundance of insect species that emerged from or that were flying over *Buchenavia tomentosa* (Combretaceae) fruits. **Sand** – fruits individually kept in autoclaved sand; **Culture** – fruits individually kept in culture medium; **Ten fruits** – ten fruits kept in autoclaved sand; **Field** – flies collected flying over fruit in the field.

Table 2 – Shannon-Wiener index, species richness and total abundance of drosophilids that emerged from *B. tomentosa* fruits in the different treatments.

Table 3 – Means and standard deviations of wing length of *D. nebulosa* and *Z. indianus*, for sex and for each treatment evaluated.

Table 4 – Analysis of variance (ANOVA) results for wing length of *D. nebulosa* and *Z. indianus* for sex and for each treatment evaluated.

Table 5 – Analysis of covariance (ANCOVA) results for wing length of *D. nebulosa* and *Z. indianus* for sex and for the treatments **Sand** and **Culture**. Co-variable was the density of individuals that emerged from each fruit.

Table 6 – Analysis of covariance (ANCOVA) results for wing length of *D. nebulosa* and *Z. indianus* for sex and for the treatments **Sand** and **Culture**. Co-variable was the relative abundance of each species.

Figure 1 – Wing of a female of *D. cuaso* indicating wing length measured (r-m vein to the end of the R_{4+5} vein).

Figure 2 – UPGMA dendrogram constructed with Morisita-Horn's similarity index comparing the treatments **Sand**, **Culture** and **Ten Fruits**.

Figure 3 – Box-plot showing the means (square), standard deviations (rectangle) and 95% confidence interval (bars) of *D. nebulosa* wing length for sex and the different treatments, as well as the result of the Tukey test that compared treatments. Different letters represent significant differences in the ANOVA test with $\alpha = 0.05$. F – females, M – males.

Figure 4 – Box-plot showing the means (square), standard deviations (rectangle) and 95% confidence interval (bars) of *Z. indianus* wing length for sex and the different treatments, as well as the result of the Tukey test that compared treatments. Different letters represent significant differences in the ANOVA test with $\alpha = 0.05$. F – females, M – males.

Figure 5 – Chart showing the analysis of covariance (ANCOVA) regression between *D. nebulosa* wing length and density of individuals that emerged from each fruit, for sex and the treatments **Sand** and **Culture**.

Figure 6 – Chart showing the analysis of covariance (ANCOVA) regression between *Z. indianus* wing length and density of individuals that emerged from each fruit, for sex and the treatments **Sand** and **Culture**.

Figure 7 – Chart showing the analysis of covariance (ANCOVA) regression between *D. nebulosa* wing length and relative abundance of the species for each fruit for sex and the treatments **Sand** and **Culture**.

Figure 8 – Chart showing the analysis of covariance (ANCOVA) regression between *Z. indianus* wing length and relative abundance of the species for each fruit for sex and the treatments **Sand** and **Culture**.

Table 1

Order	**Family**	**Species**	**Sand**	**Culture**	**Ten fruits**	**Field**	**Total**
Diptera	Drosophilidae	*Drosophila ananassae* Doleschall, 1858	25	2	53	-	**80**
		D. cardini Sturtevant, 1916	-	-	5	3	**8**
		D. cuaso Bächli, Vilela and Ratcov, 2000	6	6	8	-	**20**
		D. malerkotliana Parshad and Paika, 1964	-	17	25	6	**48**
		D. nebulosa Sturtevant, 1916	86	143	81	57	**367**
		D. simulans Sturtevant, 1919	-	4	5	5	**14**
		D. willistoni Sturtevant, 1916	-	-	11	2	**13**
		Zaprionus indianus Gupta, 1970	627	1,187	460	23	**2,297**
	Lonchaeidae		8	-	9	-	**17**
	Sepsidae		1	-	-	-	**1**
	Sciaridae		7	-	-	-	**7**
Coleoptera	Bruchidae		1	-	-	-	**1**
	Curculionidae		3	4	6	-	**13**

	Nitidulidae	4	8	25	-	**37**
Hymenoptera	Figitidae	-	3	4	-	**7**
	Total	**768**	**1,374**	**692**	**96**	**2,930**

Table 2

	Sand	**Culture**	**Ten Fruits**	**Field**
Shannon-Wiener	0.55	0.46	1.03	1.17
Species	4	6	8	6
Abundance	744	1,359	648	96

Table 3

Treatment	**Sex**	***D. nebulosa***	***Z. indianus***
Sand	♀	1.64 ± 0.080	1.60 ± 0.142
	♂	1.51 ± 0.084	1.54 ± 0.148
Culture	♀	1.63 ± 0.059	1.72 ± 0.063
	♂	1.51 ± 0.063	1.68 ± 0.063
Ten Fruits	♀	1.61 ± 0.073	1.68 ± 0.075
	♂	1.51 ± 0.063	1.64 ± 0.072
Field	♀	1.52 ± 0.101	1.60 ± 0.102
	♂	1.43 ± 0.094	1.59 ± 0.070

Table 4

	D. nebulosa (n = 294)		*Z. indianus* (n = 1,822)	
	Test value (F)	Probability	Test value (F)	Probability
Treatment	77.4	<0.0001**	197.8	<0.0001**
Sex	168.0	<0.0001**	65.8	<0.0001**
Treatment: Sex	0.2	0.65	6.0	0.014*

*significant for $\alpha < 0.05$; ** significant for $\alpha < 0.0001$

Table 5

	D. nebulosa (n = 166)		*Z. indianus* (n = 1,414)	
	t value	p	t value	p
Treatment	0.125	0.90	0.573	0.57
Sex	-1.060	0.29	-1.430	0.15
Density	0.386	0.70	-5.079	<0.0001**
Treatment: Sex	-0.304	0.76	0.382	0.70
Treatment: Density	-0.653	0.52	3.460	<0.0005*
Sex: Density	-0.730	0.47	-0.793	0.43
Treatment: Sex: Density	0.668	0.50	0.352	0.72

*significant for $\alpha < 0.001$; ** significant for $\alpha < 0.0001$

Table 6

	D. nebulosa (n = 166)		*Z. indianus* (n = 1,414)	
	t value	p	t value	p
Treatment	-2.06	0.041*	3.33	0.0009***
Sex	-4.36	< 0.00001***	1.40	0.16
Relative abundance	-2.28	0.023*	4.26	0.00002***
Treatment: Sex	2.03	0.044*	-1.02	0.31
Treatment: Relative abundance	2.37	0.019*	-2.79	0.005**
Sex: Relative abundance	2.66	0.009**	-1.93	0.053
Treatment: Sex: Relative abundance	-2.53	0.012*	1.27	0.20

*significant for $\alpha < 0.05$; **significant for $\alpha < 0.01$; ***significant for $\alpha < 0.001$

Figure 1

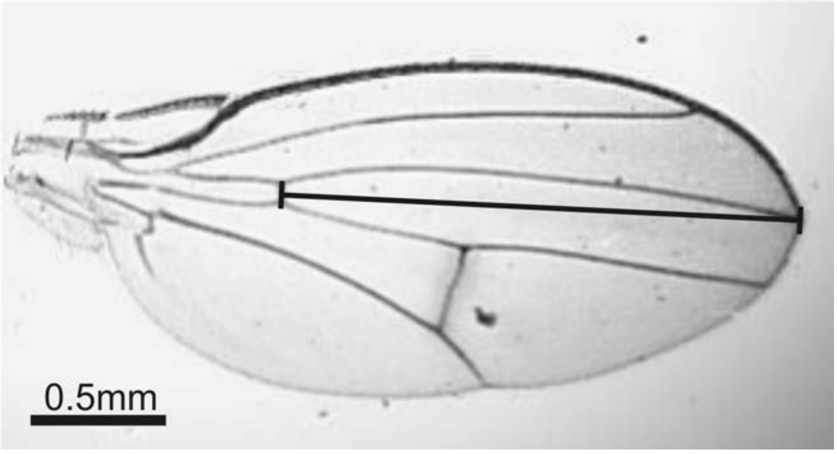


Figure 2

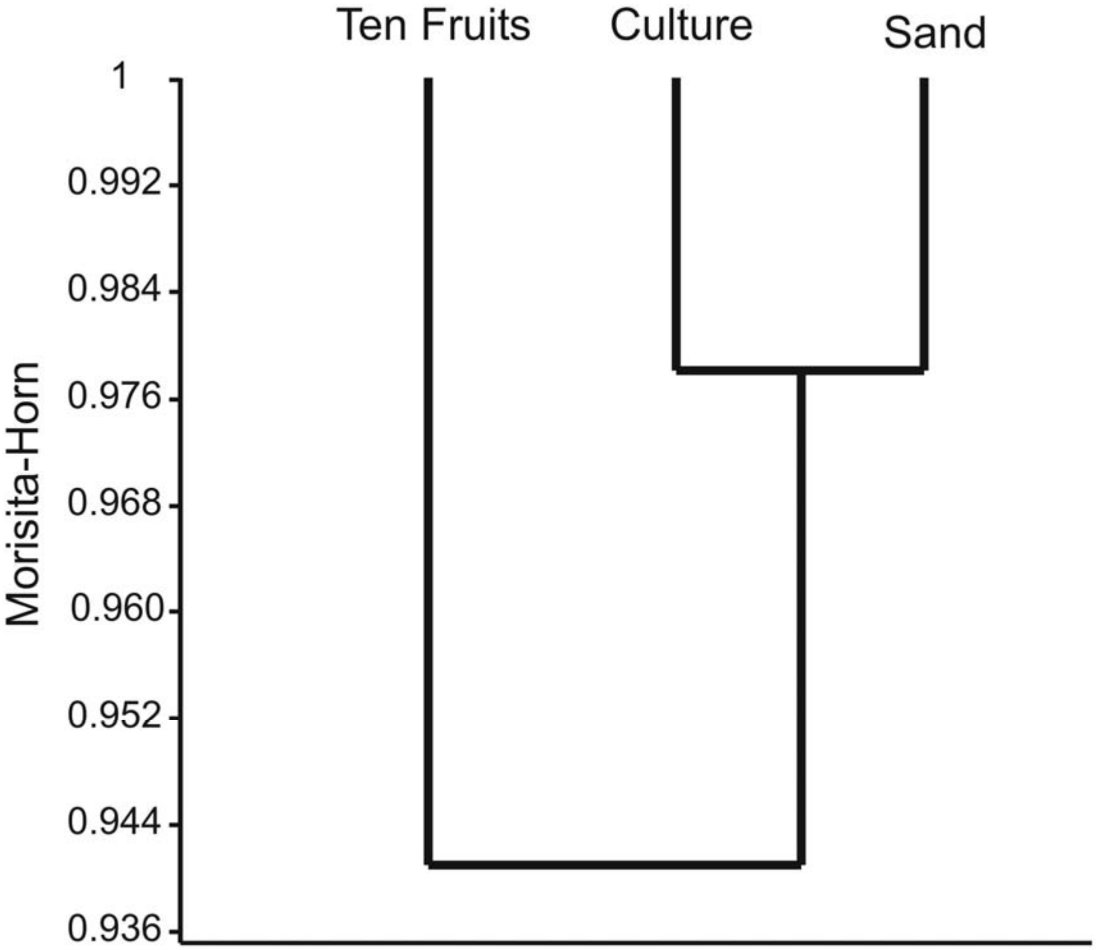

Ten Fruits
Culture
Sand
Morisita-Horn
1
0.992
0.984
0.976
0.968
0.960
0.952
0.944
0.936

Figure 3

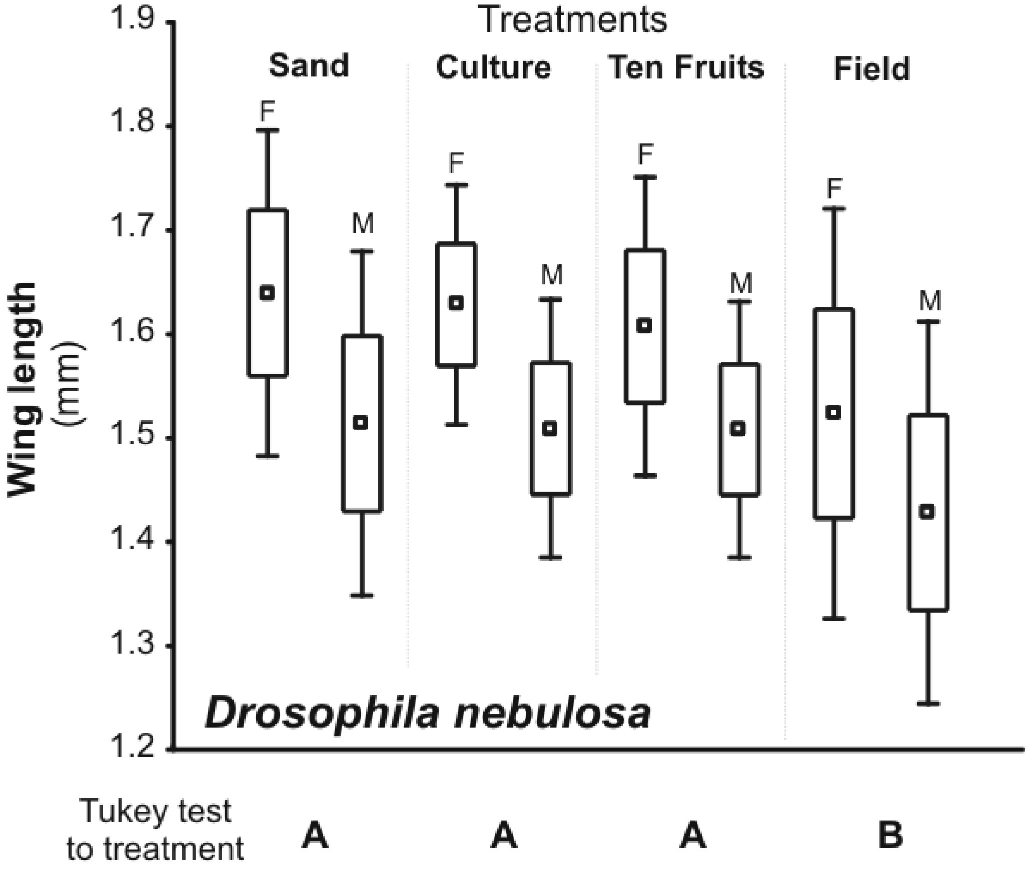

Treatments
Sand
Culture
Ten Fruits
Field
F
M
Wing length (mm)
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
Drosophila nebulosa
Tukey test to treatment
A
A
A
B

Figure 4

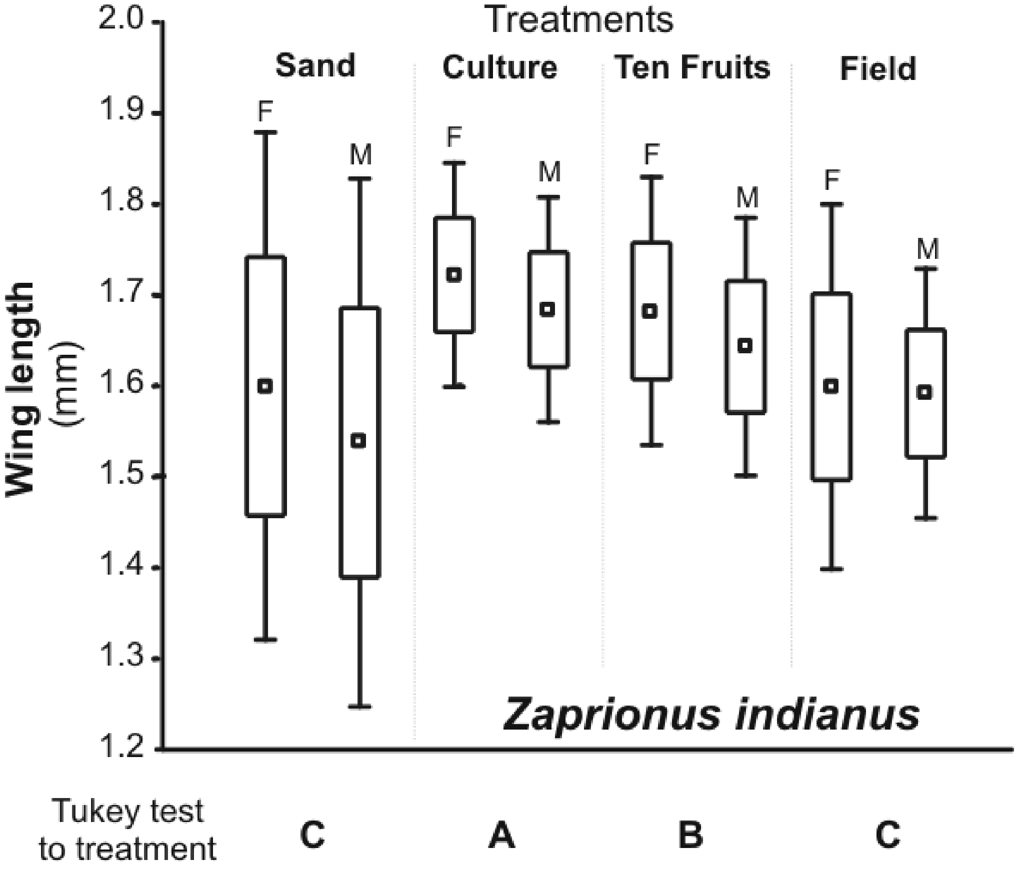

Treatments
Sand
Culture
Ten Fruits
Field
F
M
Wing length (mm)
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
Zaprionus indianus
Tukey test to treatment
C
A
B
C

Figure 5

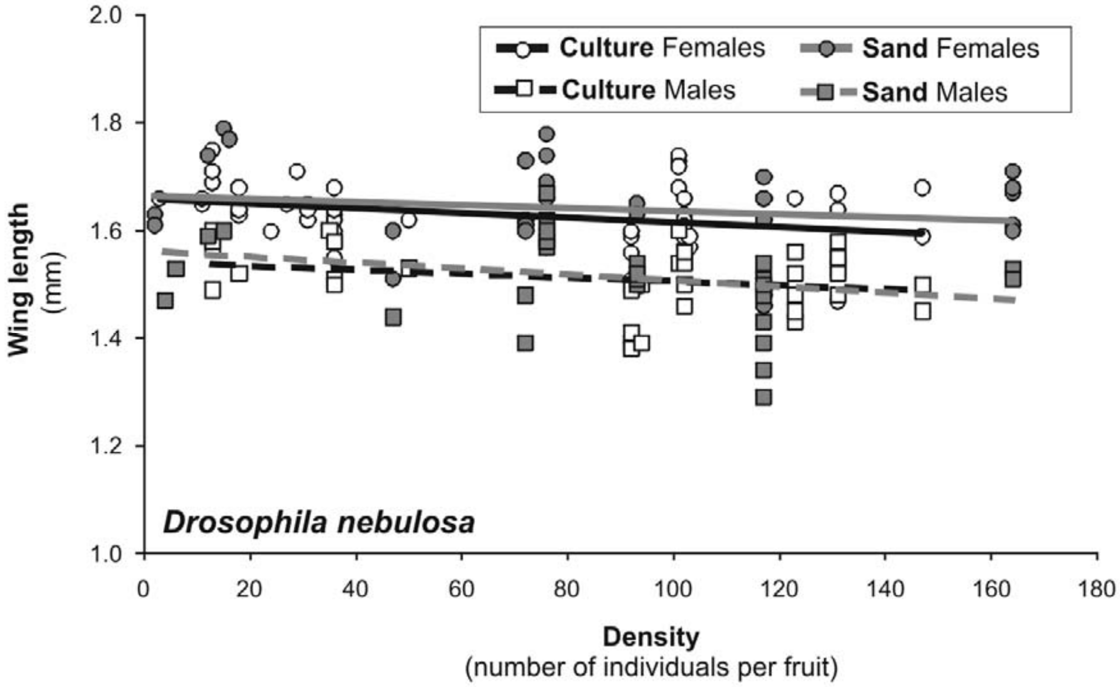

2.0
1.8
1.6
1.4
1.2
1.0
Wing length (mm)
0
20
40
60
80
100
120
140
160
180
Density (number of individuals per fruit)
Culture Females
Sand Females
Culture Males
Sand Males
Drosophila nebulosa

Figure 6

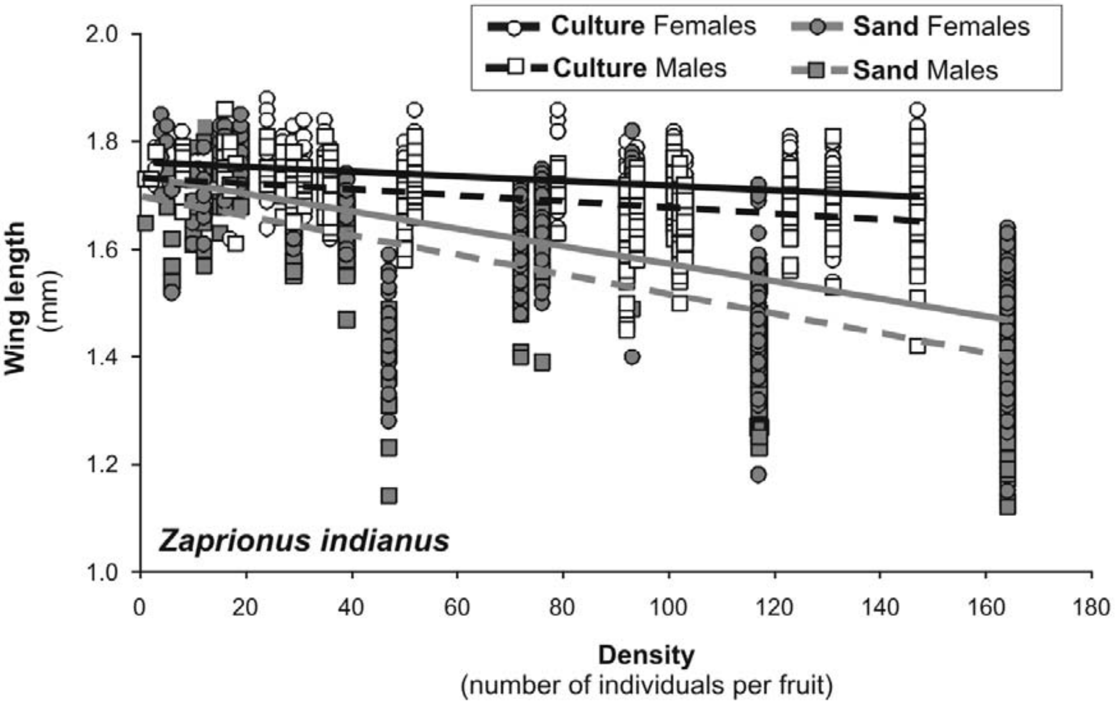
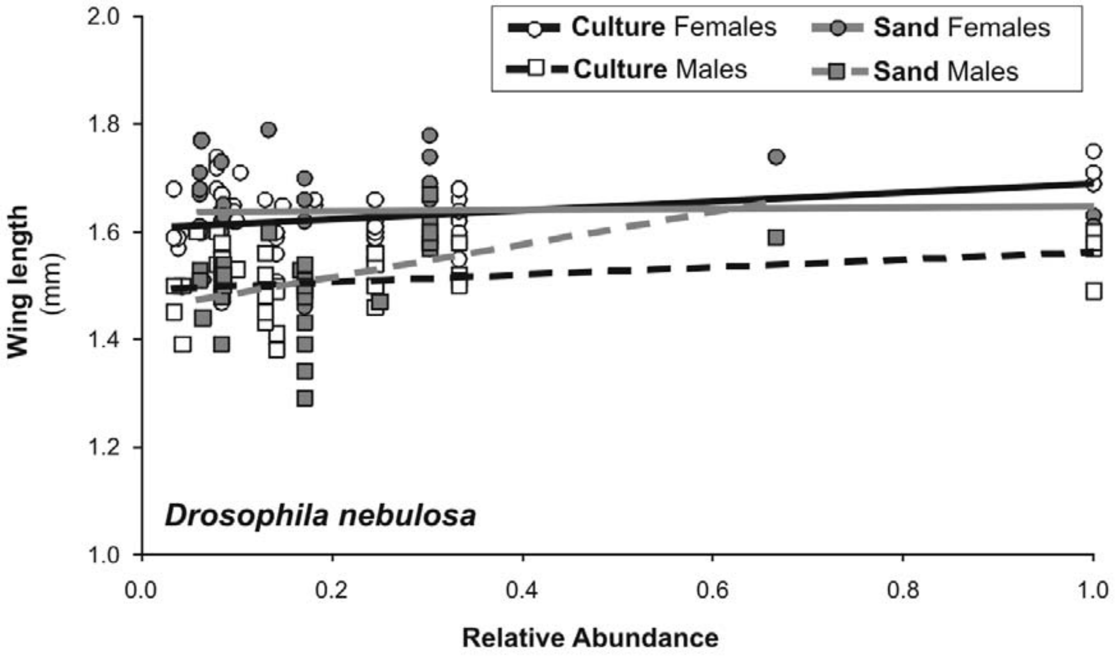
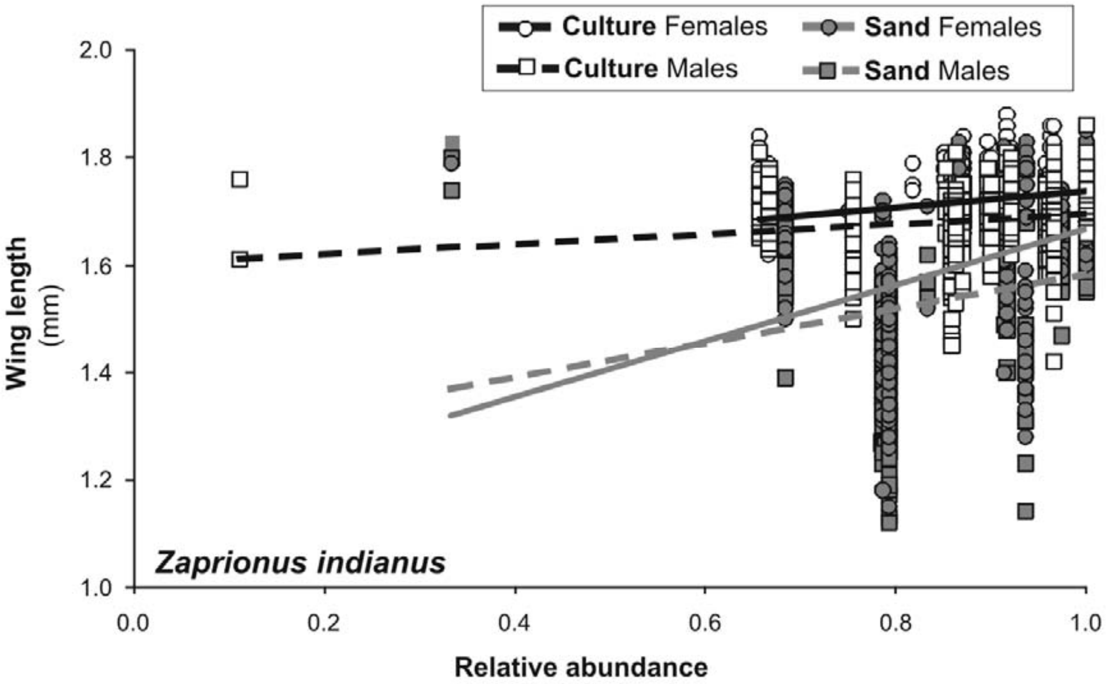

Culture Females
Culture Males
Sand Females
Sand Males
Wing length (mm)
2.0
1.8
1.6
1.4
1.2
1.0
Zaprionus indianus
0
20
40
60
80
100
120
140
160
180
Density (number of individuals per fruit)

Figure 7



Culture Females
Sand Females
Culture Males
Sand Males
Wing length (mm)
2.0
1.8
1.6
1.4
1.2
1.0
Drosophila nebulosa
0.0
0.2
0.4
0.6
0.8
1.0
Relative Abundance

Figure 8


Culture Females
Culture Males
Sand Females
Sand Males
Wing length (mm)
2.0
1.8
1.6
1.4
1.2
1.0
0.0
0.2
0.4
0.6
0.8
1.0
Relative abundance
Zaprionus indianus

CAPÍTULO 4

DROSOPHILIDAE (DIPTERA) ASSOCIATED TO FUNGI: DIFFERENTIAL USE OF RESOURCES IN ANTHROPIC AND ATLANTIC RAIN FOREST AREAS

Artigo submetido à revista *Iheringia, série Zoologia*

Title: Drosophilidae (Diptera) associated to fungi: differential use of resources in anthropic and Atlantic Rain Forest areas

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Abstract

This study investigates the Drosophilidae species associated to fruiting bodies of fungi in forested and anthropic environments of the Atlantic Rain Forest biome, in South and Southeastern Brazil. Specimen collections gave rise to 1,184 drosophilids of 48 species from the genera *Drosophila*, *Hirtodrosophila*, *Leucophenga*, *Mycodrosophila*, *Scaptomyza*, *Zaprionus* and *Zygothrica*. The *Drosophila* species collected on fungi, as well as *Zaprionus indianus*, had previously been recorded colonizing fruits, demonstrating their versatility in resource use. Most of these species belongs to the *immigrans-tripunctata* radiation of *Drosophila*. This radiation yet owns primarily mycophagous species groups and, now, with our records, almost all its groups, even those that it was supposed to be frugivorous, have species breeding and/or feeding on fungi. The colonization fauna observed on fruiting bodies varies for fungi species, depending on the time they take to decompose. Our data indicate that the faster one fungus species decomposes, the more generalists are the drosophilids species that colonize it. The environment also influences the fauna of drosophilids that colonizes fungi, since the species that resort to fungi are more generalist in environments with higher degradation rates.

Keywords: *Drosophila*, mycophagous insects, feeding sites, breeding sites.

Resumo

Foi realizado um estudo das espécies de Drosophilidae associadas aos corpos de frutificação de fungos em ambientes florestais e antrópicos no Bioma Mata Atlântica, no Sul e Sudeste do Brasil. Foram coletados 1.184 drosofilídeos de 48 espécies, pertencentes aos gêneros *Drosophila*, *Hirtodrosophila*, *Leucophenga*, *Mycodrosophila*, *Scaptomyza*, *Zaprionus* e *Zygothrica*. As espécies de *Drosophila* coletadas, assim como *Zaprionus indianus*, já haviam sido registradas em frutos, evidenciando sua versatilidade na utilização dos recursos. A maioria destas espécies pertence à radiação *immigrans-tripunctata* de *Drosophila*. Esta radiação já abrigava grupos de espécies primariamente micófagos e, agora, com nossos registros, quase todos os seus grupos, mesmos aqueles que se presumiam ser frugívoros, possuem espécies utilizando fungos como sítios de oviposição e/ou alimentação. A fauna colonizadora dos corpos de frutificação varia entre as espécies de fungos, em função do tempo em que se decompõem. Nossos dados indicam que quanto mais rápido se decompõe uma espécie de fungo, mais generalistas são as espécies de drosofilídeos que a coloniza. O ambiente também influencia a fauna de drosofilídeos que os coloniza, uma vez que as espécies que utilizam os fungos são mais generalistas em ambientes mais degradados.

Palavras-chaves: *Drosophila*, insetos micófagos, sítios de alimentação, sítios de oviposição.

Introduction

Mycophagy has manifested itself several times in the evolution of Drosophilidae, and it is very likely that it derived from detrivorous habits (THROCKMORTON, 1975). Some genera, like *Drosophila*, *Leucophenga* and *Scaptomyza* may have acquired the habit in an independent fashion (LACY, 1984; HANSKI, 1989; COURTNEY *et al.*, 1990). Yet, apparently this characteristic is synapomorphic in drosophilids of the *Zygothrica* genus group, which includes the genera *Hirtodrosophila*, *Mycodrosophila*, and *Zygothrica* as main representatives (GRIMALDI, 1990).

Almost all studies on the ecology of mycophagous drosophilids have been conducted in North America, Europe and Japan (COURTNEY *et al.*, 1990; BURLA *et al.*, 1991; TODA *et al.*, 1999; YAMASHITA & HIJII, 2007). These studies indicate that *Drosophila* is a genus that abounds in this kind or resource, and can even represent the majority of Diptera that emerge from this substrate (TODA *et al.*, 1999). These investigations also offer evidences that most mycophagous *Drosophila* species known belong to the *pinicola*, *quinaria*, *testacea* and *tripunctata* groups, all of which are included in the *immigrans-tripunctata* radiation (REMSEN & O'GRADY, 2002; MARKOW & O'GRADY, 2005). Concerning the Neotropical region, the information available about this guild is scarce. However, some samples were obtained from the 1940's up to 1960's (FROTA-PESSOA, 1945; 1951; CORDEIRO, 1952; BURLA, 1956; MOURÃO *et al.*, 1965), in studies whose the aims were not to investigate the ecology of these species.

Apart from these samplings, in a revision of the *Zygothrica* genus, GRIMALDI (1987) collected individuals in Peru and observed that few species of the genus oviposit in fungi, while some use them as courtship site. VAL & KANESHIRO (1988) carried out a survey in the Atlantic Rain Forest, where the individuals were baited with commercial fungi. In such study, *Zygothrica* was the second most abundant genus, with almost 50 species identified. Recently, ROQUE *et al.* (2006) collected drosophilids that were flying over and emerging from fruiting bodies of *Pleurotus* sp. (Tricholomataceae, Agaricales) and of one other undetermined fungus species in the Cerrado Biome, Central Brazil, where 20 species from five genera of Drosophilidae were collected, and *Drosophila* was the most abundant.

Some mycophagous species of *Drosophila*, found in temperate zones, were used as model in several studies on the ecology and brought significant contributions to this field. These studies indicate that several generalist species occasionally use fungi, which are colonized when in more advanced decomposition stages (COURTNEY *et al.*, 1990; YAMASHITA & HIJII, 2007). However, the diets of these species depends crucially on the microorganisms associated to the decomposing substrate (KIMURA, 1980). On the other hand, it has been observed that the more specialized the drosophilid is, the earlier it manages to colonize fruiting bodies of fungi (KIMURA, 1980; HANSKI, 1989). In general, these drosophilids are obligatory mycophagous organisms, both at the larval and adult stages (COURTNEY *et al.*, 1990).

Specialization towards mycophagy in insects is debated at length, and the maintenance of communities of these insects is mainly related to temporal and spatial predictability of the fungi they take as resource (COURTNEY *et al.*, 1990; TODA & KIMURA, 1997). Other factors, like toxicity of fungi, apparently play a secondary role in the mycophagous communities, considering that fungi composition is highly homogeneous (JAENIKE *et al.*, 1983; HANSKI, 1989; COURTNEY *et al.*, 1990).

Spatial predictability depends on the distribution of fruiting bodies in a given area, and this distribution in turn depends on the association these fungi present — for example, fungi associated to mycorrhizae are usually more predicted than those that associate with decomposing vegetal material (COURTNEY *et al.*, 1990). YAMASHITA & HIJII (2006) found evidence that spatial predictability is not important in the maintenance of communities of mycophagous insects as compared to temporal variability, which is related to temporal predictability. This predictability is linked to the time the fruiting bodies remains available for insect and other animals, before they are completely decomposed (LACY, 1984; HANSKI, 1989; COURTNEY *et al.*, 1990). At any rate, the last authors stated that the more predicted the fungi are, the higher is the degree of specialization of drosophilids towards them.

Although these studies have produced important insights into the ecology of mycophagous drosophilids, it is necessary to take into account that they were conducted in temperate zones, where the diversity of genera and species of Drosophilidae are lower than the found in other regions. In Australia, for example, a country which potentially have a fauna of drosophilids possibly as rich as that inhabiting the Neotropical Region, a comprehensive survey pointed out a slight superimposition of niches between mycophagous species (VAN KLINKEN & WALTER, 2001). Therefore, it becomes necessary to discover whether the processes and patterns found in temperate zones are applicable in tropical zones.

The aim of the present study is to contribute to the understanding of the processes driving the colonizing patterns of mycophagous drosophilids, by analyzing and comparing the fauna associated to fruiting bodies of fungi in Atlantic Rain Forest *stricto sensu* areas,and antropic areas, in the South and Southeast of Brazil.

Material and Methods

Drosophilids and fungi were collected in six areas in South (states of Rio Grande do Sul and Santa Catarina) and Southeast regions of Brazil (state of São Paulo). Samplings were conducted in environments of the Atlantic Rain Forest *stricto sensu* and in anthropic areas, near buildings or gardens.

Adult flies that were flying over fructification bodies of fungi were captured by sweeping with an entomological net or with an entomological aspirator. Some fructification bodies were collected and kept in glass vials with sterilized sand. Vials were maintained in a controlled temperature chamber at 24 ± 1°C. Water was added whenever necessary to prevent dehydration. Emerged adults were aspired daily.

Additionally, two samplings were conducted using 40 traps made according to TIDON & SENE (1988), baited with decomposing commercial fungi *Agaricus bisporus* (J.E. Lange) Pilát (Agaricaceae, Agaricales). Traps were kept in the field for three days. Apart from this, such baits were brought to the laboratory and reared as previously described, to verify the ability of larvae of the attracted species to grow up in such commercial fungi.

The identification of the drosophilids was based on the external morphology and on the male genitalia (prepared according to WHEELER & KAMBYSELLIS, 1966, and modified by KANESHIRO, 1969). Voucher specimens were deposited in the Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (MCN-FZB), and Museu de Zoologia, Universidade de São Paulo (MZUSP). The identification of the fungi was conducted using a dichotomic key (GUERRERO & HOMRICH, 1999).

A Detrended Correspondence Analysis (DCA) (HILL & GAUCH, 1980) was conducted to test an association between the fauna that flew over the fruiting bodies and the fungi taxa. Another DCA was used to test an association between the fauna that emerged from fruiting bodies and the fungi taxa. These analyses were conducted using the software R 2.5.0 (R DEVELOPMENT CORE TEAM, 2007), with the VEGAN package 1.8-8 (OKSANEN *et al.*, 2007).

Results

A total of 1,184 individuals belonging to 48 Drosophilidae species was collected. Each one of these species was associated to at least six fungi taxa (Tables 1-3). Of the drosophilid genera collected, *Drosophila* was the richest (33 species) and most abundant in all environments sampled, even when the genus was compared with other exclusively mycophagous species, like *Hirtodrosophila* (five species), *Leucophenga* (two species) and *Mycodrosophila* (two species).

Considering all the sampled sites, ninety individuals were collected flying over fructification bodies, totaling 21 fly species, of which 14 belonged to the genus *Drosophila* (Table 1). The prevalence of *Drosophila* was also observed in the samples collected using fungi baits (Table 2), in which 25 of the 28 species and 230 of the 275 individuals captured belonged to this genus.

In the DCA conducted for the specimens collected flying over fruiting bodies (Figure 1), the components 1 and 2 accounted for 40.9% of data variation. A distinction between specialist and generalist species was observed. The generalist species of Drosophilidae have dots located closer to the intersection of the chart axes, and occur mainly in association with *Coprinus comatus* (O. F. Müll) Pers. (Agaricaceae, Agaricales). The dots of the more specialist drosophilids are farther to the intersection of chart axes.

Specimens of four fungi families were collected and brought to the laboratory, of which 820 drosophilids emerged (Table 3). The genus *Drosophila* was once again the richest and most abundant, with ten species and 273 individuals. In the collections carried out in Joinville, the species that emerged from the baits were: *D. atrata* Burla & Pavan, 1953; *D. cuaso* Bächli, Vilela & Ratcov, 2000; *D. fumipennis* Duda 1925; *D. griseolineta* Duda, 1927; *D. roehrae* Pipkin & Heed, 1964; *Drosophila* sp.gu2 and *Leucophenga* sp.2.

In the DCA for the species that emerged from the fructification bodies (Figure 2), the components 1 and 2 accounted for 14.8% of data variation. The fungi collected in anthropized areas (*C. comatus*, *Macrolepiota* sp., *Marasmius* sp. And Agaricales *latu sensu*) were more homogeneous with regard to the compositions of the emerging fauna of Drosophilidae (highlighted by the proximity of dots amongst themselves and of the intersection of chart axes). Apart from this, the fauna emerged from Polyporaceae was typical, and distinct from that of other fungi collected. The samples of Atlantic Rain Forest area were likewise more heterogeneous as regards composition of colonizing species, since the respective dots in the chart are far away from the point in which axes cross, and the species that colonized the fungi collected in the woods were observed exclusively in these samples.

Discussion

Most fungi families collected present fast decomposition rates and low predictability (GUERRERO & HOMRICH, 1999; YAMASHITA & HIJII, 2007). This may be the reason why the *Drosophila* species have been more successful in the colonization of these fungi, since most of these flies had been recorded in other types of resources, specially fruits (CARSON, 1971; VAL *et al.*, 1981). The species of *calloptera*, *cardini*, *guarani* and *tripunctata* groups of *Drosophila*, all belonging to the *immigrans-tripunctata* radiation (REMSEN & O'GRADY, 2002; MARKOW & O'GRADY, 2005), were frequent in the fungi collected by us (except for Polyporaceae), and in a study conducted in central Brazil by ROQUE *et al.* (2006). Most of the species belonging to the *testacea* and *quinaria* groups of *Drosophila*, which also belong to such radiation, are obligatory mycophagous flies. As a whole, the results indicate that mycophagy is far more common than previously thought for this radiation, even for several Neotropical species. The characteristics related to the use of fungi by species of the *immigrans-tripunctata* radiation may thus be synapomorphic, since the species of all its groups have been recorded colonizing fungi, except those of the *pallidipennis* group. However, we cannot reject the hypothesis of homoplasy.

The occurrence of *Hirtodrosophila*, *Leucophenga*, *Mycodrosophila*, *Scaptomyza* and *Zygothrica* in fungi sthengthen the existing literature records (GRIMALDI, 1987; KANESHIRO & VAL, 1988; COURTNEY *et al.*, 1990). Nevertheless, the presence of *Zaprionus* in our samples attracted our interest, as the only species observed in the Neotropics — *Z. indianus* — is considered to be frugivorous. Adults of this species were collected over fruiting bodies of *Phallus* sp. (Phallaceae, Phallales) in anthropized areas of Ribeirão Preto (São Paulo, Brazil), and two individuals emerged from fungi collected by ROQUE *et al.* (2006). Taken together, these data demonstrate the versatility of this species, which recently invaded the American continent and that is considered a pest for fruit production.

The drosophilid fauna associated to Polyporaceae was distinct from the fungi of other families, considering both breeding and feeding sites. The dominance of species of

Hirtodrosophila, *Mycodrosophila* and *Zygothrica* may be linked to the higher temporal predictability of fruiting bodies of this family, as suggested by YAMASHITA & HIJII (2007), since its decomposition process takes longer. It is probable that the species of these genera are more specialist than those of *Drosophila*, as there is a negative trade-off between capacity to colonize stiffer fungi (like Polyporaceae) and polyphagy (HANSKI, 1989; COURTNEY *et al.*, 1990).

In contrast, the fauna emerging from the Agaricaceae, Auriculariaceae, Marasmiaceae and Phallaceae families, which assemble fungi that decompose more quickly, was far more homogeneous, specially in anthropized areas, with a high dominance of *Drosophila* species. Conversely, in forested areas the fauna sampled is more heterogeneous, even for the fast-decomposing fungi. Apart from this, it is possible that the richness of the *Mycodrosophila* and *Zygothrica* that colonize fungi is higher in forests.

Our results suggest that adult drosophilids are more generalist as to the utilization of feeding resources as compared to larvae (breeding sites), since the number of species collected flying over fungi is greater than the number of species that emerge from these organisms. Indeed, COURTNEY *et al.* (1990) mention that feeding sites adults use may be distinct from the breeding sites of larvae.

Apparently, there is some degree of restriction in the distribution of the collected species of the *cardini* group of *Drosophila* (*D. cardini* Sturtevant, 1916, *D. cardinoides* Dobzhansky & Pavan, 1943 and *D. neocardini* Streisinger, 1946), since these species were observed only in fungi of anthropic areas. The low abundance of such species in forest areas, in contrast with the high abundance observed in anthropic ones, was also recorded by GOTTSCHALK *et al.* (2007), though using banana baits. On the other hand, the collected species of the *tripunctata* and *guarani* groups were observed in both sampled environments. As for the *calloptera* group, it seemingly undergoes some degree of restriction to forest areas, in spite of the low abundance observed — results which have also been observed in collections that used fruit baits (DE TONI *et al.*, 2007).

Many Drosophilidae species collected by us had been recorded feeding or breeding on fruit. Nevertheless, the species of the *tripunctata*, *guarani*, *cardini* and *calloptera* groups of *Drosophila* were the most frequent in our samples. Apart from this, the time taken for fruiting bodies to decompose seemed to be a key factor in fungi colonization by drosophilids, as the species with wider feeding niche were the most abundant and frequent in those fungi that decompose faster. On the other hand, the species that were not frequently collected in other types of resource presented a closer relationship with Polyporaceae fungi, which decomposes more slowly. Finally, it is possible that the use of fungi as a trophic resource has played a more significant role — in comparison to previous notions — in the evolutive success of Neotropical species belonging to the *immigrans-tripunctata* radiation of *Drosophila*.

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Legends

Table 1 – Drosophilidae species collected flying over fruiting bodies of fungi in different sites in Brazil.

Table 2 – Drosophilidae species collected using baits prepared with commercial fungi in Piraí, Joinville, SC (Atlantic Rain Forest) (26°17’37,9”S; 49°00’56,4”W).

Table 3 –Drosophilidae species emerged from fruiting bodies of fungi in different sites in Brazil.

Figure 1 – Detrended Correspondence Analysis results for the feeding sites data. DCA1 – component 1; DCA2 – component 2. Circles: Drosophilidae species; Cross and underlined text: fungi species collected in anthropized environment; Cross and underlined text in bold: fungi species collected in the Atlantic Rain Forest.

Figure 2 – Detrended Correspondence Analysis results for the breeding sites data. DCA1 – component 1; DCA2 – component 2. Circles: Drosophilidae species; Cross and underlined text: fungi species collected in anthropized environment; Cross and underlined text in bold: fungi species collected in the Atlantic Rain Forest.

Table 1

Genus	**Group**	**Species**	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**	**Total**
Drosophila	*calloptera*	*D. atrata* Burla & Pavan, 1953	-	-	-	-	2	-	**2**
		D. calloptera Schiner, 1868	-	-	-	-	1	-	**1**
	cardini	*D. cardini* Sturtevant, 1916	-	-	-	3	-	-	**3**
		D. cardinoides Dobzhansky & Pavan, 1943	-	1	-	2	-	-	**3**
		D. neocardini Streisinger, 1946	-	-	-	1	-	-	**1**
	guarani	*D. griseolineata* Duda, 1927	4	5	-	-	-	6	**15**
		D. maculifrons Duda, 1927	-	1	-	-	-	-	**1**
	immigrans	*D. immigrans* Sturtevant, 1921	-	2	-	-	-	-	**2**
	melanogaster	*D. kikkawai* Burla, 1954	-	1	-	-	-	-	**1**
	tripunctata	*D. cuaso* Bächli, Vilela & Ratcov, 2000	-	2	-	-	-	4	**6**
		D. mediopunctata Dobzhansky & Pavan, 1943	3	3	-	-	-	1	**7**
		D. paraguayensis Duda, 1927	-	-	-	-	-	10	**10**

		D. roehrae Pipkin & Heed, 1964	-	-	-	-	-	5	**5**
	willistoni	*D. willistoni* subgroup	3	3	-	-	-	-	**6**
Hirtodrosophila	*hirticornis*	*H. gilva* (Burla, 1956)	-	-	-	-	-	1	**1**
		Hirtodrosophila sp.ob1 (sp.Z3*)	-	-	-	-	-	4	**4**
Leucophenga		*Leucophenga* sp.	-	-	-	2	-	-	**2**
Mycodrosophila		*M. projectans* (Sturtevant, 1916)	1	-	-	-	-	-	**1**
Zaprionus	*vittiger*	*Z. indianus* Gupta, 1970	-	-	12	-	-	-	**12**
Zygothrica	*hypandriata*	*Z. hypandriata* Burla, 1956	-	2	-	-	-	-	**2**
		Zygothrica sp.	-	-	-	5	-	-	**5**
Total			**11**	**20**	**12**	**13**	**3**	**31**	**90**

F1 – *Coprinus comatus* (Agaricaceae) – *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 15.VII.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

F2 – *C. comatus* – *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 04.VIII.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

F3 – *Phallus* sp. (Phallaceae) – *Campus* of Universidade de São Paulo, Ribeirão Preto, SP – 20.III.2006 (anthropic area) (21°10’11.7”S; 47°51’33.4”W)

F4 – Agaricales *sensu lato* – *Campus* of Universidade de São Paulo, Ribeirão Preto, SP – 22.I.2007 (anthropic area) (21°10’11.7”S; 47°51’33.4”W)

F5 – Polyporaceae – Morro da Lagoa da Conceição, Florianópolis, SC – 07.IV. 2007 (Atlantic Rain Forest) (27°35’26.8”S; 48°28’32.9”W)

F6 – Group of several undetermined fungi species – Morro da Lagoa da Conceição, Florianópolis, SC – 07.IV. 2007 (Atlantic Rain Forest) (27°35’26.8”S; 48°28’32.9”W)

* Same species introduced by GOTTSCHALK *et al.* (2007)

Table 2

Genus	group	Species	U1	U2	Total
Drosophila	*calloptera*	*D. atrata* Burla & Pavan, 1953	1	5	**6**
	canalinea	not identified	-	1	**1**
	coffeata	*D. coffeata* Williston, 1896	-	2	**2**
		D. fuscolineata Duda, 1925	-	2	**2**
	guarani	*D. griseolineata* Duda, 1927	-	1	**1**
		Drosophila sp.gu2 (sp.G1*)	14	2	**16**
		Drosophila sp.gu5	-	1	**1**
	morelia	*D. fluminensis* Vilela & Bächli, 2004	2	-	**2**
	repleta	*D. onca* Dobzhansky & Pavan, 1943	-	1	**1**
		not identified	1	1	**2**
	tripunctata	*D. bandeirantorum* Dobzhansky & Pavan, 1943	1	-	**1**
		D. bifilum Frota-Pessoa, 1954	-	1	**1**

	D. cuaso Bächli, Vilela & Ratcov, 2000	6	32	**38**
	D. mediopicta Frota-Pessoa, 1954	-	5	**5**
	D. nappae Vilela, Valente & Basso-da-Silva, 2004	-	5	**5**
	D. neoguaramunu Frydenberg, 1956	-	4	**4**
	D. paraguayensis Duda, 1927	74	35	**109**
	D. roehrae Pipkin & Heed, 1964	-	2	**2**
	D. setula Heed & Wheeler, 1957	-	2	**2**
	Drosophila sp.tp8 (sp.T3*)	1	1	**2**
	Drosophila sp.tp4	-	1	**1**
willistoni	*D. capricorni* Dobzhansky & Pavan, 1943	-	1	**1**
	D. fumipennis Duda, 1925	-	3	**3**
	willistoni subgroup	-	1	**1**
Not assigned to group	*Drosophila* sp.dr2	1	15	**16**
	Drosophila sp.fungi1	-	4	**4**

Hirtodrosophila	*Hirtodrosophila* sp.ob1 (sp.Z3[*])	-	27	**27**
	Hirtodrosophila sp.ob2 (sp.Z4[*])	2	14	**16**
Leucophenga	*Leucophenga* sp.2	2	-	**2**
Total		**105**	**170**	**275**

U1 – 03.XI.2005; U2 – 22.V.2006

[*] Same species introduced by GOTTSCHALK *et al.* (2007)

Table 3

Genus	**Group**	**Species**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**	**B11**	**B12**	**Total**
Drosophila	*cardini*	*D. cardini* Sturtevant, 1916	-	-	-	-	-	-	-	-	-	39	-	2	**41**
		D. cardinoides Dobzhansky & Pavan, 1943	-	28	-	-	-	-	4	-	-	28	97	8	**165**
		D. neocardini Streisinger, 1946	-	5	-	-	-	-	-	-	-	2	-	-	**7**
	guarani	*Drosophila* sp.gu2 (sp.G1*)	-	-	-	-	-	-	-	2	-	-	-	-	**2**
	immigrans	*D. immigrans* Sturtevant, 1921	-	-	-	-	-	-	-	-	-	-	-	1	**1**
	melanogaster	*D. kikkawai* Burla, 1954	-	-	-	-	-	-	-	-	-	-	6	4	**10**
	tripunctata	*D. cuaso* Bächli, Vilela & Ratcov, 2000	-	-	-	-	-	-	-	12	-	1	-	-	**13**
		D. mediovittata Frota-Pessoa, 1954	-	-	-	-	-	-	-	-	-	-	1	1	**2**
		D. nappae Vilela, Valente & Basso-da-Silva, 2004	-	-	-	-	-	-	-	-	-	17	10	-	**27**

		D. paraguayensis Duda, 1927	-	-	-	-	-	5	-	-	-	-	-	-	**5**
Hirtodrosophila	*hirticornis*	*H. gilva* (Burla, 1956)	-	-	-	-	-	-	-	-	181	-	-	-	**181**
	thoracis	*H. thoracis* (Williston, 1896)	-	142	-	3	-	3	18	-	-	-	-	-	**166**
	not assigned to group	*H. ramulosa* (Burla, 1956)	-	-	-	-	-	-	-	-	19	-	-	-	**19**
Leucophenga		*Leucophenga* sp.1	34	-	-	-	-	-	16	-	-	-	-	-	**50**
Mycodrosophila		*M. projectans* (Sturtevant, 1916)	-	-	9	21	2	4	-	-	-	-	1	-	**37**
		Mycodrosophila sp.2	-	-	3	-	-	-	-	-	-	-	-	-	**3**
Scaptomyza		*S. hirsuta* (cf.) Wheeler, 1949	-	-	-	-	-	-	-	-	-	-	1	1	**2**
Zygothrica	*atriangula*	*Z. poeyi* (Sturtevant, 1921)	-	-	-	-	-	1	-	-	-	-	-	-	**1**
	hypandriata	*Z. hypandriata* Burla, 1956	-	-	-	-	-	-	-	-	-	-	1	63	**64**
		Zygothrica sp.1	-	-	13	-	-	-	-	-	-	-	-	-	**13**
		Zygothrica sp.2	-	1	10	-	-	-	-	-	-	-	-	-	**11**
Total			**34**	**176**	**35**	**24**	**2**	**13**	**38**	**14**	**200**	**87**	**117**	**80**	**820**

B1 – *Macrolepiota* sp. (Agaricaceae) – *Campus* of Universidade Federal de Santa Catarina, Florianópolis, SC – 07.III.2005 (anthropic area) (27°36’12.9”S; 48°31’21.9”W)

B2 – *Marasmius* sp. (Marasmiaceae) – *Campus* of Universidade Federal de Santa Catarina, Florianópolis, SC – 07.III.2005 (anthropic area) (27°36’12.9”S; 48°31’21.9”W)

B3 – Polyporaceae – Morro da Lagoa da Conceição, Florianópolis, SC – 07.III.2005 (Atlantic Rain Forest) (27°35’26.8”S; 48°28’32.9”W)

B4 – Polyporaceae – Morro da Lagoa da Conceição, Florianópolis, SC – 07.III.2005 (Atlantic Rain Forest) (27°35’26.8”S; 48°28’32.9”W)

B5 – Polyporaceae- *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 07.VI.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

B6 – Polyporaceae – Biguaçu, SC – 13.XI.2006 (Atlantic Rain Forest) (27°29’09.8”S; 48°39’17.7”W)

B7 – Agaricales *sensu lato* – *Campus* of Universidade Federal de Santa Catarina, Florianópolis, SC – 24.V.2005 (anthropic area) (27°36’12.9”S; 48°31’21.9”W)

B8 – *Auricularia* sp. (Auriculariaceae) – Piraí, Joinville, SC – 03.XI.2005 (Atlantic Rain Forest) (26°17’37.9”S; 49°00’56.4”W)

B9 – *Auricularia* sp. (Auriculariaceae) – Biguaçu, SC – 13.XI.2006 (Atlantic Rain Forest) (27°29’09.8”S; 48°39’17.7”W)

B10 – *Coprinus comatus* (Agaricaceae) – *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 16.IV.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

B11 – *C. comatus* (Agaricaceae) – *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 15.VII.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

B12 – *C. comatus* (Agaricaceae) – *Campus* of Universidade Federal do Rio Grande do Sul, Porto Alegre, RS – 04.VIII.2005 (anthropic area) (30º04’16.1”S; 51º07’13.7”W)

* Same species introduced by GOTTSCHALK *et al.* (2007)

Figure 1

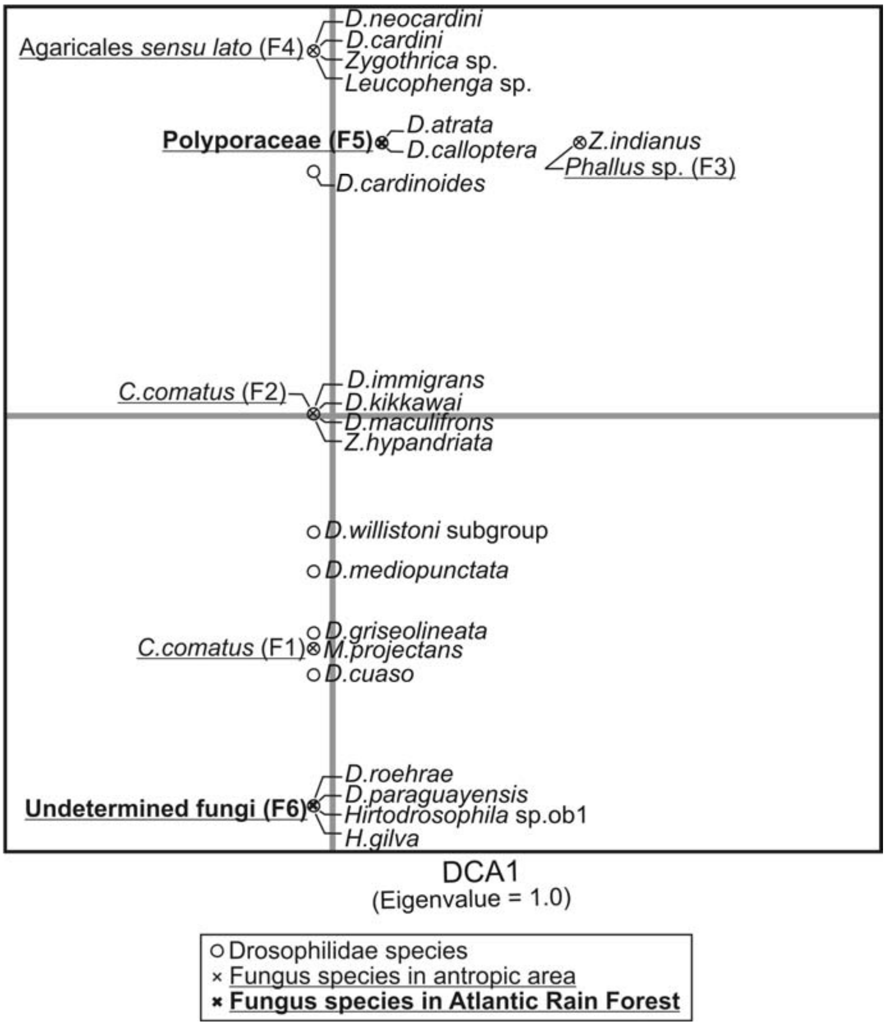
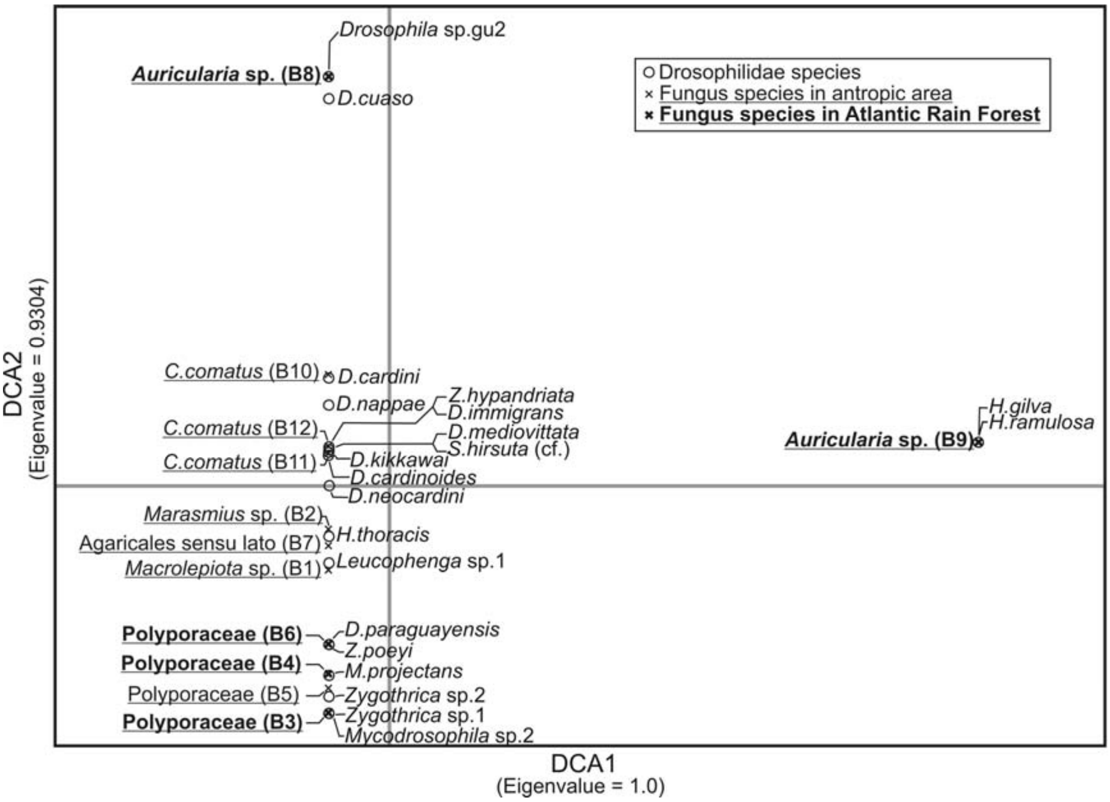

D.neocardini
Agaricales sensu lato (F4)
D.cardini
Zygothrica sp.
Leucophenga sp.
D.atrata
Polyporaceae (F5)
D.calloptera
Z.indianus
Phallus sp. (F3)
D.cardinoides
DCA2
(Eigenvalue = 0.9474)
D.immigrans
C.comatus (F2)
D.kikkawai
D.maculifrons
Z.hypandriata
D.willistoni subgroup
D.mediopunctata
D.griseolineata
C.comatus (F1)
M.projectans
D.cuaso
D.roehrae
D.paraguayensis
Undetermined fungi (F6)
Hirtodrosophila sp.ob1
H.gilva
DCA1
(Eigenvalue = 1.0)
○ Drosophilidae species
× Fungus species in antropic area
× Fungus species in Atlantic Rain Forest

Figure 2


Drosophila sp.gu2
Auricularia sp. (B8)
D.cuaso
○ Drosophilidae species
× Fungus species in antropic area
× Fungus species in Atlantic Rain Forest
C.comatus (B10)
D.cardini
D.nappae
Z.hypandriata
D.immigrans
C.comatus (B12)
D.mediovittata
S.hirsuta (cf.)
C.comatus (B11)
D.kikkawai
D.cardinoides
D.neocardini
H.gilva
H.ramulosa
Auricularia sp. (B9)
Marasmius sp. (B2)
H.thoracis
Agaricales sensu lato (B7)
Macrolepiota sp. (B1)
Leucophenga sp.1
Polyporaceae (B6)
D.paraguayensis
Z.poeyi
Polyporaceae (B4)
M.projectans
Polyporaceae (B5)
Zygothrica sp.2
Polyporaceae (B3)
Zygothrica sp.1
Mycodrosophila sp.2
DCA2
(Eigenvalue = 0.9304)
DCA1
(Eigenvalue = 1.0)

CAPÍTULO 5

DIPTERA, DROSOPHILIDAE: HISTORICAL OCCURRENCE IN BRAZIL

Artigo submetido à revista *Checklist*

Diptera, Drosophilidae: historical occurrence in Brazil

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Abstract

This study presents a literature review of Drosophilidae (Diptera) species occurrence in Brazil. The number of species recorded is 304, with *Drosophila* being the genus with most species observed, followed by *Zygothrica*, *Hirtodrosophila* and *Diathoneura*, which belong to the Drosophilinae subfamily. *Drosophila* was shown to be the most investigated taxon in the family, with the best resolved species distribution. The low number of records of species from other genera points to the paucity of studies specifically designed to investigate these species. Records of species for some regions of the country like the north and northeast, as well as for some biomes like Caatinga, Pantanal and the Pampas, are likewise rare. Apart from the banana bait, different collection methods may be necessary, like the collection at other oviposition resources, the use of baits other than fermenting fruit, and the adoption of sampling approaches that do not use baits.

Introduction

Drosophilidae species have been described since 1787, when Fabricius characterized *Musca funebris*, which later was repositioned in a new genus and became *Drosophila funebris*, the type-species of the family. Today, Drosophilidae encompass 3,952 species distributed in 73 genera belonging to two subfamilies (Bächli 2007), Steganinae and Drosophilinae. Two monotypical genera, *Apacrochaeta* Duda 1927 and *Sphyrnoceps* de Meijere 1916, have not been included in any subfamily.

Drosophilinae is the most diversified subfamily, with 3,240 species distributed across 44 genera (Bächli 2007), among which *Drosophila* Fallén 1823 is the largest, with 1,149 species recorded. When compared to the data obtained by Ashburner (1989), the number of *Drosophila* species is smaller, because some of the subgenera it originally contained were raised to genus level, such as *Scaptodrosophila* (Duda 1923), *Hirtodrosophila* (Duda 1923) and *Lordiphosa* (Basden 1961) (Grimaldi 1990a). Moreover, several Hawaiian species and the *Antopocerus* genus (Kaneshiro 1976) were incorporated into the genus *Idiomyia* Grimshaw 1901, while the subgenus *Engiscaptomyza* (Kaneshiro 1969), also native to Hawaii, was relocated to *Scaptomyza* Hardy 1849 (Grimaldi 1990a; O'Grady et al. 2003).

The subfamily Steganinae, which conserves several primitive characteristics of the family, nowadays comprises 702 species that belong to 29 genera (Bächli 2007). The Drosophilidae genera and respective number of species are listed in Table 1.

→TABLE 1

Sturtevant (1921) studied the distribution of Drosophilidae species known in the different biogeographic zones, and originally found 82 species distributed across 13 genera in Neotropical region. Yet, nowadays these numbers are downsized to 70 and 10, respectively, as the genera *Curtonotum* (Macquart 1843), *Blaesochaetophora* (Czerny 1904) and *Aulacigaster* (Macquart 1835), which contained 12 of the species listed by Sturtevant, have been relocated into other families.

More specifically, Sturtevant (1921) reports the presence of six genera and 23 species of the family in South America. With the increase in the number of studies on the Neotropical fauna, some species lists were prepared in certain countries, specially for the *Drosophila* genus, like Mexico (Patterson and Mainland 1944), El Salvador (Heed 1957), Colombia (Hunter 1969), Venezuela (Hunter 1970) and Chile (Brncic 1987). These lists include the one prepared for Brazil by Mourão et al. (1965).

Thus, the lists and nomenclature studies were somehow common for *Drosophila* in the past (apart from those already mentioned, there are the studies by Patterson and Wheeler (1949), Patterson and Stone (1952) and Wheeler (1959)). Yet, the survey made by Val et al. (1981) has so far been the largest compilation of data on Neotropical drosophilids, addressing relevant knowledge of species distribution and ecology. Considering the recent taxonomy studies, specially those by G. Bächli, D. Grimaldi and C.R. Vilela, as well as the species and ecology surveys conducted, mainly those by F.M. Sene, R. Tidon, F.C. Val and V.L.S. Valente and coworkers, the panorama of Drosophilidae species distribution and diversity in Brazil has indeed been enlarged.

Material and Methods

This study is a compilation of data obtained from a wide-ranging literature review of the records of Drosophilidae species in Brazil. The authors are aware that some of the extant records may not have been recovered in the survey process. The information retrieved was not necessarily wholly generated in studies on Drosophilidae taxonomy or ecology, since the studies consulted include those focused on evolution, population genetics, descriptive and comparative biology of the genus, for which several records were made over collections directed to find certain species. Only the Brazilian states where each species was recorded are indicated in the geographic distribution information.

Results and Discussion

The present literature review found 304 Drosophilidae species distributed in 18 genera in Brazil (Table 2, Appendix I). Among the genera recorded, *Chymomyza* Czerny 1903, *Cladochaeta* Coquillett 1900, *Dettopsomyia* Lamb 1914, *Diathoneura* Duda 1924, *Drosophila*, *Hirtodrosophila*, *Microdrosophila* Malloch 1921, *Mycodrosophila* Oldenberg 1914, *Neotanygastrella* Duda 1925, *Scaptodrosophila*, *Scaptomyza*, *Zaprionus* Coquillett 1901 and *Zygothrica* Wiedemann 1830 belong to the Drosophilinae subfamily; in turn, *Amiota* Loew 1862, *Leucophenga* Mik 1886, *Pseudiastata* Coquillett 1908, *Rhinoleucophenga* Hendel 1917 and *Stegana* Meigen 1830 rank under the Steganinae subfamily. Figure 1 shows the number of species recorded for each genus, revealing two prominent genera: *Drosophila* and *Zygothrica*. Ashburner (1989) mentions the probability that the American species of the *Gitona* genus in fact belong to *Rhinoleucophenga*. This classification has been accepted by Bächli (2007) and we followed suit. The genus *Microdrosophila* was collected by Val and Kaneshiro (1988) in the state of São Paulo, though no species was determined in that study. The authors point to these species as likely non-described species, and therefore they are not shown in Figure 1.

→FIGURE 1

Thirteen species recorded are exotic — *Dettopsomyia formosa* Lamb 1914, *D. nigrovittata* Malloch 1924, *Drosophila ananassae* Doleschall 1858, *D. busckii* Coquillett 1901, *D. immigrans* Sturtevant 1921, *D. kikkawai* Burla 1954, *D. malerkotliana* Parshad and Paika 1964, *D. melanogaster* Meigen 1830, *D. simulans* Sturtevant 1919, *D. virilis* Sturtevant 1916, *Scaptodrosophila latifasciaeformis* Duda 1940, *S. lebanonensis* Wheeler 1949 and *Zaprionus indianus* Gupta 1970 — though the majority of the total number is endemic to the New World (Malogolowkin 1946; Hardy 1959; Wheeler 1981; Grimaldi and Nguyen 1999). Yet, only *Cladochaeta*, *Diathoneura*, *Pseudiastata* and *Rhinoleucophenga* are genera for which all species are endemic to the New World (Malogolowkin 1946; Hardy 1959; Wheeler 1981; Grimaldi and Nguyen 1999). All other genera have species also in other biogeographic regions, such as *Zygothrica*, which up to the 1980's was considered an exclusive Neotropical genus (Burla, 1956) and for which some species from Africa and Samoa were only recently described (Grimaldi 1990b; Prigent and Toda 2006).

→TABLE 2

Drosophila was the genus with most species and the most comprehensively studied in Brazil, which is reflected in the largest size and abundance of *Drosophila* and *Sophophora* subgenera. This should come as no surprise, as *Drosophila* is widely employed in genetic, evolutionary and behavioral studies worldwide (Powell 1997). Apart from being a model organism in several fields of genetics and evolutionary biology, *Drosophila* has gained the same status in ecology and conservation investigations (Martins, 2001; Tidon et al. 2005). In the light of the fact that *Drosophila* is strongly attracted by baits prepared with fermented fruit, a considerable number of researchers have chosen the approach to collect specimens for their studies. This feeding preference of drosophilids has made the collection methodology quite popular among researchers on the area, which explains why most studies resort to this kind of bait (Pavan 1959; Sene et al. 1980; Tidon 2006; De Toni et al. 2007; among others). This bait attracts mainly the frugivorous species, such as most drosophilid species recorded in Brazil, while species that are only seldom attracted include fungivorous, florivorous, cactophilic and leaf-mining species, and/or species that feed on decomposing wood or that show parasitic/predatory behavior.

This large volume of information on one same taxon is highly relevant for the knowledge on the dynamics of the Neotropical fauna, as it is only based on model organisms or taxa that researchers may clarify issues related to biodiversity, species interaction, metapopulation dynamics, endemism areas and others.

In spite of the several studies on *Drosophila* conducted in Brazil as a whole, these studies do not evenly cover all the country's territory (Table 3, Figure 2). Most species have been recorded in southeastern Brazil, where the research on *Drosophila* actually started with some studies conducted for specific collection sites. Some surveys have lately been carried out in southern Brazil, specially on the coast of the State of Santa Catarina, where recent species surveys are being conducted by research groups of P.R.P. Hofmann and V.L.S. Valente.

→TABLE 3

Generally speaking, the northeastern region of the country has produced a relatively small number or records (exception is the State of Bahia). Northern Brazil likewise remains little explored, as the number of species expected for the region should be at least similar to that for southeastern and southern Brazil, due to the Amazon biome. If the endemism rates are similar across the different Brazilian biomes, then the Amazon should have the highest species richness, as the area the biome covers exceeds that of the Atlantic Forest biome. The main records for species from the north were generated in ground-breaking papers, such as those by Duda (1925; 1927), and some more recent investigations (Martins 2001; Silva and Martins 2004; De Toni et al. 2005).

→FIGURE 2

Another relevant aspect to comment on is the lack of information on other genera, apart from *Drosophila*, as all species records are for the states of São Paulo and Rio de Janeiro. These records are sporadic, and the number of studies conducted to investigate these groups in Brazil is very small, when compared to the number of studies on *Drosophila*. For example, most records for *Rhinolecophenga* are from one study only (Malogolowkin 1946). The absence of records may be associated to the need for a taxonomic review for some genera, like *Amiota*, *Leucophenga*, *Microdrosophila*, *Mycodrosophila*, *Pseudiastata*, *Rhinoleucophenga*, *Scaptomyza* and *Stegana*. The majority of species from these genera was described before the 1970's, and the characteristics adopted in the descriptions are unsatisfactory for an ideal characterization of the material collected, since detailed descriptions of male genitalia are required to properly identify the specimens collected.

Apart from this, of the 304 Drosophilidae species in Brazil, 95 have one single record only, of which number 43 belong to *Drosophila* and the other 52 to the genera *Chymomyza* (four species), *Cladochaeta* (two species), *Diathoneura* (eight species), *Hirtodrosophila* (nine species), *Leucophenga* (three species), *Mycodrosophila* (one species), *Neotanygastrella* (one species), *Rhinoleucophenga* (five species), *Scaptodrosophila* (one species), *Scaptomyza* (one species) and *Stegana* (one species) (Appendix I).

Val et al. (1981) mention that a large number of Drosophilidae has not been given the deserved attention by researchers. Such scenario has not changed since 1981. Grimaldi (1987) and Grimaldi and Nguyen (1999) report the paucity of information on the genera *Zygothrica* and *Cladochaeta* in South America, specially in Brazil, for which only four species of the second have been collected within the 124 species described.

Yet another aspect that points to the workload expected for researchers on drosophilids, a considerable number of our species has few records, and for which only the type locality is known, in many cases (Val et al. 1981). The records for *Zygothrica* in the state of São Paulo, for instance, were practically all listed by Val and Kaneshiro (1988).

This scenario is common for most Neotropical Diptera families (Brown 2005). Many Diptera species have not even been formally described. Wheeler (1986) estimated that roughly 30% of *Drosophila* species had yet to be described. Such value was very likely and underestimation, as after 20 years the number of *Drosophila* species of that time increased by 27%, and even so there is little doubt that all *Drosophila* species have been described. In 1988, Val and Kaneshiro stated that nearly 50% of the *Drosophila* species captured in the "Estação Biológica de Boracéia" in the state of São Paulo (the Brazilian state most thoroughly sampled) had never been described. The same was observed for the recent collections conducted by Medeiros and Klaczko (2004). In like manner, similar situation was seen in the State of Santa Catarina, where roughly 60 Drosophilidae species collected are yet to be described.

In order to assemble a comprehensive databank for ecological and environmental studies, it is important to complete the roll call of *Drosophila* species with banana baits across the remaining Brazilian territory. Such importance is explained by the great value drosophilids have as model organisms, even as bioindicators, for a variety of studies (Parsons 1991; Martins 2001; Tidon 2006). At the same time, it is crucial to describe any new species being collected in the territory.

Moreover, as a considerable part of drosophilid material deposited in zoological collections remains uncharacterized, a review of some genera — as said before — and of that material gains relevance to the assessment of Brazilian biodiversity. Also, collection strategies that resort to fruits other than banana are needed, such as the (1) collection at resources onto which Drosophilidae species lay their eggs — as native fruits, fungi, flowers and decomposing leaves, (2) collection using baits with other fermenting fruits, and (3) sampling approaches that do not utilize baits. With this in mind, Malaise baits, which have proved their efficiency to capture Diptera (Brown 2005), could be used. Also, these sample collections should include the different Brazilian biomes — the Atlantic Forest, the Amazon, the Cerrado, the Caatinga, Pantanal and Pampas (IBGE 2006), as the last three are mostly unexplored for the occurrence of the Drosophilid fauna.

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Table 1 – Genera of the Drosophilidade family (based on Bächli 2007), listed in alphabetical order. Number of species described for the taxon in brackets.

Drosophilidae Rondani 1856 (3952 spp.)	(Continued Drosophilinae)
Drosophilinae Rondani 1856 (3235 spp.)	*Styloptera* Duda 1924 (10 spp.)
Baeodrosophila Wheeler and Takada 1964 (5 spp.)	*Tambourella* Wheeler 1957 (3 spp.)
Balara Bock 1982 (1 sp.)	*Zaprionus* Coquillett 1901 (56 spp.)
Bialba Bock 1989 (1 sp.)	*Zapriothrica* Wheeler 1956 (5 spp.)
Celidosoma Hardy 1965 (1 sp.)	*Zaropunis* Tsacas 1990 (1 sp.)
Chymomyza Czerny 1903 (56 spp.)	*Zygothrica* Wiedemann 1830 (124 spp.)
Cladochaeta Coquillett 1900 (124 spp.)	**Steganinae** Hendel 1917 (712 spp.)
Collessia Bock 1982 (5 spp.)	*Acletoxenus* McAlpine 1968 (4 spp.)
Colocasiomyia de Meijere 1914 (26 spp.)	*Allopygaea* Tsacas 2000 (3 spp.)
Dettopsomyia Lamb 1914 (13 spp.)	*Amiota* Loew 1862 (116 spp.)
Diathoneura Duda 1924 (39 spp.)	*Apenthecia* Tsacas 1983 (12 spp.)
Dichaetophora Duda 1940 (61 spp.)	*Apsiphortica* Okada 1971 (2 spp.)
Dicladochaeta Malloch 1932 (1 sp.)	*Cacoxenus* Loew 1858 (36 spp.)
Drosophila Fallen 1823 (1149 spp.)	*Crincosia* Bock 1982 (3 spp.)
Hirtodrosophila (Duda 1923) (158 spp.)	*Electrophortica* Hennig 1965 (1 sp.)
Hypselothyrea de Meijere 1906 (30 spp.)	*Eostegana* Hendel 1913 (13 spp.)
Idiomyia Grimshaw 1901 (380 spp.)	*Erima* Kertesz 1899 (1 sp.)
Jeannelopsis Seguy 1938 (3 spp.)	*Gitona* Meigen 1830 (15 spp.)
Laccodrosophila Duda 1927 (5 spp.)	*Hyalistata* Wheeler 1960 (6 spp.)

Liodrosophila Duda 1922 (64 spp.)
Lissocephala Malloch 1929 (32 spp.)
Lordiphosa (Basden 1961) (58 spp.)
Marquesia Malloch 1932 (2 spp.)
Microdrosophila Malloch 1921 (77 spp.)
Miomyia Grimaldi 1987 (1 sp.)
Mulgravea Bock 1982 (14 spp.)
Mycodrosophila Oldenberg 1914 (118 spp.)
Neotanygastrella Duda 1925 (18 spp.)
Palmomyia Grimaldi *in* Grimaldi *et al.* 2003 (1 sp.)
Palmophila Grimaldi *in* Grimaldi *et al.* 2003 (2 spp.)
Paraliodrosophila Duda 1925 (4 spp.)
Paramycodrosophila Duda 1924 (16 spp.)
Phorticella Duda 1923 (11 spp.)
Poliocephala Bock 1989 (1 sp.)
Protochymomyza Grimaldi 1987 (1 sp.)
Samoaia Malloch 1934 (7 spp.)
Scaptodrosophila (Duda 1923) (279 spp.)
Scaptomyza Hardy 1849 (262 spp.)
Sphaerogastrella Duda 1922 (10 spp.)

Leucophenga Mik 1886 (205 spp.)
Luzonimyia Malloch 1926 (4 spp.)
Mayagueza Wheeler 1960 (1 sp.)
Neorhinoleucophenga Duda 1924 (2 spp.)
Paraleucophenga Hendel 1914 (8 spp.)
Paraphortica Duda 1934 (1 sp.)
Pararhinoleucophenga Duda 1924 (2 spp.)
Parastegana Okada 1971 (3 spp.)
Phortica Schiner 1862 (97 spp.)
Pseudiastata Coquillett 1908 (6 spp.)
Pseudocacoxenus Duda 1925 (1 sp.)
Pseudostegana Okada 1978 (33 spp.)
Pyrgometopa Kertesz 1901 (1 sp.)
Rhinoleucophenga Hendel 1917 (18 spp.)
Soederbomia Hendel 1938 (1 sp.)
Stegana Meigen 1830 (116 spp.)
Trachyleucophenga Hendel 1917 (1 sp.)

Incertae sedis (2 spp.)

Apacrochaeta Duda 1927 (1 sp.)
Sphyrnoceps de Meijere 1916 (1 sp.)

Table 2 – Genera, subgenera, groups and number of species of Drosophilidae recorded in Brazil, in alphabetical order (complete data in Appendix I).

Subfamily	**Genus**	**Subgenus**	**Group**	**Number of Species**
Drosophilinae	*Chymomyza*		*aldrichii* Okada 1976	3
			procnemis Okada 1976	2
	Cladochaeta		*armata* Grimaldi and Nguyen 1999	1
			bomplandi Grimaldi and Nguyen 1999	1
			Not assigned to group	2
	Dettopsomyia			2
	Diathoneura	*Diathoneura* Duda 1924		12
	Drosophila	*Dorsilopha* Sturtevant 1942	*busckii* Sperlich 1980	1
		Drosophila Fállen 1823	*annulimana* Pavan and Cunha 1947	9

			antioquia Vilela and Bächli 2000	1
			aureata Wasserman 1982	1
			bromeliae Patterson and Stone 1952	4
			calloptera Freire-Maia and Pavan 1950	4
			canalinea Wheeler 1957	6
			caponei Ratcov and Vilela 2007	1
			cardini Sturtevant 1942	6
			coffeata Vilela and Bächli 1990	3
			dreyfusi Patterson and Stone 1952	6
			flavopilosa Wheeler et al. 1962	6

			guarani Dobzhansky and Pavan 1943	6
			immigrans Sturtevant 1942	1
			mesophragmatica Brncic and Koref-Santibanez 1957	2
			morelia Vilela and Bächli 2004	2
			onycophora Vilela and Bächli 1990	2
			pallidipennis Patterson and Stone 1952	1
			peruensis Ratcov and Vilela 2007	3
			peruviana Throckmorton 1974	1
			polychaeta Sturtevant 1942	1
			repleta Sturtevant 1942	33

			sticta Clayton and Wheeler 1975	1
			tripunctata Sturtevant 1942	42
			virilis Patterson 1941	1
			Not assigned to group	2
		Phloridosa Sturtevant 1942		2
		Siphlodora Patterson and Mainland 1944		1
		Sophophora Sturtevant 1939	*melanogaster* Sturtevant 1927	5
			saltans Sturtevant 1940	12
			willistoni Sturtevant 1940	13
		Not assigned to subgenera		2
	Hirtodrosophila		*hirticornis* (Burla 1956)	4

			magnarcus (Frota-Pessoa 1951)	4
			thoracis (Grimaldi 1987)	2
			Not assigned to group	6
	Mycodrosophila			3
	Neotanygastrella			2
	Scaptodrosophila		*latifasciaeformis* (Burla 1954)	1
			rufifrons (Papp et al. 1999)	1
	Scaptomyza	*Mesoscaptomyza* Hackman 1959	*vittata* Wheeler 1952	2
			Not assigned to group	1
	Zaprionus	*Zaprionus* Coquillett 1901	*armatus* Chassagnard and Tsacas 1993	1
	Zygothrica		*atriangula* Burla 1956	6
			bilineata Grimaldi 1987	1

			candens Burla 1956	1
			dispar Burla 1956	15
			fuscina Grimaldi 1987	2
			hypandriata Grimaldi 1987	3
			orbitalis Grimaldi 1987	1
			virgatalba Grimaldi 1987	1
			vittatifrons Burla 1956	6
			vittimaculosa Grimaldi 1987	2
			Not assigned to group	16
Steganinae	*Amiota*	*Amiota* Loew 1862		1
	Leucophenga	*Leucophenga* Mik 1886		6
	Pseudiastata	*Pseudiastata* Coquillett 1908		2
	Rhinoleucophenga			8

	Stegana	*Ceratostylus* Enderlein 1922		1
		Steganina Wheeler 1960		1

Table 3 – Number of *Drosophila* species and other genera recorded in each Brazilian state.

Region	Brazilian states		*Drosophila*	Other genera
North	Acre	AC	10	1
	Amapá	AP	0	1
	Amazonas	AM	34	5
	Pará	PA	42	24
	Rondônia	RO	1	7
	Roraima	RR	5	1
	Tocantins	TO	2	0
Northeast	Alagoas	AL	0	0
	Bahia	BA	41	6
	Ceará	CE	2	0
	Maranhão	MA	11	3
	Paraíba	PB	11	1
	Pernambuco	PE	7	2
	Piauí	PI	2	2
	Rio Grande do Norte	RN	8	1
	Sergipe	SE	1	0
Center-West	Distrito Federal	DF	44	2
	Goiás	GO	20	1
	Mato Grosso	MT	23	7
	Mato Grosso do Sul	MS	31	4
Southeast	Espirito Santo	ES	16	3
	Minas Gerais	MG	61	3

	Rio de Janeiro	RJ	54	53
	São Paulo	SP	120	57
South	Paraná	PR	42	2
	Rio Grande do Sul	RS	56	5
	Santa Catarina	SC	107	18

Figure 1 – Proportion of recorded species in Brazil for each Drosophilidade genera. Number of species recorded is shown in brackets. The genus *Microdrosophila* are not shown in the figure though Val and Kaneshiro (1988) point that its species were probably non-described species in Brazil.

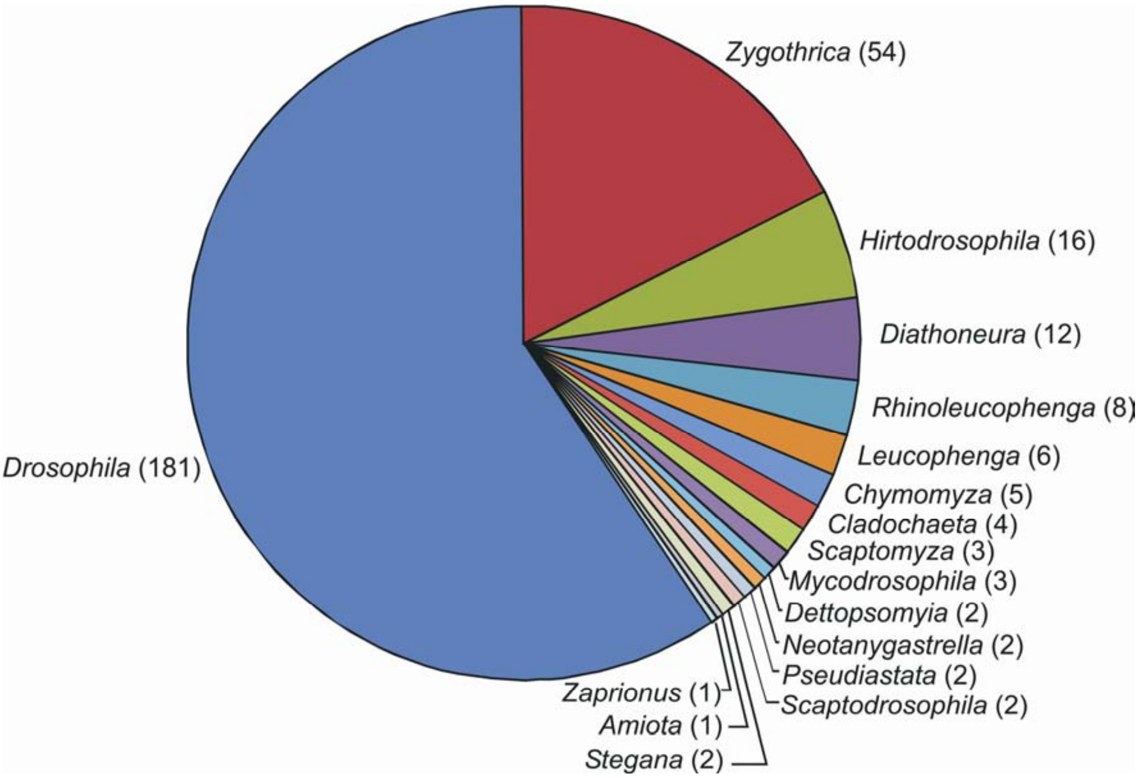
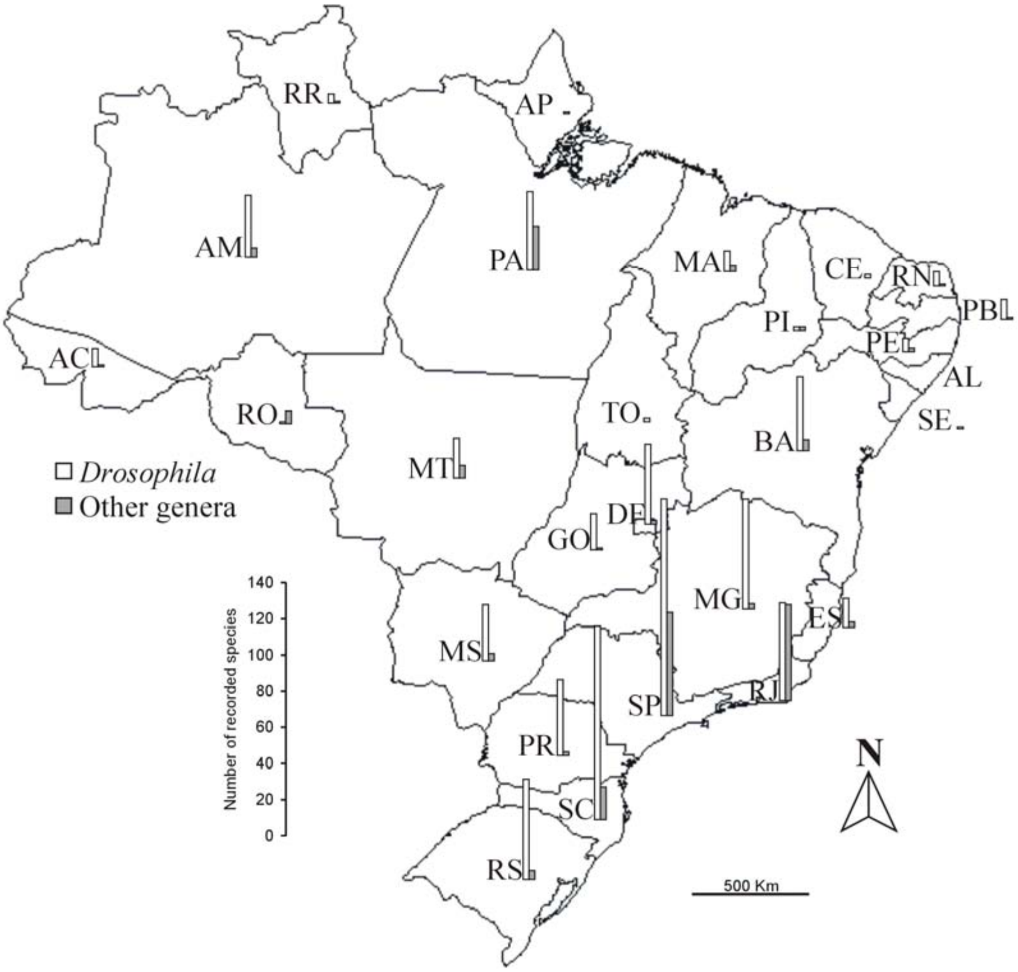


Figure 2 – Number of *Drosophila* species and other genera recorded in each Brazilian state. The code for each state is presented in Table 3.



Appendix I – List of Drosophilidae species occurring in Brazil. The municipality of the type locality is informed, when available. Numbers after each Brazilian state in the geographical distribution show the studies in which records are made. The code for each state is presented in Table 3.

Drosophilidae family

Drosophilinae subfamily

Chymomyza genus

aldrichii group

1. ***Chymomyza bicoloripes*** (Malloch)

Drosophila bicoloripes Malloch 1926:31.

Chymomyza maculipennis Hendel 1936:97.

Type locality: Higuito, San Mateo, Costa Rica.

Geographical distribution: **PA** [1].

2. ***Chymomyza laevilimbata*** Duda

Chymomyza laevilimbata Duda 1927:65.

Type locality: Pichis, Peru.

Geographical distribution: [localities not mentioned] [2, 3].

3. ***Chymomyza mesopecta*** Wheeler

Chymomyza mesopecta Wheeler 1968:435.

Type locality: Lima, Peru.

Geographical distribution: **SC** [4].

procnemis group

4. ***Chymomyza pectinifemur*** Duda

Chymomyza pectinifemur Duda 1927:66.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [5].

5. ***Chymomyza procnemis*** (Williston)

Drosophila procnemis Williston 1896:412.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **MT** [6].

Cladochaeta genus

armata group

6. ***Cladochaeta armata*** (Frota-Pessoa)

Clastopteromyia armata Frota-Pessoa 1947:195.

Type locality: Campos de Jordão, São Paulo, Brazil.

Geographical distribution: **SP** [7, 8]; **RJ** [7]; **SC** [8].

bomplandi group

7. ***Cladochaeta bomplandi*** (Malloch)

Diathoneura bomplandi Malloch 1934:438.

Type locality: Bonpland, Misiones, Argentina.

Geographical distribution: **SP** [7, 8]; **SC** [8, 9].

Not assigned to group

8. ***Cladochaeta minuta*** (Duda)

Diathoneura minuta Duda 1925:182.

Type locality: Buenaventura, Colombia.

Geographical distribution: **RJ** [5, 7].

9. ***Cladochaeta travassosi*** (Frota-Pessoa)

Clastopteromyia travassosi Frota-Pessoa 1947:214.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [7, 8].

Dettopsomyia genus

10. ***Dettopsomyia formosa*** Lamb

Dettopsomyia formosa Lamb 1914:350.

Type locality: Mahe, Seychelles.

Geographical distribution: [localities not mentioned] [3].

11. ***Dettopsomyia nigrovittata*** (Malloch)

Drosophila nigrovittata Malloch 1924:352.

Dettopsomyia argentifrons Okada 1956:55.

Type locality: Sydney, Australia.

Geographical distribution: [localities not mentioned] [3].

Diathoneura genus

Diathoneura subgenus

12. ***Diathoneura albinota*** (Wheeler)

Clastopteromyia albinota Wheeler, 1957:108.

Type locality: Cerro la Campana, Panama.

Geographical distribution: [localities not mentioned] [10].

13. ***Diathoneura bicolor*** (Frota-Pessoa)

Clastopteromyia bicolor Frota-Pessoa 1947:211.

Type locality: Campos de Jordão, São Paulo, Brazil.

Geographical distribution: **SP** [7].

14. ***Diathoneura borgmeieri*** Duda

Diathoneura borgmeieri Duda 1927:92.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [5, 7, 11].

15. ***Diathoneura brasiliensis*** Duda

Diathoneura brasiliensis Duda 1927:93.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [5, 7, 11]; **SC** [9, 12].

16. ***Diathoneura carrerai*** (Frota-Pessoa)

Clastopteromyia carrerai Frota-Pessoa 1947:200.

Type locality: Cantareira, São Paulo, Brazil.

Geographical distribution: **SP** [7, 13, 14].

17. ***Diathoneura cavalcantii*** (Frota-Pessoa)

Clastopteromyia cavalcantii Frota-Pessoa 1947:204.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [7].

18. ***Diathoneura iheringi*** (Frota-Pessoa)

Clastopteromyia iheringi Frota-Pessoa 1947:206.

Type locality: Petrópolis, Rio de Janeiro, Brazil

Geographical distribution: **RJ** [7].

19. ***Diathoneura lopesi*** (Frota-Pessoa)

Clastopteromyia lopesi Frota-Pessoa 1947:213.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [7]; **BA** [15].

20. ***Diathoneura opaca*** (Williston)

Drosophila opaca Williston 1896:411.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **RJ** [7].

21. ***Diathoneura montei*** (Frota-Pessoa)

Clastopteromyia montei Frota-Pessoa 1947:210.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [7, 13].

22. ***Diathoneura pilifrons*** (Frota-Pessoa)

Clastopteromyia pilifrons Frota-Pessoa 1947:208.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [7].

23. ***Diathoneura splendida*** (Williston)

Drosophila splendida Williston 1896:412.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **RJ** [7].

Drosophila genus

Dorsilopha subgenus

busckii group

24. ***Drosophila busckii*** Coquillett

Drosophila busckii Coquillett 1901:18 (as *buskii* lapsus).

Drosophila rubrostriata Becker 1908:155.

Drosophila plurilineata Villeneuve 1911:83.

Type locality: Washington, USA.

Geographical distribution: **BA** [16]; **DF** [17, 18, 19, 20, 21]; **GO** [22]; **MG** [16, 23, 24]; **MS** [17]; **PR** [25]; **RJ** [5, 17]; **RS** [26, 27, 28, 29, 30, 31]; **SC** [9, 12, 17, 32]; **SP** [14, 17, 33, 34].

Drosophila subgenus

annulimana group

25. ***Drosophila annulimana*** Duda

Drosophila annulimana Duda 1927:117

Type locality: Mapiri, Bolivia.

Geographical distribution: **AM** [35]; **MG** [24]; **SC** [9, 12, 32, 36]; **SP** [14, 17, 22, 25, 37, 38, 39].

26. ***Drosophila aragua*** Vilela and Pereira

Drosophila aragua Vilela and Pereira 1982:237.

Type locality: Santa Maria da Serra, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **SP** [33, 38, 39].

27. ***Drosophila araicas*** Pavan and Nacrur

Drosophila araicas Pavan and Nacrur 1950:264.

Type locality: Pirassununga, São Paulo, Brazil.

Geographical distribution: **AM** [35]; **PA** [13]; **SP** [40].

28. ***Drosophila arapuan*** Cunha and Pavan

Drosophila arapuan Cunha and Pavan, in Pavan and Cunha 1947:36.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [41]; **SC** [9]; **SP** [13, 38, 39].

29. ***Drosophila ararama*** Pavan and Cunha

Drosophila ararama Pavan and Cunha 1947:28.

Type locality: Bertioga, São Paulo, Brazil.

Geographical distribution: **BA** [15, 17]; **DF** [20, 21]; **MG** [24]; **MS** [17]; **PA** [38]; **SC** [12, 36]; **SP** [13, 17, 34, 39, 41, 42].

30. ***Drosophila arassari*** Cunha and Frota-Pessoa

Drosophila arassari Cunha and Frota-Pessoa, in Pavan and Cunha 1947:32.

Type locality: Campos de Jordão, São Paulo, Brazil.

Geographical distribution: **MG** [17]; **SC** [9, 12, 32, 36]; **SP** [13, 38, 41].

31. ***Drosophila arauna*** Pavan and Nacrur

Drosophila arauna Pavan and Nacrur 1950:268.

Type locality: Pirassununga, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **SP** [13, 38, 40].

32. ***Drosophila schineri*** Pereira and Vilela

Drosophila schineri Pereira and Vilela 1987:15.

Type locality: Peruíbe, São Paulo, Brazil.

Geographical distribution: **RS** [43]; **SC** [9, 12; 32]; **SP** [38, 44].

33. ***Drosophila tarsata*** Schiner

Drosophila tarsata Schiner 1868:240.

Type locality: Venezuela.

Geographical distribution: **SC** [9, 45].

antioquia group

34. ***Drosophila freiremaiai*** Vilela and Bächli

Drosophila freiremaiai Vilela and Bächli 2000:58.

Type locality: Marko, Amazonas, Brazil.

Geographical distribution: **AM** [46].

aureata group

35. ***Drosophila aureata*** Wheeler

Drosophila aureata Wheeler 1957:83.

Type locality: San Jose, Costa Rica.

Geographical distribution: **MG** [24].

bromeliae group

36. ***Drosophila aguape*** Val and Marques

Drosophila aguape Val and Marques 1996:224.

Type locality: Taiamã, Mato Grosso, Brazil.

Geographical distribution: **MT** [47].

37. ***Drosophila bromeliae*** Sturtevant

Drosophila bromeliae Sturtevant 1921:72.

Type locality: Havana, Cuba.

Geographical distribution: **SP** [48].

38. ***Drosophila bromelioides*** Pavan and Cunha

Drosophila bromelioides Pavan and Cunha 1947:7.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **BA** [15]; **MG** [24]; **RJ** [49]; **RS** [26, 50]; **SC** [9, 12, 32, 50]; **SP** [41].

39. ***Drosophila speciosa*** Silva and Martins

Drosophila speciosa Silva and Martins 2004:435.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **PA** [51].

calloptera group

40. ***Drosophila atrata*** Burla and Pavan

Drosophila atrata Burla and Pavan 1953:307.

Type locality: Pirassununga, São Paulo, Brazil.

Geographical distribution: **BA** [52]; **DF** [20, 21]; **MG** [52]; **PA** [52]; **RJ** [17, 52]; **RS** [26]; **SC** [9, 12, 32, 45, 53]; **SP** [13, 14, 17, 39, 52, 54].

41. ***Drosophila calloptera*** Schiner

Drosophila calloptera Schiner 1868:239.

Paramycodrosophila tephritoptera Hendel 1936:95.

Type locality: Venezuela.

Geographical distribution: **AC** [52]; **AM** [52]; **PA** [1, 52]; **PE** [52]; **RJ** [5, 52]; **SC** [9]; **SP** [52, 55, 56].

42. ***Drosophila quadrum*** (Wiedemann)

Trypeta quadrum Wiedemann 1830:507.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **SC** [9, 12, 32, 36]; **SP** [14, 17, 39, 52]; **RS** [26, 52].

43. ***Drosophila schildi*** Malloch

Drosophila schildi Malloch 1924:10.

Paramycodrosophila poeciloptera Duda 1925:226.

Drosophila poecila Burla and Pavan 1953:311.

Type locality: Higuito, San Mateo, Costa Rica.

Geographical distribution: **DF** [20, 21]; **RJ** [5]; **SC** [9]; **SP** [39, 52].

canalinea group

44. ***Drosophila albomarginata*** Duda

Drosophila albomarginata Duda 1927:173.

Type locality: Mapiri, Bolivia.

Geographical distribution: **SP** [39].

45. ***Drosophila canalinea*** Patterson and Mainland

Drosophila canalinea Patterson and Mainland 1944:50.

Type locality: San Juan, Veracruz, Mexico.

Geographical distribution: **AM** [35]; **CE** [57]; **GO** [58]; **PA** [58]; **SP** [34, 39, 58].

46. ***Drosophila davidgrimaldii*** Vilela and Bächli

Drosophila davidgrimaldii Vilela and Bächli 1990:58.

Type locality: Suiza, Turrialba, Costa Rica.

Geographical distribution: **PA** [11].

47. ***Drosophila hendeli*** Vilela and Bächli

Drosophila hendeli Vilela and Bächli 1990:59.

Type locality: Santarém, Pará, Brazil.

Geographical distribution: **PA** [11].

48. ***Drosophila piratininga*** Ratcov and Vilela

Drosophila piratininga Ratcov and Vilela 2007:337.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **PR** [59], **SP** [59].

49. ***Drosophila sampa*** Ratcov and Vilela

Drosophila sampa Ratcov and Vilela 2007:339.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [59].

caponei group

50. ***Drosophila caponei*** Pavan and Cunha

Drosophila caponei Pavan and Cunha 1947:4.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **MG** [23, 24]; **SC** [9, 12, 32]; **SP** [13, 22, 39, 41, 60].

cardini group

cardini subgroup

51. ***Drosophila cardini*** Sturtevant

Drosophila cardini Sturtevant 1916:336.

Type locality: Havana, Cuba.

Geographical distribution: **AM** [35, 61, 62]; **BA** [16, 63]; **DF** [18, 19, 20, 21, 63]; **MG** [16, 24, 23, 63]; **MS** [63]; **PA** [64]; **PB** [63]; **PR** [25, 63]; **RJ** [43, 63, 64]; **RN** [63]; **RS** [28, 63]; **SC** [12, 32, 63]; **SP** [14, 25, 39, 63, 64].

52. ***Drosophila cardinoides*** Dobzhansky and Pavan

Drosophila cardinoides Dobzhansky and Pavan 1943:21.

Type locality: Iporanga, São Paulo, Brazil.

Geographical distribution: **AC** [22]; **AM** [22, 35, 48, 64]; **BA** [22, 63]; **DF** [19, 20, 21, 63]; **ES** [63]; **GO** [22]; **MA** [22]; **MG** [23, 24, 56]; **MS** [63]; **PA** [22, 58, 64, 65]; **PR** [22, 63]; **RJ** [37, 63]; **RO** [22]; **RR** [22]; **RS** [22, 26, 27, 28, 29, 30, 31, 43, 63, 65, 66, 67]; **SC** [9, 12, 32, 36, 45, 63]; **SP** [13, 14, 22, 37, 58, 63, 64, 68].

53. ***Drosophila neocardini*** Streisinger

Drosophila neocardini Streisinger 1946:111.

Type locality: Teffé, Amazonas, Brazil.

Geographical distribution: **AC** [22]; **AM** [13, 22, 57, 69]; **BA** [22, 63]; **DF** [20, 21]; **MG** [23, 24, 56]; **MS** [63]; **PR** [63]; **RJ** [64, 65]; **RS** [30, 31, 63]; **SC** [9, 12, 32, 36, 45, 53, 63]; **SP**: [14, 22, 39, 63, 64, 70].

54. ***Drosophila neomorpha*** Heed and Wheeler

Drosophila neomorpha Heed and Wheeler 1957:33.

Type locality: Arima Valley, Trinidad.

Geographical distribution: **MT** [53]; **PA** [53]; **SC** [53].

55. ***Drosophila parthenogenetica*** Stalker

Drosophila parthenogenetica Stalker 1953:347.

Type locality: Atlixco, Puebla, Mexico.

Geographical distribution: **AM** [53]; **MT** [53]; **PA** [53]; **SC** [53].

56. ***Drosophila polymorpha*** Dobzhansky and Pavan

Drosophila polymorpha Dobzhansky and Pavan 1943:19.

Type locality: Bertioga, São Paulo, Brazil.

Geographical distribution: **AC** [22]; **AM** [35]; **BA** [15, 22, 63]; **DF** [18, 19, 20, 21, 63]; **ES** [63]; **GO** [71]; **MA** [22, 58]; **MG** [16, 24, 37, 56, 63]; **MS** [63]; **MT** [22]; **PA** [22, 56, 58]; **PR** [22, 25, 58, 63]; **RJ** [22, 37, 63]; **RR** [22]; **RS** [22, 26, 27, [28, 29, 30, 31, 37, 43, 63, 65, 67, 72]; **SC** [9, 12, 32, 36, 45, 53, 63, 73]; **SP** [13, 14, 22, 25, 33, 34, 37, 39, 55, 56, 58, 60, 63].

coffeata group

57. ***Drosophila coffeata*** Williston

Drosophila coffeata Williston 1896:409.

Drosophila flavolineata Duda 1927:157.

Drosophila umbripennis Hendel 1936:99.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **PA** [1, 11, 74]; **SC** [32]; **SP** [57].

58. ***Drosophila fuscolineata*** Duda

Drosophila fuscolineata Duda 1925:213.

Drosophila castanea Patterson and Mainland 1944:51.

Drosophila fumosa Pavan and Cunha 1947:31.

Type locality: Suiza, Turrialba, Costa Rica.

Geographical distribution: **DF** [20, 21]; **GO** [58]; **MG** [23, 24]; **PA** [58]; **SC** [9, 12, 32]; **SP** [22, 34, 39, 41, 58].

59. ***Drosophila pagliolii*** Cordeiro

Drosophila pagliolii Cordeiro 1963:401.

Type locality: Santa Maria, Rio Grande do Sul, Brazil.

Geographical distribution: **DF** [75]; **RS** [75].

dreyfusi group

60. ***Drosophila briegeri*** Pavan and Breuer

Drosophila briegeri Pavan and Breuer 1954:459.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **BA** [76]; **SC** [9, 12]; **SP** [13, 39, 77, 78].

61. ***Drosophila camargoi*** Dobzhansky and Pavan

Drosophila camargoi Dobzhansky and Pavan, in Pavan 1950:6.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AC** [22, 74]; **AM** [35, 74]; **MA** [74]; **PA** [13, 22, 56, 58, 74, 77].

62. ***Drosophila decemseriata*** Hendel

Drosophila decemseriata Hendel 1936:98.

Type locality: Santarém, Pará, Brazil.

Geographical distribution: **PA** [1, 11].

63. ***Drosophila dreyfusi*** Dobzhansky and Pavan

Drosophila dreyfusi Dobzhansky and Pavan 1943:61.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **MG** [24]; **SC** [9, 12, 36]; **SP** [13, 14, 17, 37, 39, 48, 77].

64. ***Drosophila krugi*** Pavan and Breuer

Drosophila krugi Pavan and Breuer 1954:462.

Type locality: Cantareira, São Paulo, Brazil.

Geographical distribution: **SP** [13, 14, 39, 77, 78].

65. ***Drosophila wingei*** Cordeiro

Drosophila wingei Cordeiro 1964:1.

Type locality: Torres, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [76].

flavopilosa group

66. ***Drosophila cestri*** Brncic

Drosophila cestri Brncic 1978:651.

Type locality: Sapucaia, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [13, 43, 79, 80]; **SP** [81, 82, 83].

67. ***Drosophila corderoi*** Brncic

Drosophila cordeiroi Brncic 1978:649.

Type locality: Porto Alegre, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [13, 79]; **SP** [81, 82, 83].

flavopilosa subgroup

68. ***Drosophila flavopilosa*** Frey

Drosophila flavopilosa Frey 1919:14.

Drosophila dentata Duda 1927:201 (pre-occupied).

Type locality: Valparaiso, Chile.

Geographical distribution: **RS** [79].

69. ***Drosophila hollisae*** Vilela and Pereira

Drosophila hollisae Vilela and Pereira 1992:478.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [82, 83].

nesiota subgroup

70. ***Drosophila incompta*** Wheeler and Takada

Drosophila incompta Wheeler and Takada, in Wheeler et al. 1962:408.

Type locality: Almirante, Bocas del Toro, Panama.

Geographical distribution: **RS**: [13, 43, 79, 80, 84]; **SP** [81, 82, 83].

71. ***Drosophila mariaehelenae*** Vilela

Drosophila mariaehelenae Vilela 1984:64.

Type locality: Santa Izabel, São Paulo, Brazil.

Geographical distribution: **SP** [81, 82, 83].

guarani group

72. ***Drosophila alexandrei*** Cordeiro

Drosophila alexandrei Cordeiro 1951:1.

Type locality: Emboaba, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [85].

guarani subgroup

73. ***Drosophila guaru*** Dobzhansky and Pavan

Drosophila guaru Dobzhansky and Pavan 1943:37.

Type locality: Amalia, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **SC** [9]; **SP** [11, 13, 25, 34, 37, 39].

74. ***Drosophila ornatifrons*** Duda

Drosophila ornatifrons Duda 1927:162.

Drosophila guarani Dobzhansky and Pavan 1943:36.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **AM** [35]; **BA** [16]; **DF** [18, 20, 21]; **MG** [23, 24]; **PR** [25]; **RJ** [5, 11, 37]; **RS** [26, 28, 29, 72]; **SC** [9, 12, 32, 36]; **SP** [11, 13, 14, 17, 25, 37, 39, 42, 55, 70].

guaramunu subgroup

75. ***Drosophila griseolineata*** Duda

Drosophila griseolineata Duda 1927:161.

Type locality: Mapiri, Bolivia.

Geographical distribution: **BA** [17]; **ES** [17]; **MG** [16, 24, 56]; **PR** [17, 22]; **RJ** [11, 13, 17, 37]; **RS** [17, 26, 27, 28, 29, 30, 31, 43, 66, 72]; **SC** [9, 12, 17, 36, 45, 53]; **SP** [14, 17, 22, 37, 39, 55, 58, 70].

76. ***Drosophila guaraja*** King

Drosophila guaraja King 1947:48.

Drosophila pulla Pavan and Cunha 1947:10.

Type locality: Campos de Jordão, São Paulo, Brazil.

Geographical distribution: **MG** [17, 23, 24]; **PR** [25]; **SC** [9, 12, 32]; **SP** [11, 13, 14, 41, 86].

77. ***Drosophila maculifrons*** Duda

Drosophila maculifrons Duda 1927:122.

Drosophila guaramunu Dobzhansky and Pavan 1943:39.

Type locality: Rosalina, Peru.

Geographical distribution: **DF** [17, 18, 20, 21]; **ES** [17]; **MG** [23, 24]; **MT** [22, 58]; **MS** [17]; **PR** [17, 22, 25, 58]; **RJ** [37]; **RS** [17, 22, 26, 27, 28, 29, 43, 66, 67, 72]; **SC** [9, 12, 32, 36]; **SP** [11, 13, 14, 17, 22, 25, 37, 39, 55, 56, 58, 60].

immigrans group

immigrans subgroup

78. ***Drosophila immigrans*** Sturtevant

Drosophila immigrans Sturtevant 1921:83.

Drosophila brouni Hutton 1901:91.

Drosophila cilifemur Villeneuve 1923:28.

Drosophila flexipilosa Pipkin 1964:238.

Type locality: New York, New York, USA.

Geographical distribution: **BA** [16]; **DF** [17, 19, 20]; **MG** [23, 24]; **MT** [58]; **MS** [17]; **PE** [17, 22]; **PR** [25]; **RJ** [17]; **RS** [26, 27, 28, 29, 31, 43, 67, 72]; **SC** [9, 12, 32, 36, 45]; **SP** [14, 17, 22, 25, 34, 39, 58, 60].

mesophragmatica group

79. ***Drosophila gaucha*** Jaeger and Salzano

Drosophila gaucha Jaeger and Salzano 1953:205.

Type locality: Muitos Capões, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [26, 27, 28, 29, 43, 87, 88, 89]; **SC** [12]; **SP** [88, 89].

80. ***Drosophila mesophragmatica*** Duda

Drosophila mesophragmatica Duda 1927:205.

Drosophila andina Dobzhansky and Pavan 1943:59.

Type locality: Cuzco, Peru.

Geographical distribution: **SC** [9]; **SP** [41].

morelia group

81. ***Drosophila carioca*** Vilela and Bächli

Drosophila carioca Vilela and Bächli 2004:48.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [90].

82. ***Drosophila fluminensis*** Vilela and Bächli

Drosophila fluminensis Vilela and Bächli 2004:54.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [90].

onychophora group

83. ***Drosophila colmenares*** Hunter

Drosophila colmenares Hunter 1988:305.

Type locality: Bogotá, Colombia.

Geographical distribution: **SC** [9].

84. ***Drosophila freilejoni*** Hunter

Drosophila freilejoni Hunter 1979:373.

Type locality: Bogotá, Colombia.

Geographical distribution: **SC** [9].

pallidipennis group

85. ***Drosophila pallidipennis*** Dobzhansky and Pavan

Drosophila pallidipennis Dobzhansky and Pavan 1943:32.

Type locality: Iporanga, São Paulo, Brazil.

Geographical distribution: **BA** [16, 17]; **DF** [20, 21]; **MG** [16, 23, 24]; **MT** [58]; **MS** [17]; **PA** [58]; **PR** [17, 25]; **RJ** [17, 91]; **RS** [17, 30, 31, 92]; **SC** [9, 12, 17, 32, 36, 45]; **SP** [11, 13, 14, 17, 22, 25, 34, 37, 39, 42, 48, 58, 68].

peruensis group

86. ***Drosophila atalaia*** Vilela and Sene

Drosophila atalaia Vilela and Sene 1982:343.

Type locality: Arraial do Cabo, Rio de Janeiro, Brazil.

Geographical distribution: **ES** [93]; **MS** [93]; **RJ** [93].

87. ***Drosophila boraceia*** Vilela and Val

Drosophila boraceia Vilela and Val 2004:46.

Type locality: Salesópolis, São Paulo, Brazil.

Geographical distribution: **SP** [94].

88. ***Drosophila pauliceia*** Ratcov & Vilela

Drosophila pauliceia Ratcov & Vilela 2007:305.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SC**[12]; **SP**[95].

peruviana group

89. ***Drosophila peruviana*** Duda

Drosophila peruviana Duda 1927:204.

Type locality: Urubamba, Peru.

Geographical distribution: **PA** [22, 58, 74].

polychaeta group

90. ***Drosophila polychaeta*** Patterson and Wheeler

Drosophila polychaeta Patterson and Wheeler 1942:102.

Drosophila pattersoni Hardy 1952:470.

Drosophila baole Burla 1954:187.

Drosophila asper Lin and Tseng 1971:69.

Type locality: Galveston, Texas, USA.

Geographical distribution: [localities not mentioned] [22].

repleta group

fasciola subgroup

91. ***Drosophila carolinae*** Vilela

Drosophila carolinae Vilela 1983:5.

Type locality: Salesópolis, São Paulo, Brazil.

Geographical distribution: **PR** [25, 96, 97]; **SC** [12, 98]; **SP** [14, 96, 99].

92. ***Drosophila coroica*** Wasserman

Drosophila coroica Wasserman 1962:125.

Type locality: Coroico, La Paz, Bolivia.

Geographical distribution: **MS** [99]; **PR** [25, 97, 99]; **SP** [25, 33, 34, 97, 100].

93. ***Drosophila ellisoni*** Vilela

Drosophila ellisoni Vilela 1983:7.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AM** [34, 96]; **PA** [96]; **SC** [96, 98]; **SP** [97, 100].

94. ***Drosophila fascioloides*** Dobzhansky and Pavan

Drosophila fascioloides Dobzhansky and Pavan 1943:42.

Type locality: Bertioga, São Paulo, Brazil.

Geographical distribution: **PA**[101]; **PR**[25, 96]; **RJ**[97, 100]; **SC**[9, 12, 96, 98]; **SP**[14, 22, 25, 37, 39, 96, 97, 99].

95. ***Drosophila ivai*** Vilela

Drosophila ivai Vilela 1983:14.

Type locality: Juçara, Paraná, Brazil.

Geographical distribution: **MS**[96]; **PR**[96]; **SP**[39].

96. ***Drosophila mapiriensis*** Vilela and Bächli

Drosophila mapiriensis Vilela and Bächli 1990:93.

Type locality: Mapiri, Bolivia.

Geographical distribution: **SC**[12, 98].

97. ***Drosophila moju*** Pavan

Drosophila moju Pavan 1950:19.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AM**[35]; **PA**[22, 74, 101]; **SC**[9].

98. ***Drosophila mojuoides*** Wasserman

Drosophila mojuoides Wasserman 1962:121.

Type locality: Arima Valley, Trinidad.

Geographical distribution: **PA**[96].

99. ***Drosophila onca*** Dobzhansky and Pavan

Drosophila onca Dobzhansky and Pavan 1943:40.

Type locality: Iporanga, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **ES** [99]; **MG** [24]; **PR** [25, 96, 97, 99, 100]; **RS** [97]; **SC** [9, 12, 32, 45, 96, 98]; **RJ** [99]; **SP** [37, 39, 60, 96, 99, 102].

100. ***Drosophila papei*** Bächli and Vilela

Drosophila papei Bächli and Vilela 2002:235.

Type locality: Aragua, Venezuela.

Geographical distribution: **SC** [12, 98].

101. ***Drosophila pictilis*** Wasserman

Drosophila pictilis Wasserman 1962:125.

Type locality: La Libertad, El Salvador.

Geographical distribution: **SC** [32]; **SP** [39].

102. ***Drosophila pictura*** Wasserman

Drosophila pictura Wasserman 1962:121.

Type locality: Saint George, Trinidad.

Geographical distribution: **SC** [98]; **SP** [39].

103. ***Drosophila querubimae*** Vilela

Drosophila querubimae Vilela 1983:24.

Type locality: Guaratuba, São Paulo, Brazil.

Geographical distribution: **SC** [12, 98]; **SP** [39, 96, 99].

104. *Drosophila rosinae* Vilela

Drosophila rosinae Vilela 1983:25.

Type locality: Peruíbe, São Paulo, Brazil.

Geographical distribution: **BA** [16, 96, 97, 99, 100]; **ES** [96]; **MG** [24]; **RJ** [96]; **RN** [57]; **SP** [96, 99].

105. *Drosophila senei* Vilela

Drosophila senei Vilela 1983:27.

Type locality: Ibiúna, São Paulo, Brazil.

Geographical distribution: **SC** [9]; **SP** [39, 96].

hydei subgroup

106. *Drosophila hydei* Sturtevant

Drosophila hydei Sturtevant 1921:101.

Drosophila marmoria Hutton 1901:91 (suppressed).

Drosophila setosa Dobzhansky and Pavan 1943:46.

Type locality: Lakeland, Florida, USA.

Geographical distribution: **BA** [15, 16, 96, 99]; **DF** [18, 19, 20, 21]; **ES** [96]; **MG** [16, 23, 24, 96, 99]; **MS** [96, 99]; **PB** [96, 99]; **RS** [30, 31, 43]; **SC** [9, 12, 32, 45, 98]; **SP** [34, 37, 96, 99].

mercatorum subgroup

107. *Drosophila mercatorum* Patterson and Wheeler

Drosophila mercatorum Patterson and Wheeler 1942:93.

Drosophila carinata Grimshaw 1901:70 (suppressed).

Type locality: Santa Barbara, California, USA.

Geographical distribution: **AM**[35]; **BA**[16, 96, 99]; **DF**[18, 19, 20, 21, 96, 99]; **ES**[96, 99]; **GO**[96]; **MG**[16, 23, 24, 96, 99]; **MS**[47, 96, 99]; **PB**[96, 99]; **PR**[25, 96, 99]; **RJ**[57, 96, 99, 103]; **RS**[27, 28, 29, 30, 31, 43, 67, 72, 92, 99, 102]; **SC**[9, 12, 32, 36, 45, 96, 98, 99]; **SP**[14, 22, 25, 33, 34, 39, 96, 99, 100].

108. ***Drosophila paranaensis*** Barros

Drosophila paranaensis Barros 1950:266.

Drosophila pseudomercatorum Magalhães and Malogolowkin-Cohen 1974:363.

Drosophila paramercatorum Magalhães and Malogolowkin-Cohen 1974:365.

Type locality: Porto Capitão Heitor, Paraná, Brazil.

Geographical distribution: **AM**[96]; **BA**[96, 99]; **DF**[19, 20, 21, 96, 99]; **GO**[96]; **MG**[23, 24]; **MS**[96, 99, 104]; **MT**[96]; **PR**[25, 96, 99]; **SC**[96]; **SP**[25, 33, 34, 39, 96, 99].

mulleri subgroup

109. ***Drosophila aldrichi*** Patterson

Drosophila aldrichi Patterson, in Patterson and Crow 1940:251.

Type locality: Austin, Texas, USA.

Geographical distribution: **AM**[96]; **MS**[96]; **PR**[96, 99].

110. ***Drosophila antonietae*** Tidon-Sklorz and Sene

Drosophila antonietae Tidon-Sklorz and Sene 2001:142.

Type locality: Jundiaí, São Paulo, Brazil.

Geographical distribution: **MS**[105]; **PR**[25, 105, 106]; **RS**[105, 106]; **SP**[25, 34, 105, 106, 107].

111. ***Drosophila borborema*** Vilela and Sene

Drosophila borborema Vilela and Sene 1977:296.

Type locality: Milagres, Bahia, Brazil.

Geographical distribution: **BA** [16, 96, 99, 102, 107, 108, 109]; **MG** [16]; **PE** [96]; **PB** [96, 99]; **RN** [96, 99].

112. ***Drosophila buzzatii*** Patterson and Wheeler

Drosophila buzzatii Patterson and Wheeler 1942:97.

Drosophila tigrina Buzzati-Traverso 1943:44.

Drosophila versicolor Mather 1955:573.

Type locality: Cordoba, Argentina.

Geographical distribution: **BA** [16, 96, 99, 102]; **MG** [16, 23, 24, 96, 102, 109]; **MS** [57, 96, 99]; **PB** [96, 99]; **PE** [96]; **PR** [25, 96, 99]; **RS** [27, 28, 29, 66, 96, 99, 102]; **SC** [96]; **SP** [25, 34, 38, 107, 109].

113. ***Drosophila gouveai*** Tidon-Sklorz and Sene

Drosophila gouveai Tidon-Sklorz and Sene 2001:144.

Type locality: Altinópolis, São Paulo, Brazil.

Geographical distribution: **BA** [105, 107]; **DF** [20]; **GO** [105]; **MG** [105]; **MS** [105]; **PE** [105]; **SP** [105].

114. ***Drosophila meridionalis*** Wasserman

Drosophila meridionalis Wasserman 1962:88.

Type locality: Angra dos Reis, Rio de Janeiro, Brazil.

Geographical distribution: **BA** [96, 99]; **ES** [96]; **MG** [23, 96]; **MS** [96, 99]; **PB** [96, 99]; **PR** [25, 96, 99]; **RJ** [96, 99, 110]; **RS** [96, 99, 102, 111]; **SC** [9, 12, 96, 98, 99, 102]; **SP** [25, 96, 99, 102, 111].

115. ***Drosophila nigricruria*** Patterson and Mainland

Drosophila nigricruria Patterson and Mainland, in Patterson 1943:136.

Drosophila hoeckeri Brncic 1957:76.

Type locality: El Mediñena, Jalisco, Mexico.

Geographical distribution: **BA** [22, 96]; **DF** [20, 21]; **GO** [22]; **MG** [16, 23, 24, 96]; **MS** [58]; **PR** [25]; **SC** [12, 98]; **SP** [22, 33, 34, 39, 58, 96].

116. ***Drosophila serido*** Vilela and Sene

Drosophila serido Vilela and Sene 1977:295.

Type locality: Milagres, Bahia, Brazil.

Geographical distribution: Due to the complex taxonomic history of the species, and as it initially was mistakenly considered to be *D. antonietae*, *D. gouveai* or *D. seriema*, its geographic distribution was restricted to that mentioned in the review of the cluster *buzatti* by Manfrin and Sene[112], which includes the states of **BA**; **CE**; **ES**; **MG**; **PB**; **PE**; **PR**; **RJ**; **RN**; **SC**; **SE**; **SP.**

117. ***Drosophila seriema*** Tidon-Sklorz and Sene

Drosophila seriema Tidon-Sklorz and Sene 1995:139.

Type locality: Grão Mogol, Minas Gerais, Brazil.

Geographical distribution: **BA** [107, 109, 113, 114]; **MG** [16, 24, 109, 113, 114].

repleta subgroup

118. ***Drosophila eleonorae*** Tosi, Martins, Vilela and Pereira

Drosophila eleonorae Tosi, Martins, Vilela and Pereira 1990:21.

Type locality: Altamira, Pará, Brazil.

Geographical distribution: **GO** [115]; **MT** [115]; **PA** [115]; **SP** [115].

119. ***Drosophila fulvimacula*** Patterson and Mainland

Drosophila fulvimacula Patterson and Mainland 1944:42.

Type locality: Jalapa, Veracruz, Mexico.

Geographical distribution: **AM** [35, 56]; **PA** [116].

120. ***Drosophila limensis*** Pavan and Patterson

Drosophila limensis Pavan and Patterson, in Pavan and Cunha 1947:26.

Type locality: Lima, Lima, Peru.

Geographical distribution: **SC** [12, 98].

121. ***Drosophila pseudorepleta*** Vilela and Bächli

Drosophila pseudorepleta Vilela and Bächli 1990:95.

Type locality: Hohenau, Paraguay.

Geographical distribution: **MG** [23, 24].

122. ***Drosophila repleta*** Wollaston

Drosophila repleta Wollaston 1858:117.

Drosophila pygmaea Duda 1927:125 (pre-occupied, as *repleta* var. *pygmaea*).

Drosophila punctulata Loew 1862:232.

Drosophila punctata Johnson 1913:202 (lapsus).

Drosophila nigropunctata van der Wulp, 1892:216.

Drosophila melanopalpa Patterson and Wheeler 1942:77.

Drosophila maculiventris van der Wulp 1897:142.

Drosophila brunneipalpa Dobzhansky and Pavan 1943:53.

Drosophila betari Dobzhansky and Pavan 1943:48.

Drosophila austrorepleta Dobzhansky and Pavan 1943:50.

Drosophila adspersa Mik 1886:328.

Type locality: Funchal, Madeira Island.

Geographical distribution: **AM**[35]; **BA**[96, 99]; **DF**[20, 99]; **GO**[96]; **MG**[24]; **MS**[96, 99]; **MT**[47, 96]; **PR**[99]; **RJ**[96]; **SC**[9, 12, 32, 96, 98]; **SP**[37, 39, 96].

123. ***Drosophila zottii*** Vilela

Drosophila zottii Vilela 1983:92.

Type locality: Santa Izabel, São Paulo, Brazil.

Geographical distribution: **MG**[24]; **RS**[28, 29, 30, 31, 43, 96]; **SC**[9, 32, 45, 98]; **SP**[96].

sticta group

124. ***Drosophila sticta*** Wheeler

Drosophila sticta Wheeler 1957:96.

Type locality: Lancetilla, Honduras.

Geographical distribution: **SP**[39, 83].

tripunctata group

i subgroup

125. ***Drosophila mediocris*** Frota-Pessoa

Drosophila mediocris Frota-Pessoa 1954:275.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ**[117]; **SP**[117].

126. ***Drosophila nappae*** Vilela, Valente and Basso-da-Silva

Drosophila nappae Vilela, Valente and Basso-da-Silva 2004:233.

Type locality: Porto Alegre, Rio Grande do Sul, Brazil.

Geographical distribution: **MG** [53]; **RJ** [53, 117]; **RS** [27, 28, 29, 30, 31, 43, 53, 72]; **SC** [9, 12, 36, 53, 118]; **SP** [14, 22, 39, 53, 70, 117].

127. ***Drosophila neoguaramunu*** Frydenberg

Drosophila neoguaramunu Frydenberg 1956:57.

Type locality: Tingo Maria, Peru.

Geographical distribution: **DF** [20]; **SC** [9 (mentioned as *D. angustibucca*), 12, 118]; **SP** [39].

128. ***Drosophila platitarsus*** Frota-Pessoa

Drosophila platitarsus Frota-Pessoa 1954:276.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [13, 117]; **SC** [9, 45]; **SP** [13, 117].

129. ***Drosophila setula*** Heed and Wheeler

Drosophila setula Heed and Wheeler 1957:18.

Type locality: Fusagasuga, Colombia.

Geographical distribution: **SC** [9, 12, 98, 118]; **SP** [14, 39].

ii subgroup

130. ***Drosophila bodemannae*** Pipkin and Heed

Drosophila bodemannae Pipkin and Heed 1964:257.

Type locality: Cerro Campana, Panama, Panama.

Geographical distribution: **SC**[9].

131. ***Drosophila cuaso*** Bächli, Vilela and Ratcov

Drosophila cuaso Bächli, Vilela and Ratcov 2000:80.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SC**[12, 32, 118]; **SP**[39, 70, 119].

132. ***Drosophila medioimpressa*** Frota-Pessoa

Drosophila medioimpressa Frota-Pessoa 1954:300.

Type locality: Montes Claros, Minas Gerais, Brazil.

Geographical distribution: **DF**[20]; **MG**[13, 24, 117]; **SC**[9, 12, 118]; **SP**[14, 39].

133. ***Drosophila mediopunctata*** Dobzhansky and Pavan

Drosophila mediopunctata Dobzhansky and Pavan 1943:26.

Type locality: Itanhaém, São Paulo, Brazil.

Geographical distribution: **BA**[15, 16]; **DF**[20, 21]; **MG**[23, 24, 120, 121]; **PR**[25, 117, 123]; **RJ**[120, 122, 124]; **RS**[28, 29, 30, 31, 43, 66, 67, 72, 117, 120, 121, 124]; **SC**[9, 12, 32, 36, 45, 118]; **SP**[13, 14, 25, 34, 37, 39, 57, 68, 70, 117, 120, 124, 125, 126].

134. ***Drosophila mediosignata*** Dobzhansky and Pavan

Drosophila mediosignata Dobzhansky and Pavan 1943:24.

Type locality: Iporanga, São Paulo, Brazil.

Geographical distribution: **RJ**[37]; **RS**[30, 31, 43, 72]; **SC**[9]; **SP**[11, 13, 37, 39, 55, 119].

135. ***Drosophila morena*** Frota-Pessoa

Drosophila morena Frota-Pessoa 1954:283.

Type locality: Feliz, Rio Grande do Sul, Brazil.

Geographical distribution: **RS**[117].

136. ***Drosophila paraguayensis*** Duda

Drosophila paraguayensis Duda 1927:185.

Drosophila medionotata Frota-Pessoa 1954:288.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **DF**[20, 21]; **MG**[13, 24, 117, 119]; **RJ**[5, 11, 13, 117, 119]; **RS**[29, 30, 31]; **SC**[9, 12, 32, 36, 45, 118]; **SP**[11, 13, 14, 70, 117, 119].

137. ***Drosophila prosimilis*** Duda

Drosophila prosimilis Duda 1927:194 (*nomen dubium* sensu Bächli et al. 2000).

Type locality: Pichis, Peru.

Geographical distribution: **RJ**[37, 117]; **SP**[37].

138. ***Drosophila roehrae*** Pipkin and Heed

Drosophila roehrae Pipkin and Heed 1964:270.

Type locality: Cerro Campana, Panama.

Geographical distribution: **SC**[9, 12, 32, 118]; **SP**[39].

139. ***Drosophila unipunctata*** Patterson and Mainland

Drosophila unipunctata Patterson and Mainland, in Patterson 1943:182.

Type locality: Tamazunchale, San Luis Potosi, Mexico.

Geographical distribution: **MG**[24]; **SC**[9, 118].

iii subgroup

140. ***Drosophila addisoni*** Pavan

Drosophila addisoni Pavan 1950:4.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AM**[22]; **PA**[13, 22, 74].

141. ***Drosophila bandeirantorum*** Dobzhansky and Pavan

Drosophila bandeirantorum Dobzhansky and Pavan 1943:30.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **BA**[17]; **DF**[17, 20, 21]; **MG**[23, 24]; **PR**[17, 22, 25]; **RJ**[17]; **RS**[22, 27, 28, 29, 30, 31, 72, 92]; **SC**[9, 12, 32, 36, 45, 118]; **SP**[13, 14, 17, 22, 25, 37, 39, 48, 55, 58, 70].

142. ***Drosophila bifilum*** Frota-Pessoa

Drosophila bifilum Frota-Pessoa 1954:284.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **DF**[20]; **MG**[13, 24, 117]; **SC**[118]; **SP**[13, 39, 117].

143. ***Drosophila bipunctata*** Patterson and Mainland

Drosophila bipunctata Patterson and Mainland, in Patterson 1943:194.

Type locality: Michoacan, Mexico.

Geographical distribution: **SC**[118].

144. ***Drosophila curvapex*** Frota-Pessoa

Drosophila curvapex Frota-Pessoa 1954:296.

Type locality: Feliz, Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [13, 117]; **SP** [127].

145. ***Drosophila divisa*** Duda

Drosophila divisa Duda 1927:187.

Drosophila diversa Patterson and Wheeler 1949:220 (lapsus).

Type locality: Mapiri, Bolivia.

Geographical distribution: **SC** [9].

146. ***Drosophila fairchildi*** Pipkin and Heed

Drosophila fairchildi Pipkin and Heed 1964:269.

Type locality: El Volcan, Chiriqui, Panama.

Geographical distribution: **SC** [9].

147. ***Drosophila fragilis*** Wheeler

Drosophila fragilis Wheeler 1949:191.

Type locality: Atlixco, Puebla, Mexico.

Geographical distribution: **SC** [9, 45]; **SP** [83].

148. ***Drosophila frotapessoai*** Vilela and Bächli

Drosophila frotapessoai Vilela and Bächli 1990:99.

Type locality: Umahuankilia, Peru.

Geographical distribution: **SP** [39].

149. ***Drosophila mediopicta*** Frota-Pessoa

Drosophila mediopicta Frota-Pessoa 1954:290.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **MG** [24]; **RJ** [117]; **RS** [29, 30, 31, 43, 72]; **SC** [9, 12, 32, 36, 118]; **SP** [13, 14, 39, 70, 117].

150. ***Drosophila mediopictoides*** Heed and Wheeler

Drosophila mediopictoides Heed and Wheeler 1957:24.

Type locality: Turrialba, Costa Rica.

Geographical distribution: **SC** [9].

151. ***Drosophila mediostriata*** Duda

Drosophila mediostriata Duda 1925:223.

Drosophila crocina Patterson and Mainland 1944:34.

Drosophila campestris Burla, in Pavan 1950:9.

Type locality: Suiza, Turrialba, Costa Rica.

Geographical distribution: **AC** [22]; **AM** [22]; **BA** [17, 22, 74]; **DF** [18, 20, 21]; **GO** [74]; **MA** [22]; **MG** [23, 24]; **MT** [22, 58]; **PR** [25]; **RJ** [5]; **RR** [22]; **RS** [30, 31, 43]; **SC** [9, 12, 32, 45, 118]; **SP** [14, 17, 22, 25, 39, 55, 58, 68, 70, 74, 128]; **TO** [22].

152. ***Drosophila mesostigma*** Frota-Pessoa

Drosophila mesostigma Frota-Pessoa 1954:269.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **DF** [21]; **MG** [23]; **PA** [13, 117]; **PI** [13, 117]; **SC** [9]; **SP** [39].

153. ***Drosophila nigricincta*** Frota-Pessoa

Drosophila nigricincta Frota-Pessoa 1954:289.

Type locality: Cantareira, São Paulo, Brazil

Geographical distribution: **SP** [13, 39, 117].

154. ***Drosophila paramediostriata*** Townsend and Wheeler

Drosophila paramediostriata Townsend and Wheeler 1955:62.

Type locality: Porto Rico.

Geographical distribution: **DF** [20, 21]; **SC** [12, 118]; **SP** [34, 38, 70].

155. ***Drosophila trapeza*** Heed and Wheeler

Drosophila trapeza Heed and Wheeler 1957:25.

Drosophila mirassolensis Mourão and Gallo 1967:118.

Type locality: La Lola, Costa Rica.

Geographical distribution: **MG** [24]; **SC** [32, 118]; **SP** [39, 68, 122].

156. ***Drosophila triangula*** Wheeler

Drosophila triangula Wheeler 1949:192.

Type locality: Morelia, Michoacán, Mexico.

Geographical distribution: **SC** [9].

157. ***Drosophila trifilum*** Frota-Pessoa

Drosophila trifilum Frota-Pessoa 1954:292.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **RJ** [117]; **SC** [12, 118]; **SP** [13, 39, 117].

iv subgroup

158. ***Drosophila albescens*** Frota-Pessoa

Drosophila albescens Frota-Pessoa 1954:281.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [13, 117].

159. ***Drosophila albicans*** Frota-Pessoa

Drosophila albicans Frota-Pessoa 1954:282.

Type locality: Pirassununga, São Paulo, Brazil.

Geographical distribution: **SP** [13, 117].

160. ***Drosophila albirostris*** Sturtevant

Drosophila albirostris Sturtevant 1921:78.

Type locality: Panamas.

Geographical distribution: **MG** [23]; **SP** [83].

161. ***Drosophila mediovittata*** Frota-Pessoa

Drosophila mediovittata Frota-Pessoa 1954:280.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [13, 117].

162. ***Drosophila metzii*** Sturtevant

Drosophila metzii Sturtevant 1921:78.

Type locality: Herradura, Cuba.

Geographical distribution: **SP** [39].

163. ***Drosophila pruinifacies*** Frota-Pessoa

Drosophila pruinifacies Frota-Pessoa 1954:292.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **SP** [117].

164. ***Drosophila spinatermina*** Heed and Wheeler

Drosophila spinatermina Heed and Wheeler 1957:30.

Type locality: Port of Spain, Trinidad.

Geographical distribution: **SP** [39].

165. ***Drosophila tripunctata*** Loew

Drosophila tripunctata Loew 1862:231.

Drosophila modesta Sturtevant 1916:338.

Type locality: Columbia, USA.

Geographical distribution: **SC** [9, 118].

166. ***Drosophila tristriata*** Heed and Wheeler

Drosophila tristriata Heed and Wheeler 1957:31.

Type locality: Port of Spain, Trinidad.

Geographical distribution: **SC** [9].

virilis group

virilis subgroup

167. ***Drosophila virilis*** Sturtevant, 1916

Drosophila virilis Sturtevant 1916:330.

Type locality: New York, New York, USA.

Geographical distribution: **MG** [23]; **SC** [12, 32].

Capítulo 2 Not assigned to group

168. ***Drosophila impudica*** Duda

Drosophila impudica Duda 1927:196.

Drosophila para Pavan and Burla, in Pavan 1950:22.

Type locality: Urubamba, Peru.

Geographical distribution: **BA** [16, 17]; **DF** [20]; **MS** [17]; **PA** [11, 13, 22, 56, 74]; **SP** [17].

169. ***Drosophila tuchaua*** Pavan

Drosophila tuchaua Pavan 1950:26.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AM** [35]; **PA** [13, 74].

Phloridosa subgenus

170. ***Drosophila denieri*** Blanchard

Drosophila denieri Blanchard 1938:362.

Type locality: Isla de Oro, Formosa, Argentina.

Geographical distribution: **RJ** [128, 129]; **RS** [50]; **SC** [50].

171. ***Drosophila lutzii*** Sturtevant

Drosophila lutzii Sturtevant 1916:340.

Drosophila floricola Sturtevant 1942:42.

Type locality: Havana, Cuba.

Geographical distribution: **RS** [50]; **SC** [50].

Siphlodora subgenus

172. ***Drosophila flexa*** Loew

Drosophila flexa Loew 1866:182.

Drosophila subsigmoides Patterson and Mainland 1944:26.

Type locality: Gunglach, Cuba.

Geographical distribution: **GO** [130]; **RJ** [130]; **RN** [130]; **SC** [12, 32, 131]; **SP** [39, 130].

Sophophora subgenus

melanogaster group

ananassae subgroup

173. ***Drosophila ananassae*** Doleschall

Drosophila ananassae Doleschall 1858:128.

Drosophila imparata Walker 1859:126.

Drosophila similis Lamb 1914:347 (pre-occupied).

Drosophila caribea Sturtevant 1916:335.

Drosophila errans Malloch 1933:21.

Type locality: Ambon Island, Indonesia.

Geographical distribution: **AM** [35]; **BA** [15, 17]; **MG** [23]; **PR** [22]; **RJ** [49, 132]; **RS** [28, 29]; **SC** [12, 32, 133]; **SP** [22, 34, 68].

174. ***Drosophila malerkotliana*** Parshad and Paika

Drosophila malerkotliana Parshad and Paika 1964:235.

Type locality: India.

Geographical distribution: **AM**[35, 61, 62]; **BA**[16, 17]; **DF**[17, 19, 20, 21]; **MG**[16, 17, 23, 24]; **MS**[17]; **MT**[47, 53]; **PA**[35, 53]; **PB**[17]; **PR**[17, 25]; **RJ**[17]; **RN**[17]; **RS**[134]; **SC**[9, 12, 32, 36, 45, 53]; **SP**[17, 25, 33, 34, 39, 42].

melanogaster subgroup

175. ***Drosophila melanogaster*** Meigen

Drosophila melanogaster Meigen 1830:85.

Drosophila fasciata Meigen 1830:84.

Drosophila nigriventris Macquart 1843:259(=416).

Drosophila approximata Zetterstedt 1847:2557.

Drosophila immatura Walker 1849:1108.

Drosophila ampelophila Loew 1862:231.

Drosophila uvarum Rondani 1875:145.

Drosophila ampelophaga Howard 1900:604 (lapsus).

Drosophila pilosula Becker 1908:156.

Drosophila emulata Ray-Chaudhuri and Mukherjee 1941:216.

Drosophila melanocephala de Meijere 1946:16 (lapsus).

Type locality: Germany and Austria.

Geographical distribution: **BA**[15]; **DF**[17, 19, 20, 21]; **MA**[135]; **MG**[17, 23, 43, 135]; **PI**[135]; **PR**[17, 135]; **RJ**[17]; **RS**[28, 43, 135]; **SC**[9, 12, 32, 135]; **SP**[14, 17, 34, 39, 43, 135].

176. ***Drosophila simulans*** Sturtevant

Drosophila simulans Sturtevant 1919:153.

Type locality: Lakeland, Florida, USA.

Geographical distribution: **AM**[35, 62]; **BA**[15, 16, 17]; **DF**[17, 18, 19, 20, 21]; **ES**[17]; **MG**[16, 17, 23, 24, 56]; **MT**[47, 53, 58]; **MS**[17, 47]; **PA**[53, 58]; **PB**[17]; **PR**[17, 25]; **RJ**[17]; **RN**[17]; **RS**[17, 27, 28, 29, 43, 66, 67, 72, 92]; **SC**[9, [12, 17, 32, 36, 45, 53]; **SP** [14, 17, 25, 33, 34, 39, 43, 55, 58, 60, 68].

montium subgroup

177. ***Drosophila kikkawai*** Burla

Drosophila kikkawai Burla 1954:47.

Drosophila montium de Meijere 1916:205 sensu Freire-Maia and Pavan 1949 (key).

Type locality: Brazil.

Geographical distribution: **DF** [17, 20]; **MS** [17]; **PR** [22, 41]; **RJ** [41]; **RS** [30, 31, 43, 67, 136]; **SC** [9, 12, 32, 45, 137]; **SP** [22, 41, 68].

saltans group

cordata subgroup

178. ***Drosophila neocordata*** Magalhães

Drosophila neocordata Magalhães 1956:275.

Type locality: Montes Claros, Minas Gerais, Brazil.

Geographical distribution: **BA** [17]; **ES** [17]; **MG** [13, 138, 139]; **MS** [17]; **PR** [17]; **RJ** [17]; **SP** [17].

elliptica subgroup

179. ***Drosophila neoelliptica*** Pavan and Magalhães

Drosophila neoelliptica Pavan and Magalhães, in Pavan 1950:13.

Type locality: Jaguariaiva, Paraná, Brazil.

Geographical distribution: **GO** [13, 74, 139]; **PR** [74, 139]; **RJ** [139]; **SC** [9, 12, 36]; **SP** [14, 39, 139].

180. ***Drosophila neosaltans*** Pavan and Magalhães

Drosophila neosaltans Pavan and Magalhães, in Pavan 1950:16.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **SC** [9, 12, 32, 133]; **SP** [13, 14, 17, 39, 74, 139].

parasaltans subgroup

181. ***Drosophila parasaltans*** Magalhães

Drosophila parasaltans Magalhães 1956:276.

Type locality: Rio Negro, Amazonas, Brazil.

Geographical distribution: **AM** [138, 139].

182. ***Drosophila subsaltans*** Magalhães

Drosophila subsaltans Magalhães 1956:277.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **PA** [138, 139].

saltans subgroup

183. ***Drosophila austrosaltans*** Spassky

Drosophila austrosaltans Spassky 1957:57.

Type locality: Pirassununga, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **MA** [139]; **MG** [24]; **MS** [17]; **SP** [34, 39, 42, 139, 140].

184. ***Drosophila prosaltans*** Duda

Drosophila prosaltans Duda 1927:164.

Type locality: Hohenau, Paraguay.

Geographical distribution: **AM** [35, 139]; **BA** [16, 17, 22, 139]; **MA** [22, 139]; **MG** [17, 24]; **MS** [17]; **PA** [22, 139]; **PR** [25]; **RJ** [139]; **RS** [17, 30, 31, 43, 139]; **SC** [9, 12, 17, 32]; **SP** [14, 17, 22, 25, 34, 42, 39, 55, 139]; **TO** [139].

185. ***Drosophila pseudosaltans*** Magalhães

Drosophila pseudosaltans Magalhães 1956:273.

Type locality: Cantareira, São Paulo, Brazil.

Geographical distribution: **SP** [138, 139].

186. ***Drosophila saltans*** Sturtevant

Drosophila saltans Sturtevant 1916:328.

Drosophila sellata Sturtevant 1942:39.

Type locality: Guantanamo, Cuba.

Geographical distribution: **MT** [53]; **PA** [53]; **SC** [9, 12, 45, 53]; **SE** [43].

sturtevanti subgroup

187. ***Drosophila magalhaesi*** Mourão and Bicudo

Drosophila magalhaesi Mourão and Bicudo 1967:127.

Type locality: Rio Grande do Sul, Brazil.

Geographical distribution: **RS** [141].

188. ***Drosophila pulchella*** Sturtevant

Drosophila pulchella Sturtevant 1916:327.

Drosophila bellula Williston 1896:410 (pre-occupied).

Type locality: Saint Vicente, West Indians.

Geographical distribution: **RS** [30, 31]; **SC** [133].

189. ***Drosophila sturtevanti*** Duda

Drosophila sturtevanti Duda 1927:167.

Drosophila earlei Sturtevant 1916:329.

Drosophila pilifacies Malloch 1926:29.

Drosophila biopaca Sturtevant 1942:37.

Type locality: Mapiri, Bolivia.

Geographical distribution: **AC** [22, 139]; **AM** [22, 35, 56, 139]; **BA** [15, 16, 17, 22, 139]; **DF** [17, 18, 19, 20, 21]; **ES** [17]; **GO** [22, 139]; **MA** [22, 139]; **MG** [16, 17, 23, 24, 56, 142]; **MT** [22, 47, 53, 58]; **MS** [17]; **PA** [22, 53, 56, 58, 139, 143]; **PB** [17]; **PR** [17, 25]; **RJ** [17, 22, 37, 139, 143]; **RN** [17]; **RR** [22]; **RS** [17, 43, 142]; **SC** [9, 12, 17, 32, 36, 45, 53]; **SP** [14, 17, 22, 25, 33, 34, 37, 39, 42, 58, 60, 68, 139, 141, 142, 143].

willistoni group

alagitans subgroup

190. ***Drosophila alagitans*** Patterson and Mainland

Drosophila alagitans Patterson and Mainland, in Patterson 1943:194.

Type locality: Laguna Pátzcuaro, Michoacan, Mexico.

Geographical distribution: **SC** [9].

bocainensis subgroup

191. ***Drosophila bocainensis*** Pavan and Cunha

Drosophila bocainensis Pavan and Cunha 1947:18.

Type locality: Campos de Bocaina, São Paulo, Brazil.

Geographical distribution: **DF** [20, 21]; **MT** [58]; **PR** [41, 144]; **RS** [29, 28, 30, 31, 72]; **SC** [9, 12, 133]; **SP** [13, 14, 39, 41, 55, 58, 144].

192. ***Drosophila bocainoides*** Carson

Drosophila bocainoides Carson 1954:150.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **MG** [24]; **RJ** [145]; **SC** [9, 12, 133]; **SP** [13, 14, 39, 145].

193. ***Drosophila capricorni*** Dobzhansky and Pavan

Drosophila capricorni Dobzhansky and Pavan 1943:14.

Type locality: Mongaguá, São Paulo, Brazil.

Geographical distribution: **BA** [16, 22]; **ES** [17]; **MA** [22]; **MG** [17, 23, 24]; **MT** [22, 58]; **PA** [58]; **PR** [43]; **RJ** [17, 22]; **RS** [17, 26, 28, 43]; **SC** [9, 12, 32, 36, 45]; **SP** [13, 14, 17, 22, 37, 39, 55, 56, 58, 144].

194. ***Drosophila changuinolae*** Wheeler and Magalhães

Drosophila changuinolae Wheeler and Magalhães 1962:169.

Type locality: Changuinola, Panama.

Geographical distribution: **SP** [39].

195. ***Drosophila fumipennis*** Duda

Drosophila fumipennis Duda 1925:220.

Type locality: Suiza, Turrialba, Costa Rica.

Geographical distribution: **AC** [22]; **AM** [22, 35]; **BA** [15, 22]; **DF** [17, 20]; **ES** [17]; **MA** [22]; **MG** [23]; **MT** [22, 58]; **PA** [22, 56, 58]; **PR** [22]; **RJ** [5, 22, 37]; **RS** [27, 28, 30, 31]; **SC** [9, 12, 32, 36, 45]; **SP** [14, 17, 22, 25, 37, 39, 48, 55, 58, 144].

196. ***Drosophila mangabeirai*** Malogolowkin

Drosophila mangabeirai Malogolowkin 1951:432.

Type locality: Campina, Bahia, Brazil.

Geographical distribution: **BA** [15].

197. ***Drosophila nebulosa*** Sturtevant

Drosophila nebulosa Sturtevant 1916:327.

Drosophila limbata Williston 1896:414 (pre-occupied).

Type locality: Saint Vicente, West Indians.

Geographical distribution: **AC** [22]; **AM** [17, 22, 35, 61, 62]; **BA** [15, 16, 17, 22]; **DF** [17, 18, 19, 20, 21, 43]; **ES** [17]; **GO** [22, 71]; **MA** [22]; **MG** [16, 17, 23, 24, 56]; **MT** [22, 47, 58]; **MS** [17, 47]; **PA** [22, 58]; **PB** [17]; **PR** [17, 22, 58]; **RJ** [17, 22]; **RN** [17]; **RO** [22]; **RR** [22]; **RS** [17, 22, 26, 27, 28, 29, 30, 31, 43, 72]; **SC** [9, 12, 32, 36, 45]; **SP** [14, 17, 22, 33, 34, 39, 42, 43, 56, 58, 68, 144]; **TO** [22].

198. ***Drosophila parabocainensis*** Carson

Drosophila parabocainensis Carson 1954:149.

Type locality: Feliz, Rio Grande do Sul, Brazil.

Geographical distribution: **MG** [23, 24, 145]; **RS** [13, 145, 146]; **SP** [14, 145].

willistoni subgroup

199. ***Drosophila equinoxialis*** Dobzhansky

Drosophila equinoxialis Dobzhansky 1946:209.

Type locality: Teffé, Amazonas, Brazil.

Geographical distribution: **AM** [13, 48, 61, 144, 147]; **GO** [43]; **MT** [53]; **PA** [53].

200. ***Drosophila paulistorum*** Dobzhansky and Pavan

Drosophila paulistorum Dobzhansky and Pavan, in Burla et al. 1949:301.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **AM** [61, 147, 148, 149, 150]; **BA** [149, 151]; **CE** [149, 151]; **GO** [43, 149]; **MA** [149];

MG [24, 148, 149, 150]; **MT** [53]; **PA** [43, 53, 147, 149, 150, 151]; **PE** [149]; **RJ** [148, 149, 150]; **RS** [43, 147, 152, 153]; **SC** [12, 32, 147]; **SP** [14, 37, 39, 55, 144, 147, 148, 149].

201. ***Drosophila tropicalis*** Burla and Cunha

Drosophila tropicalis Burla and Cunha, in Burla et al. 1949:302.

Type locality: Palmas, Tocantins, Brazil.

Geographical distribution: **AC** [144]; **AM** [61]; **GO** [20]; **MT** [53]; **PA** [43, 53].

202. ***Drosophila willistoni*** Sturtevant

Drosophila willistoni Sturtevant 1916:327.

Drosophila pallida Williston 1896:415 (pre-occupied).

Drosophila paulista Dobzhansky and Pavan 1943:10.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **AM** [61, 154, 155, 156]; **BA** [15, 144, 147, 155, 156]; **DF** [20]; **MG** [24, 147, 155]; **MT** [53]; **PA** [53, 147, 154, 155]; **PR** [58, 144, 147, 155]; **RJ** [37, 154, 157, 158, 159, 160, 161]; **RS** [26, 27, 28, 29, 43, 66, 67, 72, 92, 147, 152, 153, 155, 156, 161, 162, 163, 164]; **SC** [12, 32, 36, 53, 147, 155, 165]; **SP** [14, 37, 39, 55, 60, 144, 147, 154, 155, 161, 166].

Capítulo 3 Not assigned to subgenera

203. ***Drosophila atra*** Walker

Drosophila atra Walker 1853:412.

Type locality: Brazil.

Geographical distribution: [localities not mentioned] [3, 167].

204. ***Drosophila tarsalis*** Walker

Drosophila tarsalis Walker 1853:412.

Type locality: Brazil.

Geographical distribution: [localities not mentioned] [167].

Hirtodrosophila genus

hirticornis group

205. ***Hirtodrosophila gilva*** (Burla)

Drosophila gilva Burla 1956:263.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168].

206. ***Hirtodrosophila mendeli*** (Mourão, Gallo and Bicudo)

Drosophila mendeli Mourão, Gallo and Bicudo 1965:578.

Type locality: Mirassol, São Paulo, Brazil.

Geographical distribution: **SP** [169].

207. ***Hirtodrosophila morgani*** (Mourão, Gallo and Bicudo)

Drosophila morgani Mourão, Gallo and Bicudo 1967:160.

Type locality: Mirassol, São Paulo, Brazil.

Geographical distribution: **SP** [169, 170].

208. ***Hirtodrosophila subgilva*** (Burla)

Drosophila subgilva Burla 1956:263.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168].

thoracis group

209. ***Hirtodrosophila clypitata*** (Grimaldi)

Drosophila clypitata Grimaldi 1987:149.

Zygothrica clypeata Burla 1956:251.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [168].

210. ***Hirtodrosophila pleurostrigata*** (Burla)

Zygothrica pleurostrigata Burla 1956:250.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [168]; **SP** [168].

211. ***Hirtodrosophila thoracis*** (Williston)

Drosophila thoracis Williston 1896:411.

Type locality: not found

Geographical distribution: **RJ** [168].

212. ***Hirtodrosophila strigocula*** (Burla)

Zygothrica strigocula Burla 1956:250.

Type locality: Bahia, Brazil.

Geographical distribution: **BA** [168].

magnarcus group

213. ***Hirtodrosophila levigata*** (Burla)

Drosophila levigata Burla 1956:261.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [170]; **SP** [168, 170].

214. ***Hirtodrosophila magnarcus*** (Frota-Pessoa)

Drosophila magnarcus Frota-Pessoa 1951:407.

Drosophila caxiensis Cordeiro 1952:304.

Drosophila paralevigata Burla 1956:261.

Type locality: Mogi das Cruzes, São Paulo, Brazil.

Geographical distribution: **RJ** [170]; **RS** [170, 171]; **SP** [168, 170, 172].

Capítulo 4 Not assigned to group

215. ***Hirtodrosophila gavea*** Vilela and Bächli

Hirtodrosophila gavea Vilela and Bächli 2005:150.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [170].

216. ***Hirtodrosophila jordanensis*** (Frota-Pessoa)

Drosophila jordanensis Frota-Pessoa 1945:473.

Type locality: Campos de Jordão, São Paulo, Brazil.

Geographical distribution: **SP** [170, 173].

217. ***Hirtodrosophila minuscula*** Vilela and Bächli

Hirtodrosophila minuscula Vilela and Bächli 2005:154.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [170].

218. ***Hirtodrosophila pictiventris*** (Duda)

Drosophila pictiventris Duda 1925:211.

Drosophila pictiventria Patterson and Wheeler 1949:225 (lapsus).

Type locality: Costa Rica.

Geographical distribution: **PA** [170].

219. ***Hirtodrosophila ramulosa*** (Burla)

Drosophila ramulosa Burla 1956:266.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168, 170].

220. ***Hirtodrosophila subflavohalterata*** (Burla)

Drosophila subflavohalterata Burla 1956:264.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168, 170].

Mycodrosophila genus

221. ***Mycodrosophila brunnescens*** Wheeler and Takada

Mycodrosophila brunnescens Wheeler and Takada 1963:399.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **PA** [174].

222. ***Mycodrosophila elegans*** Wheeler and Takada

Mycodrosophila elegans Wheeler and Takada 1963:398.

Type locality: Canal Zone, Panama.

Geographical distribution: **PA** [174].

223. ***Mycodrosophila projectans*** (Sturtevant)

Drosophila projectans Sturtevant 1916:342.

Type locality: Saint Domingos, West Indians.

Geographical distribution: [localities not mentioned] [2, 3, 174].

Neotanygastrella genus

224. ***Neotanygastrella chymomyzoides*** Duda

Neotanygastrella chymomyzoides Duda 1927:71.

Type locality: Mapiri, Bolivia.

Geographical distribution: **PA** [1].

225. ***Neotanygastrella tricoloripes*** Duda

Neotanygastrella tricoloripes Duda 1925:224.

Bunostoma Braziliensis Frota-Pessoa 1946:176.

Type locality: Suiza, Turrialba, Costa Rica.

Geographical distribution: **PA** [1]; **RJ** [175].

Scaptodrosophila genus

latifasciaeformis group

226. ***Scaptodrosophila latifasciaeformis*** (Duda)

Drosophila latifasciaeformis Duda 1940:22.

Drosophila finitima gracilipes Duda 1940:39.

Drosophila mirim Dobzhansky and Pavan 1943:62.

Drosophila baeomyia Wheeler 1949:145.

Type locality: Katona, Uganda.

Geographical distribution: **AC** [22]; **AM** [22, 35, 61, 62]; **BA** [15, 16, 17, 22]; **DF** [17, 18, 19, 20, 21]; **GO** [22, 71]; **MA** [22]; **MG** [16, 17, 23]; **MS** [17]; **MT** [22, 47, 58]; **PA** [22, 56, 58]; **PB** [17]; **PR** [17]; **RJ** [17, 22]; **RN** [17]; **RO** [22]; **SC** [9, 12, 17, 32, 45]; **SP** [13, 14, 17, 22, 25, 37, 42, 58, 68].

rufifrons group

227. ***Scaptodrosophila lebanonensis*** (Wheeler)

Drosophila lebanonensis Wheeler 1949:143.

Drosophila pattersoni Pipkin 1956:251.

Drosophila stonei Pipkin 1956:254.

Drosophila galloi Lourenço and Mourão 1992:575.

Type locality: Beirut, Lebanon.

Geographical distribution: **RS** [176, 177].

Scaptomyza genus

Mesoscaptomyza subgenus

vittata group

228. ***Scaptomyza fuscinervis*** Malloch

Scaptomyza fuscinervis Malloch 1924:11.

Type locality: Alto Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [7]; **SP** [178].

229. ***Scaptomyza nigripalpis*** Malloch

Scaptomyza nigripalpis Malloch 1924:11.

Type locality: Alto Itatiaia, São Paulo, Brazil.

Geographical distribution: **MG** [7]; **RJ** [7]; **SP** [178].

Capítulo 5 Not assigned to group

230. ***Scaptomyza pleurolineata*** Wheeler and Takada

Scaptomyza pleurolineata Wheeler and Takada 1966:70.

Type locality: Popayan, Colombia.

Geographical distribution: **SP** [7, 179].

Zaprionus genus

Zaprionus subgenus

armatus group

vittiger subgroup

231. ***Zaprionus indianus*** Gupta

Zaprionus indianus Gupta 1970:63 (como *Z. indiana* – lapsus).

Zaprionus inermis Seguy 1938:343 (preocuped).

Zaprionus paravittiger Godbole and Vaidya 1972:135.

Zaprionus collarti Tsacas 1980:147.

Type locality: India.

Geographical distribution: **BA** [180]; **DF** [18, 19, 20, 21, 181]; **MA** [181]; **MG** [182]; **MT** [180]; **PA** [53, 180, 181]; **RJ** [180]; **RO** [181]; **RS** [30, 31, 67]; **SC** [9, 12, 32, 45, 53]; **SP** [181, 183].

Zygothrica genus

atriangula group

232. ***Zygothrica atriangula*** Duda

Zygothrica atriangula Duda, 1927:57.

Type locality: Pichis Peru.

Geographical distribution: **PA** [1, 168]; **RJ** [168]; **SP** [14, 168].

233. ***Zygothrica parapoeyi*** Burla

Zygothrica parapoeyi Burla 1956:242.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

234. ***Zygothrica paraptilialis*** Burla

Zygothrica paraptilialis Burla 1956:246.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [168].

235. ***Zygothrica poeyi*** (Sturtevant)

Drosophila poeyi Sturtevant 1921:76.

Type locality: Havana, Cuba.

Geographical distribution: **RJ** [168]; **SC** [184].

236. ***Zygothrica subcandens*** Burla

Zygothrica subcandens Burla 1956:245.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

237. ***Zygothrica virgatinigra*** Burla

Zygothrica virgatinigra Burla 1956:252.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

bilineata group

238. ***Zygothrica bilineata*** (Williston)

Drosophila bilineata Williston 1896:409.

Zygothrica gemma Burla 1956:249.

Type locality: Saint Vicente, West Indians.

Geographical distribution: **MT** [185]; **PA** [185]; **PR** [185]; **RJ** [168, 185]; **RO** [185]; **RS** [185]; **SC** [12, 184]; **SP** [14].

candens group

239. ***Zygothrica candens*** Burla

Zygothrica candens Burla 1956:244.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

dispar group

aldrichi subgroup

240. ***Zygothrica aldrichi*** Sturtevant

Zygothrica aldrichi Sturtevant 1920:157.

Type locality: Panama.

Geographical distribution: **PA** [1].

241. ***Zygothrica joeyesco*** Grimaldi

Zygothrica joeyesco Grimaldi 1987:234.

Type locality: Raleigh, Suriname.

Geographical distribution: **RO** [186].

242. ***Zygothrica mediovitta*** Grimaldi

Zygothrica mediovitta Grimaldi 1987:238.

Type locality: Mizaruni-Potaro, English Guiana.

Geographical distribution: **PA** [186].

243. ***Zygothrica microeristes*** Grimaldi

Zygothrica microeristes Grimaldi 1987:218.

Type locality: Belém, Pará, Brazil.

Geographical distribution: **AM** [186]; **ES** [186]; **PA** [186]; **MT** [186]; **RO** [186].

244. ***Zygothrica neoaldrichi*** Burla

Zygothrica neoaldrichi Burla 1956:222.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168, 186]; **SP** [14].

245. ***Zygothrica nigropleura*** Grimaldi

Zygothrica nigropleura Grimaldi 1987:230.

Type locality: Salesópolis, São Paulo, Brazil.

Geographical distribution: **SC** [184]; **SP** [186].

246. ***Zygothrica paraldrichi*** Burla

Zygothrica paraldrichi Burla 1956:223.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **AM** [186]; **PA** [186]; **RJ** [168, 186]; **RO** [186]; **SP** [14].

247. ***Zygothrica pilipes*** Hendel

Zygothrica pilipes Hendel 1936:93.

Type locality: Santarém, Pará, Brazil.

Geographical distribution: **AM** [186]; **AP** [186]; **PA** [1, 186]; **RO** [186].

248. ***Zygothrica radialis*** Grimaldi

Zygothrica radialis Grimaldi 1987:240.

Type locality: Mizaruni-Potaro, English Guiana.

Geographical distribution: **PA** [186].

249. ***Zygothrica somatia*** Grimaldi

Zygothrica somatia Grimaldi 1987:236.

Type locality: Monte Dourado, Pará, Brazil.

Geographical distribution: **PA** [186].

250. ***Zygothrica zygia*** Grimaldi

Zygothrica zygia Grimaldi 1987:209.

Type locality: Tabaquite, Trinidad.

Geographical distribution: **AM** [186]; **PA** [186]; **RO** [186].

caudata subgroup

251. ***Zygothrica caudata*** (Hendel)

Drosophilura caudata Hendel 1913:389.

Type locality: Santarém, Pará, Brazil.

Geographical distribution: **PA** [1, 186]; **SP** [14, 168, 186].

252. ***Zygothrica laticeps*** Burla

Zygothrica laticeps Burla 1954:246.

Type locality: Cantareira, São Paulo, Brazil.

Geographical distribution: **RJ** [168]; **SP** [168, 186].

dispar subgroup

253. ***Zygothrica dispar*** (Wiedemann)

Achias dispar Wiedemann 1830:556.

Type locality: Brazil.

Geographical distribution: **ES** [186]; **PA** [1]; **PI** [186]; **RJ** [49, 144, 168, 186, 187]; **SC** [12, 32, 184]; **SP** [14, 48, 83, 168, 186].

254. ***Zygothrica prodispar*** Duda

Zygothrica prodispar Duda 1925:189.

Type locality: Pinipini, Peru.

Geographical distribution: **BA** [186]; **MT** [186]; **PA** [186]; **PI** [186]; **RJ** [49, 168, 186]; **SC** [12, 32, 184, 186]; **SP** [14, 168, 186].

fuscina group

255. ***Zygothrica fuscina*** Burla

Zygothrica fuscina Burla 1956:257.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

256. ***Zygothrica venustipoeyi*** Burla

Zygothrica venustipoeyi Burla 1956:238.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [168].

hypandriata group

257. ***Zygothrica hypandriata*** Burla

Zygothrica hypandriata Burla 1956:246.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RJ** [168]; **SC** [184]; **SP** [14, 168].

258. ***Zygothrica lanceolata*** Burla

Zygothrica lanceolata Burla 1956:246.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SC** [184]; **SP** [14, 168].

259. ***Zygothrica spiculirostris*** Burla

Zygothrica spiculirostris Burla 1956:255.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

orbitalis group

260. ***Zygothrica orbitalis*** (Sturtevant)

Drosophila orbitalis Sturtevant 1916:336.

Zygothrica nitidifrons Duda 1927:55.

Drosophila ochracella Hendel 1936:98.

Zygothrica parilis Burla 1956:220.

Type locality: Ilha Taboga, Panama.

Geographical distribution: **PA** [1]; **RJ** [168]; **SC** [12, 32, 184]; **SP** [14, 168].

virgatalba group

261. ***Zygothrica virgatalba*** Burla

Zygothrica virgatalba Burla 1956:252.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

vittimaculosa group

262. ***Zygothrica sectipoeyi*** Burla

Zygothrica sectipoeyi Burla 1956:236.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

263. ***Zygothrica vitticlara*** Burla

Zygothrica vitticlara Burla 1956:226.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168].

264. ***Zygothrica vittimaculosa*** Burla

Zygothrica vittimaculosa Burla 1956:227.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **RS** [43]; **SC** [12, 184]; **SP** [14, 168].

265. ***Zygothrica vittinubila*** Burla

Zygothrica vittinubila Burla 1956:225.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ**: [168]; **SP** [14, 83, 168].

266. ***Zygothrica vittipunctata*** Burla

Zygothrica vittipunctata Burla 1956:230.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

267. ***Zygothrica zygopoeyi*** Burla

Zygothrica zygopoeyi Burla 1956:236.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

vittatifrons group

268. ***Zygothrica vittatifrons*** (Williston)

Drosophila vittatifrons Williston 1896:408.

Type locality: not found

Geographical distribution: [localities not mentioned] [2].

269. ***Zygothrica vittimarginata*** Burla

Zygothrica vittimarginata Burla 1956:229.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [168].

Capítulo 6 Not assigned to group

270. ***Zygothrica apopoeyi*** Burla

Zygothrica apopoeyi Burla 1956:240.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SC** [184]; **SP** [14, 168].

271. ***Zygothrica clavipoeyi*** Burla

Zygothrica clavipoeyi Burla 1956:238.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [168].

272. ***Zygothrica festiva*** Burla

Zygothrica festiva Burla 1956:256.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

273. ***Zygothrica gracilipoeyi*** Burla

Zygothrica gracilipoeyi Burla 1956:240.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14].

274. ***Zygothrica laevifrons*** Duda

Zygothrica laevifrons Duda 1927:56.

Type locality: Pichis, Peru.

Geographical distribution: **PA** [1].

275. ***Zygothrica laeviventris*** Duda

Zygothrica laeviventris Duda 1927:62.

Type locality: P. Novo, Brazil.

Geographical distribution: [localities not mentioned] [3, 5].

276. ***Zygothrica mesopoeyi*** Burla

Zygothrica mesopoeyi Burla 1956:241.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14].

277. ***Zygothrica pallidipoeyi*** Burla

Zygothrica pallidipoeyi Burla 1956:237.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [168]; **SP** [14].

278. ***Zygothrica palpipoeyi*** Burla

Zygothrica palpipoeyi Burla 1956:243.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [168].

279. ***Zygothrica parvipoeyi*** Burla

Zygothrica parvipoeyi Burla 1956:239.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

280. ***Zygothrica ptilialis*** Burla

Zygothrica ptilialis Burla 1956:245.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

281. ***Zygothrica vittimarmorata*** Burla

Zygothrica vittimarmorata Burla 1956:232.

Type locality: São Paulo, São Paulo, Brazil.

Geographical distribution: **SP** [168].

282. ***Zygothrica vittinotialis*** Burla

Zygothrica vittinotialis Burla 1956:230.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

283. ***Zygothrica vittipoecila*** Burla

Zygothrica vittipoecila Burla 1956:231.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [168].

284. ***Zygothrica vittisecta*** Burla

Zygothrica vittisecta Burla 1956:232.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

285. ***Zygothrica vittivirgata*** Burla

Zygothrica vittivirgata Burla 1956:228.

Type locality: Itatiaia, São Paulo, Brazil.

Geographical distribution: **SP** [14, 168].

Steganinae subfamily

Amiota genus

Amiota subgenus

286. ***Amiota steganoptera*** Malloch

Amiota steganoptera Malloch 1926:31.

Type locality: Higuito, San Mateo, Costa Rica.

Geographical distribution: [localities not mentioned] [2, 188].

Leucophenga genus

Leucophenga subgenus

287. ***Leucophenga argenteofasciata*** Kahl

Leucophenga argenteofasciata Kahl 1917:371 (as *argenteo-fasciata*).

Type locality: Santarém, Pará, Brazil.

Geographical distribution: **PA** [5, 6].

288. ***Leucophenga brazilensis*** Malloch

Leucophenga brazilensis Malloch 1924:9.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [178].

289. ***Leucophenga frontalis*** (Williston)

Drosophila frontalis Williston 1896:413.

Type locality: Saint Vicente, West Indians.

Geographical distribution: [localities not mentioned] [3].

290. ***Leucophenga hasemani*** Kahl

Leucophenga hasemani Kahl 1917:375.

Type locality: Munez Freire, Espirito Santo, Brazil.

Geographical distribution: **ES** [6].

291. ***Leucophenga maculosa*** (Coquillett)

Drosophila maculosa Coquillett, in Johnson 1895:317.

Type locality: Florida, USA.

Geographical distribution: [localities not mentioned] [2, 3].

292. ***Leucophenga obscuripennis*** (Loew)

Drosophila obscuripennis Loew 1866:183.

Type locality: Cuba.

Geographical distribution: [localities not mentioned] [3].

Pseudiastata genus

Pseudiastata subgenus

293. ***Pseudiastata brasiliensis*** Lima

Pseudiastata brasiliensis Lima 1937:179.

Type locality: São Gonçalo, Rio de Janeiro, Brazil.

Geographical distribution: **PE** [189]; **RJ** [190, 191].

294. ***Pseudiastata pseudococcivora*** Sabrosky

Pseudiastata pseudococcivora Sabrosky 1951:624.

Type locality: Canal Zone, Panama.

Geographical distribution: **BA** [189]; **PE** [189].

Rhinoleucophenga genus

295. ***Rhinoleucophenga angustifrons*** Malogolowkin

Rhinoleucophenga angustifrons Malogolowkin 1946:425.

Type locality: Angra dos Reis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [192].

296. ***Rhinoleucophenga brasiliensis*** (Lima)

Gitona brasiliensis Lima 1950:251.

Type locality: Brazil.

Geographical distribution: [localities not mentioned] [2, 3].

297. ***Rhinoleucophenga fluminensis*** (Lima)

Gitona fluminensis Lima 1950:249.

Type locality: Brazil.

Geographical distribution: [localities not mentioned] [2, 3].

298. ***Rhinoleucophenga lopesi*** Malogolowkin

Rhinoleucophenga lopesi Malogolowkin 1946:424.

Type locality: Rio de Janeiro, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [192].

299. ***Rhinoleucophenga matogrossensis*** Malogolowkin

Rhinoleucophenga matogrossensis Malogolowkin 1946:420.

Type locality: Salobra, Mato Grosso do Sul, Brazil.

Geographical distribution: **MS** [192].

300. ***Rhinoleucophenga nigrescens*** Malogolowkin

Rhinoleucophenga nigrescens Malogolowkin 1946:421.

Type locality: Salobra, Mato Grosso do Sul, Brazil.

Geographical distribution: **MS** [192].

301. ***Rhinoleucophenga obesa*** (Loew)

Drosophila obesa Loew 1872:102.

Phortica hirtifrons Johnson 1913:88.

Type locality: Texas, USA.

Geographical distribution: **MT** [192]; **RJ** [192]; **SC** [12]; **SP** [192].

302. ***Rhinoleucophenga personata*** Malogolowkin

Rhinoleucophenga personata Malogolowkin 1946:422.

Type locality: Salobra, Mato Grosso do Sul, Brazil.

Geographical distribution: **MS** [192].

Stegana genus

Ceratostylus subgenus

303. ***Stegana fumipennis*** (Enderlein)

Ceratostylus fumipennis Enderlein 1922:296.

Type locality: Santa Catarina, Brazil.

Geographical distribution: **SC** [193].

Steganina subgenus

304. ***Stegana brasiliensis*** (Duda)

Protostegana brasiliensis Duda 1927:27.

Type locality: Petrópolis, Rio de Janeiro, Brazil.

Geographical distribution: **RJ** [5].

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CAPÍTULO 6

CHANGES IN BRAZILIAN DROSOPHILIDAE (DIPTERA) ASSEMBLAGES ACROSS NA URBANISATION GRADIENT

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ECOLOGY, BEHAVIOR AND BIONOMICS

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

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

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

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

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

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

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

Another important consequence of urbanisation is the biotic homogenisation, caused by the eradication of the wild fauna and flora by the introduction of exotic ones associated with the urbanisation process itself (Sukopp & Werner 1982, McKinney & Lockwood 1999, Pickett *et al.* 2001). For instance, several species of Drosophilidae are found in association with environments under anthropic influence (Parsons & Stanley 1981). These environmental changes usually define a gradient from wild to urbanised areas. Ruszczyk (1986/1987) identified this gradient in the city of Porto Alegre, southernmost Brazil, and suggested a classification for the different urbanisation levels based on the extent of plant covers and the kind and height of buildings.

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

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

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

Material and Methods

Study area. Collections were carried out in the Santa Catarina Island, city of Florianópolis, Santa Catarina State, southern Brazil. This island measures approximately 424 km² and is the location of the largest part of the city of Florianópolis, home to about 300,000 inhabitants. According to the Köeppen criteria, the climatic classification of the area is type Cfa, located in subtropical intermediate zone and belongs to the mesothermic humid group (Prefeitura Municipal de Florianópolis 2005). The variation of the monthly average of daily temperature and relative humidity, the total monthly rainfall measured in the collection period at the Meteorological Station of Instituto Nacional de Meteorologia (27º35'S; 48º34'W; altitude of 2m) are shown in Fig. 1.

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

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

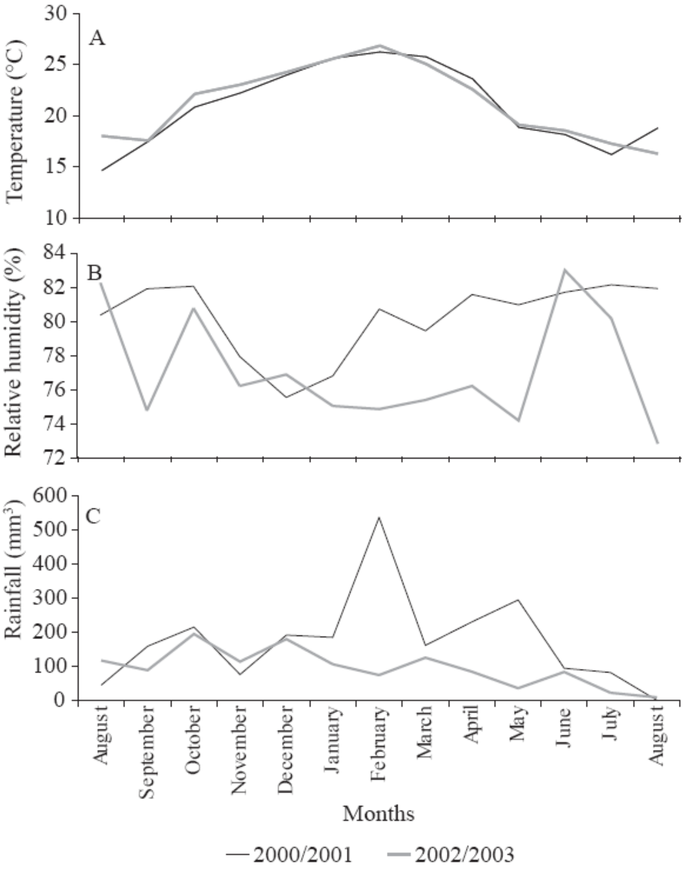

Fig. 1. Temperature and relative humidity averages and total rainfall in the months during collections in years 2000/2001 and 2002/2003.

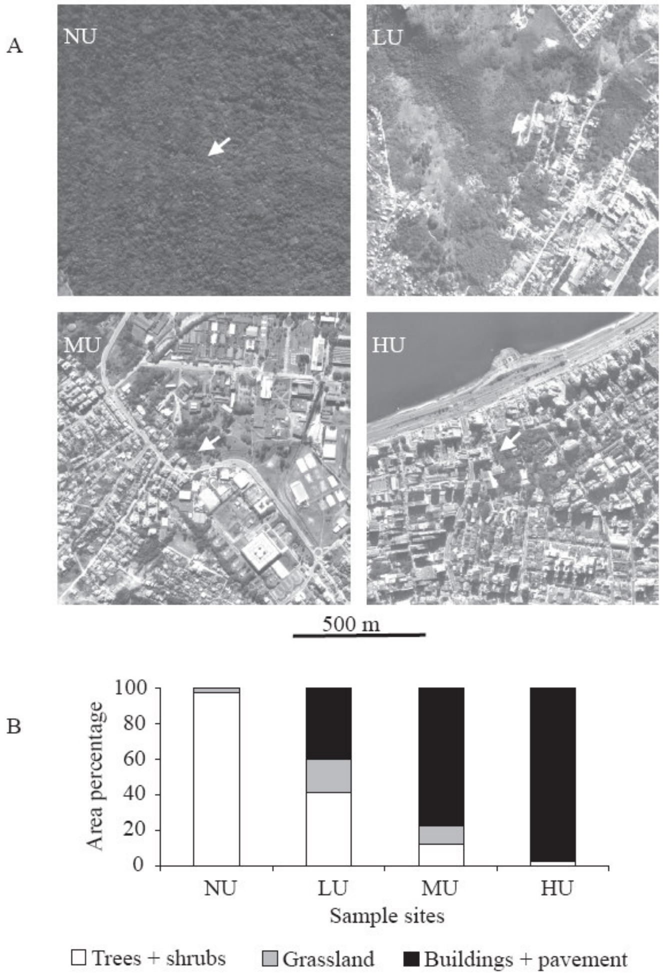

Fig. 2. (A) Aerial photographs of the collection sites and (B) the percentage of the area covered by trees+shrubs or grassland or buildings+pavement; radius = 1 km. The arrow shows where the traps were distributed. NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU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

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

Collection and identification of specimens. Ten samples were collected between August 2000 and August 2003. The samples were categorised as winter/2000 (collections between August 7th and September 1st), spring/2000 (October 25th to December 1st), summer/2001 (January 8th to February 7th), autumn/2001 (March 12th to April 21st), winter/2001 (July 9th to August 13th), winter/2002 (August 16th to September 7th), spring/2002 (November 7th to 22nd), summer/2003 (February 15th to 21st), autumn/2003 (April 9th to 16th) and winter/2003 (August 11th to 16th).

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

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

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

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

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

Results

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

The relative abundance (*pi*) of the species that reached values above 5% of the total per sample in each site is shown in Fig. 3. In NU (Fig. 3A), *Drosophila capricorni* Dobzhansky & Pavan was the best-represented species in winter, followed by the *willistoni* subgroup (*D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky & Pavan). The predominance of *D. capricorni* also occurred in spring 2000. In the remaining samples, the *willistoni* subgroup was the most representative, followed by *D. polymorpha* Dobzhansky & Pavan or *D. capricorni*. In the LU site (Fig. 3B), the *willistoni* subgroup was the most predominant taxon in winter, and *Zaprionus indianus* Gupta was the most representative species in summer and autumn 2001 and in spring 2002, followed either by the *willistoni* subgroup or by *D. simulans* Sturtevant. This latter species was predominant in spring 2000, and *D. malerkotliana* Parshad & Paika, followed by *D. simulans* prevailed in summer and autumn 2003.

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

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

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

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

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

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

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

Species	Collection sites				Total
	NU	LU	MU	HU	
Amiota sp.	0	4	0	0	4
Diathoneura brasiliensis Duda	0	1	0	0	1
* *Drosophila ananassae* Doleschall	0	80	527	293	900
Drosophila annulimana Duda	15	11	9	10	45
Drosophila ararama Pavan & da Cunha	0	0	4	6	10
Drosophila arassari da Cunha & Frota-Pessoa	1	1	1	1	4
Drosophila atrata Burla & Pavan	0	2	0	0	2
Drosophila bandeirantorum Dobzhansky & Pavan	8	8	10	75	101
Drosophila bocainensis Pavan & da Cunha	5	32	7	6	50
Drosophila bocainoides Carson	6	0	0	0	6
Drosophila briegeri Pavan & Breuer	0	1	0	0	1
Drosophila bromelioides Pavan & da Cunha	0	5	10	4	19
* *Drosophila busckii* Coquillett	0	17	12	124	153
Drosophila caponei Pavan & da Cunha	48	66	56	88	258
Drosophila capricorni Dobzhansky & Pavan	2,353	233	29	56	2,671
Drosophila cardini Sturtevant	0	0	3	0	3
Drosophila cardinoides Dobzhansky & Pavan	1	110	1,292	1,208	2,611
Drosophila carolinae Vilela	9	11	4	3	27
Drosophila dreyfusi Dobzhansky & Pavan	10	0	0	0	10
Drosophila fascioloides Dobzhansky & Pavan	0	0	0	4	4
Drosophila flexa Loew	0	1	2	3	6
Drosophila fumipennis Duda	150	105	2	4	261
Drosophila fuscolineata Duda	2	10	11	10	33
Drosophila gaucha Jaeger & Salzano	0	0	1	0	1
Drosophila griseolineata Duda	17	390	39	183	629
Drosophila guaraja King	2	11	1	77	91
Drosophila hydei Sturtevant	4	11	23	152	190
* *Drosophila immigrans* Sturtevant	34	423	220	669	1,346
* *Drosophila kikkawai* Burla	0	0	40	129	169
Drosophila limensis Pavan & Patterson	0	7	12	4	23
Drosophila maculifrons Duda	0	2	2	1	5
* *Drosophila malerkotliana* Parshad & Paika	7	2,386	24,727	21,621	48,741
Drosophila mapiriensis Vilela & Bachli	4	4	0	73	81
Drosophila mediopicta Frota-Pessoa	89	112	4	37	242
Drosophila mediopunctata Dobzhansky & Pavan	85	104	28	83	300
Drosophila mediostriata Duda	0	0	2	3	5
* *Drosophila melanogaster* Meigen	3	64	50	1,235	1,352
Drosophila mercatorum Patterson & Wheeler	280	1,221	2,374	3,584	7,459

Continue

Table 1. Continuation.

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

Continue

Table 1. Continuation.

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

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

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

Discussion

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

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

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

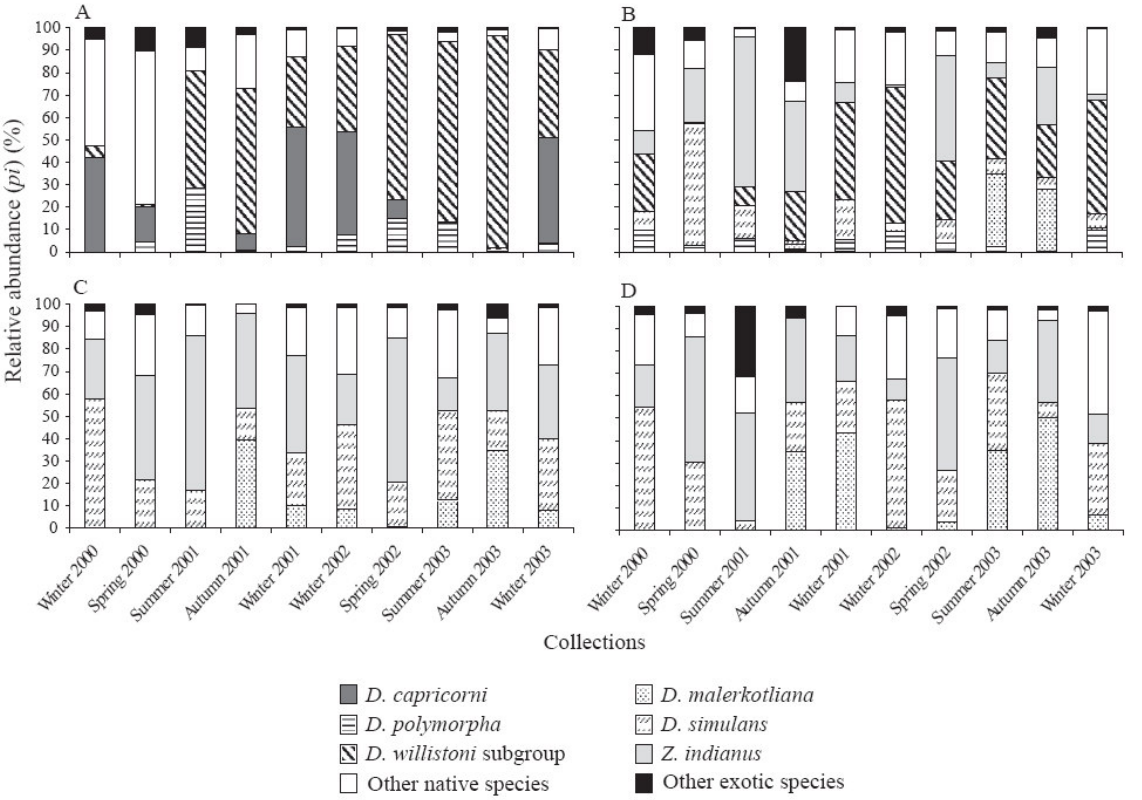

Fig. 3. Relative abundance of the main species sampled in each sampling site ($p_i > 0.05$). A) NU – not urbanized site. B) LU – low urbanisation site. C) MU – medium urbanisation site. D) HU – high urbanisation site.

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

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

The *willistoni* subgroup, typical of forests (Martins 1987, 2001; Saavedra *et al.* 1995), was very abundant in our collections, including those carried out in urbanized areas. The presence of these species in urban areas was previously related by Valente *et al.* (1993), by Valiati & Valente (1996), and recently by Silva *et al.* (2005a,b), who sampled it at high abundance in Porto Alegre, southernmost Brazil. Moreover, due to the high abundance of the exotic species in the city, the expressiveness of *willistoni* subgroup is low in areas of medium and high urbanisation.

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

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

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

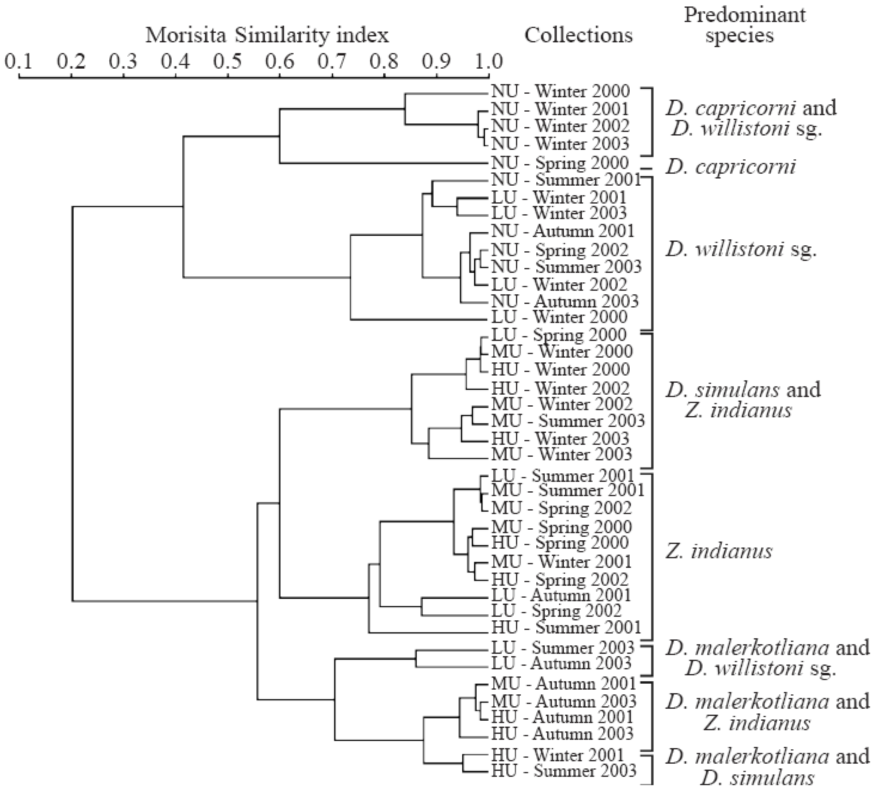

Fig. 4. UPGMA dendrogram constructed with Morisita's similarity index and the predominant species in each sample. NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site.

Table 2. Ecological indices calculated for each collection.

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

Continue

Table 2. Continuation.

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

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

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

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

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

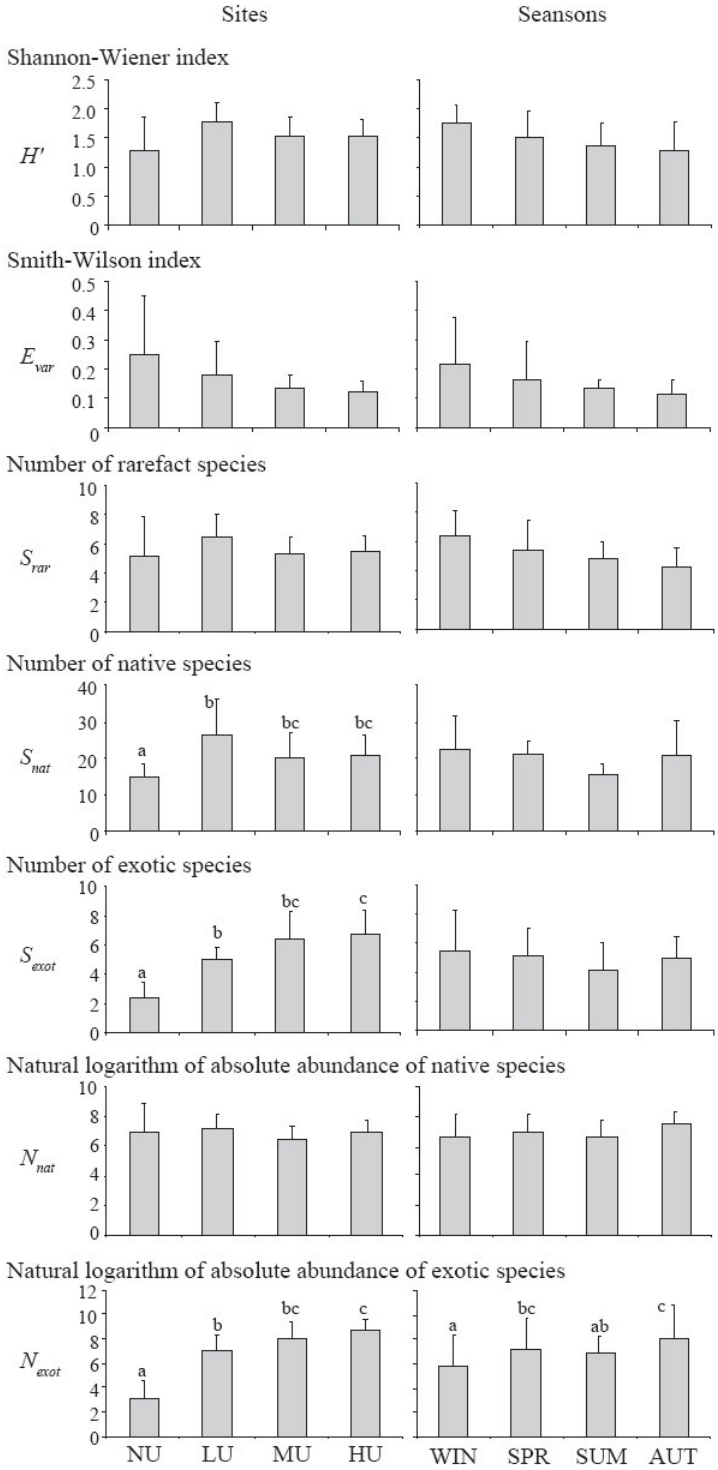

Fig. 5. Average of indices per site and per season, and significant differences. NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site, WIN – winter, SPR – spring, SUM – summer, AUT – autumn. Different letters represent significant differences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

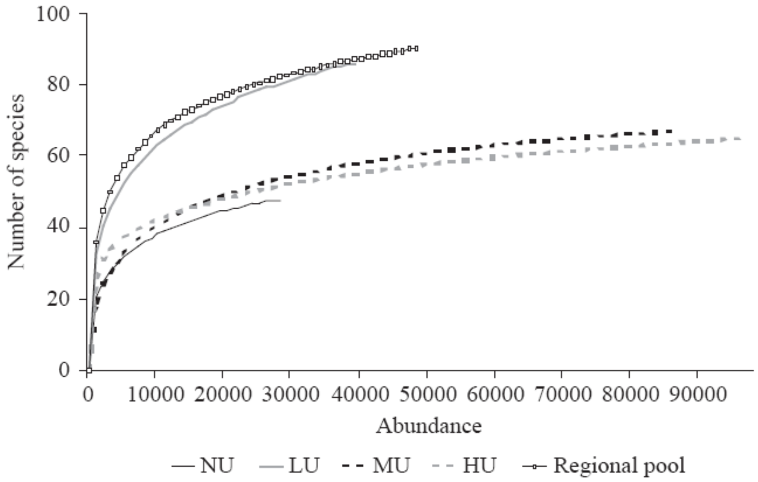

Fig. 6. Curves with rarefaction data of the collection sites and the data from regional pool (De Toni *et al.* 2007). NU – not urbanized site, LU – low urbanisation site, MU – medium urbanisation site, HU – high urbanisation site.

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

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

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

This attribute of urban gardens was also observed for other insects, as butterflies (Blair & Launer 1997, Wood & Pullin 2002, Shapiro 2002) and mosquitoes (Barbosa *et al.* 2003, Navarro-Silva *et al.* 2004). Nevertheless, Levy & Connor (2004) point that the populations found in these gardens could not be maintained due to a lack of local resources, and that these areas probably act as sink environments for these populations. Could the populations of native species of Drosophilidae survive in urban environments? This question can only be answered with further investigation of the substrata used as breeding site by these species in urban areas.

Another possibility to explain the highest richness of native species in urban areas, especially in low urbanisation sites, is the increased attractiveness of the baits in the city. It can happen by an increase in the stressing factors and a lack of natural resources in the city. Like this, the loss of richness becomes apparent when compared with the regional values. Crooks *et al.* (2004) observed that local bird diversity increases in moderately disturbed environments, but decreases in the overall regional diversity. These authors attribute this loss of richness to the biotic homogenisation of urban environments (McKinney & Lockwood 1999). It is very unlikely that the urban areas are as rich as, or even

Table 4. Niche analysis of diversity for temporal and spatial components.

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

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

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

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

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

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

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

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

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

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

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CAPÍTULO 7

CONCLUSÃO GERAL E PERSPECTIVAS

CONCLUSÃO GERAL

Dentre os objetivos de nosso estudo estava identificar como as espécies de Drosophilidae se relacionam na utilização dos recursos tróficos por suas larvas, buscando identificar quais os principais fatores que podem estar atuando na manutenção da diversidade de espécies de suas assembléias em áreas de Mata Atlântica e urbanas de Florianópolis (SC). Além disso, nosso estudo buscou verificar quais recursos tróficos são utilizados para oviposição pelas espécies de drosofilídeos e como estas espécies estariam utilizando os diferentes tipos de recursos tróficos disponíveis para criação de larvas.

Neste sentido, nosso estudo realizou uma listagem de frutos e alguns fungos utilizados como sítio de oviposição para as espécies de Drosophilidae da região de Florianópolis, e concluiu que as espécies de Drosophilidae conseguem colonizar ambientes urbanos, mas há uma grande perda da diversidade de espécies, pela ausência de espécies raras nas amostras de moscas emergentes dos frutos coletados na cidade.

Ainda, as assembléias estudadas apresentaram um caráter generalista, tanto quanto à utilização dos recursos tróficos. Nas assembléias frugívoras de Mata Atlântica verificou-se a formação de grupos ecológicos funcionais, onde certas espécies possuem uma maior similaridade na utilização dos recursos. Este tipo de organização não foi observado nas assembléias urbanas, onde há uma grande sobreposição dos nichos e uma menor diversidade de espécies. Já, as assembléias fungívoras parecem ser organizadas de acordo com a resistência e persistência dos corpos de frutificação das espécies de fungos coletadas e com o ambiente em que esses corpos estão inseridos.

As assembléias de Mata Atlântica e de áreas urbanizadas são características, mesmo quando realizamos as coletas de imaturos a partir dos sítios de oviposição e, inclusive, a disposição dos recursos varia de acordo com esta mudança no grau de antropização. Entretanto, há uma diminuição na diversidade de sítios de oviposição, que parece ser um fator limitante nas assembléias estudadas, uma vez que há correlação entre a composição vegetal e a composição de moscas em nossas amostras. Esta perda parece estar associada a uma diminuição na heterogeneidade ambiental e, conseqüentemente, a uma maior sobreposição do nicho das espécies de drosofilídeos.

Também foi verificado que espécies neotropicais da radiação *immigrans-tripunctata* do gênero *Drosophila* possuem a capacidade de colonizar tanto frutos quanto fungos, em ambientes preservados e alterados do Bioma Mata Atlântica.

Quanto ao último objetivo específico, que foi verificar se uma possível limitação de recurso para as larvas poderia estar incrementando a interação competitiva entre as mesmas, constatamos que sim, há evidências de que restrições alimentares ou nutricionais podem aumentar a interação competitiva entre espécies da família Drosophilidae. Entretanto, diferentes espécies possuem diferentes respostas a esta limitação, e ainda o aumento da competição interespecífica parece ser maior que da intraespecífica.

Além disso, foi realizado um levantamento dos registros de espécies de Drosophilidae no Brasil, sendo levantadas 304 espécies já coletadas em nosso território. A maioria dos registros se concentra no gênero *Drosophila*, o gênero mais bem estudado da família, e os estados mais bem amostrados são São Paulo, Rio de Janeiro, Rio Grande do Sul e Santa Catarina, além do Distrito Federal, onde há a presença de grupos de pesquisa enfocando as áreas de ecologia e taxonomia das espécies de Drosophilidae.

PERSPECTIVAS

Durante a realização do trabalho, alguns questionamentos e perspectivas de estudos complementares surgiram, dentre eles, a análises descritivas dos padrões da distribuição dos indivíduos de cada espécie de Drosophilidae sobre os frutos coletados, buscando identificar a importância relativa da partição de recursos e da agregação intraespecífica na manutenção da diversidade local nas áreas urbanas estudadas.

Além disso, evidenciamos a importância da identificação dos sítios de oviposição dos drosofilídeos, sendo necessária a investigação de outros tipos de recursos para um levantamento efetivo da fauna da região, incluindo flores, folhas e seivas de árvores, além da busca de eventuais hospedeiros de espécies de drosofilídeos parasitas. Ainda, evidenciamos a necessidade de um levantamento sistemático das espécies micófagas de Drosophilidae do Neotrópico, em especial do Brasil, onde poucos trabalhos foram realizados.

Ressaltamos que a atualização do banco de dados sobre a distribuição das espécies de Drosophilidae no Brasil e no Neotrópico é importante para proporcionar a realização de análises biogeográficas e ecológicas.

APÊNDICE I

STUDY OF THE DROSOPHILIDAE (DIPTERA) COMMUNITIES ON ATLANTIC FOREST ISLANDS OF SANTA CATARINA STATE, BRAZIL

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ECOLOGY, BEHAVIOR AND BIONOMICS

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

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

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

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

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

KEY WORDS: *Drosophila*, biodiversity, ecology

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

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

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

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

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

Methodology

Samples were taken as adults, flying over fermented banana bait and natural trophic resources (fermented fruits), at eight different sites (Fig. 1). Two of these sites were located on Santa Catarina Island: Morro da Lagoa da Conceição (27°35'27'S; 48°28'33'W – site A), a collecting point with *sensu strictu* secondary Atlantic Forest, in advanced process of regeneration and without recent human influence; and the Municipal Park of Lagoa do Peri (27°45'23'S; 48°32'58'W

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

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

Four sites are located on small islands near the mainland: Ratones Grande Island (27°28'58'S; 48°33'71'W - site B), located to the north of Santa Catarina Bay, approximately 0.8 km from the west coast of Santa Catarina Island; Ratones Pequeno Island (27°29'69'S; 48°33'97'W - site C), positioned a few hundred meters from Ratones Grande Island; Campeche Island (27°41'81'S; 48°28'88'W - Site H), to the east of the Island of Santa Catarina, approximately 1.5 km from the coast, being the most extreme easterly located collection site of this research; and Arvoredo Island (27°17'57'S; 48°21'23'W - Site G), situated 8 km from the north of Santa Catarina Island, being the northernmost sampling site studied in this research.

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

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

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

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

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

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

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

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

Results and Discussion

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

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

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

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

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

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

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

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

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

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

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

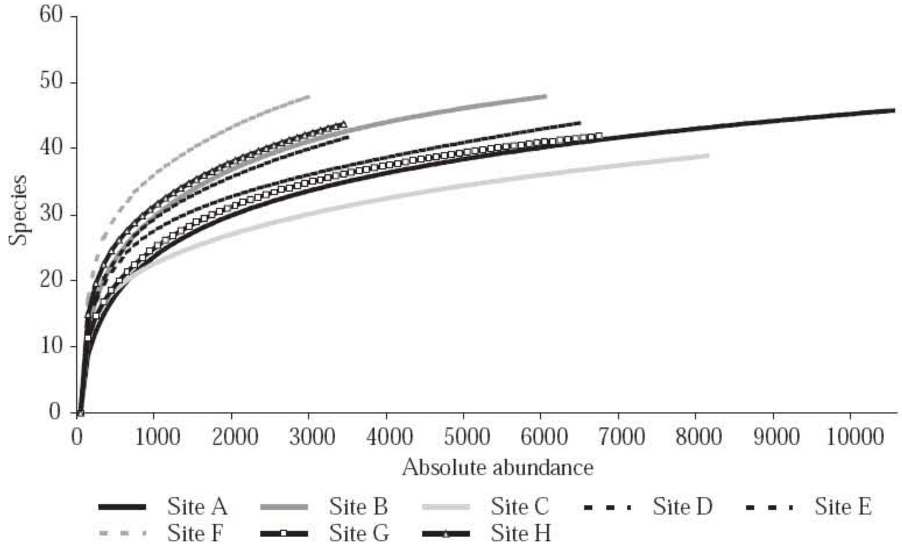

Fig. 2. Total rarefaction of species number per site.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

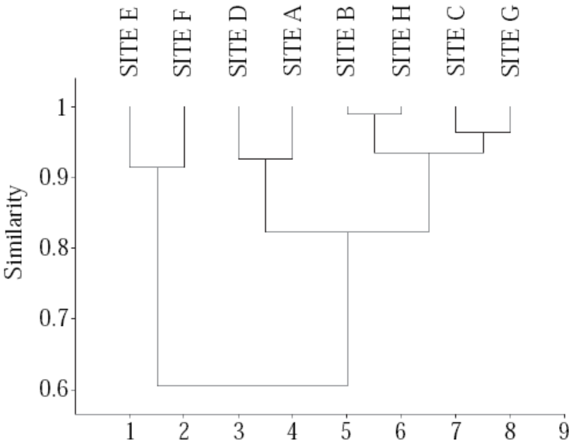

Fig. 3. Dendogram showing the similarity relationships between the studied assemblies.

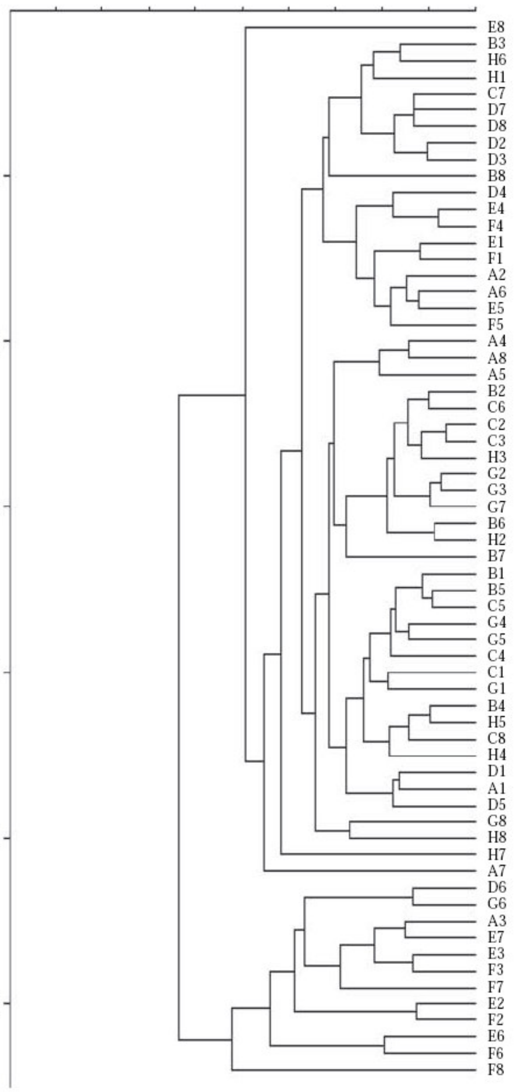

Fig. 4. Dendogram showing the similarity relationships between the studied assemblies at the different seasons. Numbers after the letter indicate the collecting site are corresponding with the months of the year.

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

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

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Annex

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

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

Continue

Table 1. Continuation.

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

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

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

Continue

Table 2. Continuation.

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

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

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

Continue

Table 3. Continuation.

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

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

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

Continue

Table 4. Continuation.

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

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

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

Continue

Table 5. Continuation.

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

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

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

Continue

Table 6. Continuation.

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

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

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

Continue

Table 7. Continuation.

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

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

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

Continue

Table 8. Continuation.

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

APÊNDICE II

A NOVEL RECORD OF DROSOPHILIDAE SPECIES IN THE CERRADO BIOME OF THE STATE OF MATO GROSSO, WSET-CENTRAL BRAZIL

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A novel record of Drosophilidae species in the Cerrado biome of the state of Mato Grosso, west-central Brazil.

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Introduction

Systematic studies on the ecology and distribution of Drosophilidae species in Brazil started in the 1940's (Dobzhansky and Pavan, 1943, 1950; Pavan, 1959). From then on, research groups were formed to investigate Drosophilidae species in different localities in Brazil, especially in the south-east and Atlantic Forest. More recently, by the end of the 1990's, systematic studies were conducted also in west-central Brazil, more specifically in the Cerrado biome (Tidon *et al.*, 2003, 2005; Tidon, 2006), in southern Brazil, in the Atlantic Forest biome (De Toni and Hofmann, 1995; Schmitz *et al.*, 2007; Gottschalk *et al.*, in press), and in the north, in the Amazonian biome (Martins, 1987, 2001).

Of the 3,952 Drosophilidae species described (Bächli, 2007), 308 have been recorded in Brazil (M.S. Gottschalk, personal communication), the majority of which are in south-eastern Brazil (Tidon-Sklorz and Sene, 1999; Medeiros and Klaczko, 2004).

Table 1. List of species with records in the state of Mato Grosso and respective references.

Species reccorded in Mato Grosso, Brazil	References
Chymomyza procnemis (Williston, 1896)	Kahl (1917)
Drosophila aguape Val & Marques, 1996	Val & Marques (1996)
D. bocainensis Pavan & Cunha, 1947	Pavan (1959)
D. capricorni Dobzhansky & Pavan, 1943	Pavan (1959), Dobzhansky & Pavan (1950)
D. eleonorae Tosi, Martins, Vilela & Pereira, 1990	Tosi *et al.* (1990)
D. equinoxialis Dobzhansky, 1946	De Toni *et al.* (2005)
D. fumipennis Duda, 1925	Pavan (1959), Dobzhansky & Pavan (1950)
D. immigrans Sturtevant, 1921	Dobzhansky & Pavan (1950)
D. maculifrons Duda, 1927	Pavan (1959), Dobzhansky & Pavan (1950)
D. malerkotliana Parshad & Paika, 1964	Val & Marques (1996), De Toni *et al.* (2005)
D. mediostriata Duda, 1925	Pavan (1959), Dobzhansky & Pavan (1950)
D. nebulosa Sturtevant, 1916	Pavan (1959), Dobzhansky & Pavan (1950), Val & Marques (1996)
D. neomorpha Heed & Wheeler, 1957	De Toni *et al.* (2005)
D. pallidipennis Dobzhansky & Pavan, 1943	Dobzhansky & Pavan (1950)
D. paranaensis Barros, 1950	Vilela (1983)
D. parthenogenetica Stalker, 1953	De Toni *et al.* (2005)
D. paulistorum Dobzhansky & Pavan *in* Burla *et al.*, 1949	De Toni *et al.* (2005)
D. polymorpha Dobzhansky & Pavan, 1943	Pavan (1959)
D. repleta Wollaston, 1858	Vilela (1983), Val & Marques (1996)
D. saltans Sturtevant, 1916	De Toni *et al.* (2005)
D. simulans Sturtevant, 1919	Dobzhansky & Pavan (1950), Val & Marques (1996), De Toni *et al.* (2005)
D. sturtevanti Duda, 1927	Dobzhansky & Pavan (1950), Pavan (1959), Val & Marques (1996), De Toni *et al.* (2005)
D. tropicalis Burla & Cunha *in* Burla *et al.*, 1949	De Toni *et al.* (2005)
D. willistoni Sturtevant, 1916	De Toni *et al.* (2005)
Rhinoleucophenga obesa (Loew, 1872)	Malogolowkin (1946)
Scaptodrosophila latifasciaeformis (Duda, 1940)	Pavan (1959), Dobzhansky & Pavan (1950), Val & Marques (1996)
Zaprionus indianus Gupta, 1970	David *et al.* (2006)
Zygothrica bilineata (Williston, 1896)	Grimaldi (1990)
Z. microeristes Grimaldi, 1987	Grimaldi (1987)
Z. prodispar Duda, 1925	Grimaldi (1987)

In the state of Mato Grosso, few studies on Drosophilidae species have been conducted, and only 30 species have been recorded (Table 1). Three biomes are observed in the state: Amazon, Pantanal and Cerrado, which covers most of the state's area. Cerrado is the second Brazilian biome in size. The prevailing vegetal physiognomy is the savannah, though forest patches are observed, in which vegetation aspect and physiognomy are varied (Valente, 2006). Estimates say that the biome comes second in species richness in the world. Yet, the Cerrado is endangered by the increase in plantation and pasture areas. Nowadays the Cerrado is considered a global conservation hotspot (Myers *et al.*, 2000).

In an effort to add to the current knowledge of drosophilid distribution in the Cerrado biome, our study lists 18 records of Drosophilidae species in the Tangará da Serra region, state of Mato Grosso, west-central Brazil, new to the region.

Figure 1. South America map indicating the municipality of Tangará da Serra, state of Mato Grosso (MT), Brazil.

Material and Methods

Sample collections were carried out in the municipality of Tangará da Serra, state of Mato Grosso (14°04'38"S; 57°03' 45"W) (Figure 1), located between Parecis and Tapirapuã mountain ranges. The prevailing vegetation class is the Seasonal Semi-deciduous Forest. Nowadays, the patches of intact original vegetation are rare in the region. This area of the Cerrado biome undergoes the influence of the Amazonian biome, receiving an expressive number of animal and plant species native to the latter. Adult fly specimens were collected (i) on specially prepared banana baits (Tidon and Sene, 1988) and (ii) flying over fruit lying in the collection site, using an entomological net, whereas larvae were collected with fruit and flowers and reared in the laboratory upon emergence of adult flies. Plant species on which individuals were collected (adult or as immature) were also recorded. As for immature individuals, the material was sent to the laboratory and stored in a controlled temperature environment (21 ± 1°C) for one month. Emerging flies were retrieved daily. Table 2 shows the dates, locations and collection approaches adopted.

The characterization of the drosophilids collected was based on external morphologic traits and male genitalia, according to Wheeler and Kambysellis (1966).

Table 2 – Date, location, collection method, and plant species collected and used as feeding or breeding sites.

	Date	Location	Collection method / resource collected
01	March 22nd 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Artocarpus heterophyllus* (Thunb.) (Moraceae) – jackfruit
02	March 22nd 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Persea americana* Mill. (Lauraceae) – avocado
03	March 25th 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Artocarpus heterophyllus* (Thunb.) (Moraceae) – jackfruit
04	March 31st 2007	Forest patch near Agricultural School	Flying over fruits of *Bactris coccinea* Barb. Rodr. (Palmae) – red club palm
05	April 13th 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Malpighia glabra* L. (Malpighiaceae) – acerola fruit
06	23rd to 26th April 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Persea americana* Mill. (Lauraceae) – avocado
07	23rd to 26th April 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Pyrus* sp. (Rosaceae) – common pear
08	24th April 2007	Park in town center	Emerged from flowers of Convolvulaceae
09	13th May 2007	Vacant lot in downtown	Emerged from flowers of Convolvulaceae
10	13th May 2007	Park in town center	Emerged from *Buchenavia tomentosa* Eichler (Combretaceae) – mirindiba fruit
11	14th May 2007	Garden of UNEMAT *Campus*	Flying over fruits of *Artocarpus heterophyllus* (Thunb.) (Moraceae) – jackfruit
12	18th May 2007	Plantation near UNEMAT *Campus*	Inside flowers of *Cucurbita pepo* L. (Cucurbitaceae) – zucchini
13	18th to 21st May 2007	Forest patch near UNEMAT *Campus*	Collection using traps according to Tidon & Sene (1988)
14	18th to 21st May 2007	Pasture area near UNEMAT *Campus*	Collection using traps according to Tidon & Sene (1988)

Results and Discussion

A total of 1,187 individuals were collected. Specimens belonged to 35 species and four genera of Drosophilidae, the majority of which associated to fruit (Table 3). The only species associated to flowers were *D. denieri* and one *Drosophila* species belonging to the *bromeliae* group, not yet described — *Drosophila* sp.1 (H.J. Schmitz, personal communication). Schmitz and Hofmann (2005) state that *D. denieri* was recorded in Argentina, Uruguay, and in the Brazilian states of Rio Grande do Sul and Santa Catarina. The authors draw attention to the hypothesis that the apparently restricted distribution of *D. denieri* is due to inappropriate collection approaches. The first record of the species in the Mato Grosso section of the Cerrado biome confirms the notion.

Table 3. Species collected in the region of Tangará da Serra, state of Mato Grosso, Brazil. Numbers indicate collections mentioned in Table 2.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	Total
Drosophila															
atrata group															
D. calloptera Schiner, 1868*	-	1	-	5	-	-	-	-	-	-	-	-	-	-	6
bromeliae group															
Drosophila sp.1	-	-	-	-	-	-	-	8	-	-	-	-	-	-	8
canalinea group															
D. canalinea Patterson & Mainland, 1944*	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2
cardini group															
D. cardini Sturtevant, 1916*	1	3	3	-	-	-	-	-	-	1	-	-	55	78	141
D. cardinoides Dobzhansky & Pavan, 1943*	-	-	-	-	-	-	-	-	-	52	-	-	-	-	52
D. polymorpha Dobzhansky & Pavan, 1943	-	-	1	-	-	1	-	-	-	-	-	-	-	-	2
melanogaster group															
D. ananassae Doleschall, 1858*	1	-	1	-	-	-	-	-	-	1	3	-	-	-	6
D. kikkawai Burla, 1954*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
D. malerkotliana Parshad & Paika, 1964	23	-	-	-	1	1	1	-	-	12	-	-	83	11	132
D. melanogaster Meigen, 1830*	-	-	-	-	-	-	-	-	-	-	2	-	-	4	6
D. simulans Sturtevant, 1919	-	-	-	-	5	-	-	-	-	-	-	-	2	5	12
repleta group															
D. hydei Sturtevant, 1921*	37	-	1	-	-	-	-	-	-	-	-	-	-	7	45
D. mercatorum Patterson & Wheeler, 1942*	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
D. moju Pavan, 1950*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
D. paranaensis (Barros, 1950)	-	-	-	-	-	-	-	-	-	-	-	-	4	1	5
D. zottii Vilela, 1983*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
saltans group															
D. prosaltans Duda, 1927*	-	-	1	-	-	-	-	-	-	-	1	-	9	2	13
D. sturtevanti Duda, 1927	-	-	1	-	-	-	-	-	-	-	3	-	25	3	32
Drosophila sp.2	-	-	-	-	-	-	-	-	-	-	2	-	2	-	4
tripunctata group															
D. cuaso Bächli, Vilela & Ratcov, 2000*	-	-	-	-	-	-	-	-	-	25	-	-	-	-	25
D. mediopunctata Dobzhansky & Pavan, 1943*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
D. mediostriata Duda, 1925	-	-	-	3	-	-	-	-	-	18	-	-	2	2	25
D. neoguaramunu Frydenberg, 1956*	-	-	-	1	-	-	-	-	-	-	-	-	1	-	2
D. paramediostriata Townsend & Wheeler, 1955*	-	7	1	-	-	-	-	-	-	-	-	-	-	-	8
D. trapeza Heed & Wheeler, 1957*	-	-	3	-	-	-	-	-	-	-	-	-	2	-	5
willistoni group															
D. nebulosa Sturtevant, 1916	-	-	-	-	2	-	2	-	-	48	-	-	2	1	55
willistoni subgroup	4	-	-	-	-	-	-	-	-	7	-	-	4	1	16
Drosophila sp.3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
not grouped															
D. denieri Blanchard, 1938*	-	-	-	-	-	-	-	-	1	-	-	24	-	-	25
Drosophila sp.4†	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
Rhinoleucophenga															
R. obesa (Loew, 1872)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Rhinoleucophenga sp.1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Rhinoleucophenga sp.2	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
Scaptodrosophila															
latifasciaeformis group															
S. latifasciaeformis (Duda, 1940)	116	8	36	-	2	4	1	-	-	-	5	-	27	168	367
Zaprionus															
vittiger group															
Z. indianus Gupta, 1970	-	-	1	-	14	-	-	-	-	33	1	-	23	105	177
Total	183	20	49	10	24	6	5	8	1	198	17	24	248	394	1187

species with first record in the state of Mato Grosso

†same *Drosophila* sp.4 mentioned in Gottschalk *et al.* (in press*)

The lack of collections in the region also explains why *D. calloptera* and *D. moju*, which distribute in the Amazon and in the Atlantic Forest (Val *et al*., 1981; De Toni *et al*., 2007; Gottschalk *et al*., in press), had not been recorded in the Cerrado before. In turn, *D. cuaso* distribution was confined to the Atlantic Forest, and the present record being the first outside that biome (Bächli *et al*., 2000).

The other species presenting novel records in the state of Mato Grosso are: *D. canalinea*, *D. cardini*, *D. cardinoides*, *D. hydei*, *D. mediopunctata*, *D. mercatorum*, *D. neoguaramunu*, *D. paramediostriata*, *D. prosaltans*, *D. trapeza* and *D. zottii*. However, these species had previously been described in other Cerrado regions (Sene *et al*., 1980; Martins, 2001; De Toni *et al*., 2007). For the first time in the state the following species of the *melanogaster* groups were recorded: *D. ananassae*, *D. kikkawai,* and *D. melanogaster*. These species are cosmopolitan, exotic to the Neotropical region, and are very common in open areas of all South American continent (Ferreira and Tidon, 2005; Gottschalk *et al*., in press).

In spite of the efforts by Brazilian researchers to obtain representative samples of Drosophilidae in the country's territory as a whole, the biogeographic and ecological studies conducted have failed to cover an expressive extension of the territory, leaving several areas totally unexplored or poorly sampled. Considering the current stage of degradation of most biomes, a considerable body of evidence on species distribution might now be irremediably lost, let alone the fact that the extent of endemism areas that have vanished is unknown.

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ANEXOS

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BRYANT, J. P. 1915. Woody plant-mammals interactions. *In*: ROSENTHAL, G. A. & BEREMBAUM, M. R. eds. **Herbivores: their interactions with secondary plants metabolites**. San Diego, Academic. v.2, p.344-365.

HOLME, N. A.; BARNES, M. H. G.; IWERSON, C. W. R.; LUTKEN, B. M. & MCINTYRE, A. D. 1988. **Methods for the study of marine mammals**. Oxford, Blackwell Scientific. 527p.

PLATNICK, N. I. 2002. **The world spider catalog, version 3.0**. American Museum of Natural History. Disponível em: <http://research.amnh.org/entomology/spiders/catalog81-87/index.html>. Acesso em: 10.05.2002.

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13. A listagem do material examinado deve dispor as localidades de Norte a Sul e de Oeste a Leste e as siglas das instituições compostas preferencialmente de até 4 letras, segundo o modelo abaixo:

VENEZUELA, **Sucre:** San Antonio del Golfe, (Rio Claro, 5º57'N 74º51'W, 430m) 5♀, 8.VI.1942, S. Karpinski col. (MNHN 2547). PANAMÁ, **Chiriquí:** Bugaba (Volcán de Chiriquí), 3♂, 3♀, 24.VI.1901, Champion col. (BMNH 1091). BRASIL, **Goiás:** Jataí (Fazenda Aceiro), 3♂ , 15.XI.1915, C. Bueno col. (MZSP); **Paraná:** Curitiba, ♀, 10.XII.1925, F. Silveira col. (MNRJ); **Rio Grande do Sul:** São Francisco de Paula (Fazenda Kraeff, Mata com Araucária, 28º30'S 52º29'W, 915m), 5♂ , 17.XI.1943, S. Carvalho col. (MCNZ 2147).

14. Enviar, juntamente com as cópias impressas, cópia do manuscrito em meio digital (disquete, zip disk ou CDROM, devidamente identificado) em arquivo para Microsoft Word (*.doc) ou em formato “Rich Text” (*.rtf). Para as imagens digitalizadas, utilizar resolução mínima de 300 dpi e arquivos Bitmap TIFF (*.tif). Enviar as imagens nos arquivos originais (não inseridas em arquivos do MS Word, MS Power Point e outros), rotulados de forma auto-explicativa (e. g. figura01.tif). Gráficos e tabelas devem ser inseridos em arquivos separados (Microsoft Word ou Excel). Para arquivos vetoriais utilizar formato Corel Draw (*.cdr).

15. As provas não serão enviadas aos autores, exceto em casos especiais.

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Instructions for Species Lists

Cover Page

Title: Taxonomic group, locality (optional), State, Country

e.g.: *Fish, Conewango Creek, Allegheny River Drainage, New York, USA.*

Author(s): Name(s) with respective institution and author for correspondence (provide e-mail):

e.g.:

Diego F. Cisneros-Heredia[1,3]
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[3]*Corresponding author: diegofrancisco_cisneros@yahoo.com*

Second Page (the first to be numbered)

Abstract

Up to 150 words

Introduction

Brief

Materials and Methods

✓ Study Site
✓ Data Collection (any sort of permits/authorizations should be mentioned in this section)
✓ Data Analysis (optional)

Results and Discussion

Please, suggest the placement of Tables and Figures in the text

Acknowledgements (optional)

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Journal articles with usual volume and issue number

Orr, J. W. 2004. *Lopholiparis flerxi*: a new genus and species of Snailfish (Scorpaeniformes: Liparidae) from the Aleutian Islands, Alaska. Copeia 2004(3): 551-555.

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Prado, J. and C. E. M. Bicudo. 2002. Theses as media for effective publication: new data for an old problem. Taxon 51: 525-527.

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Book

Nelson, J. S., E. J. Crossman, H. Espinosa-Perez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. Bethesda, Maryland. American Fisheries Society, Special Publication 29. 386 p.

Material from the World Wide Web

Frost, D. R. 2004. Amphibian Species of the World: an online reference. Version 3.0. Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA. Captured on 04 February 2005.

TABLES

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TITLE: Taxonomic Group, *Species name*(s) (or taxa name): category (extended distribution, reduced distribution, historical occurrence, filling gaps, other)

AUTHOR NAMES AND INSTITUTIONS

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```
<taxaList>
   <taxon class="Actinopterygii" family="Acestrorhynchinae" genus="Acestrorhynchus" species="falcatus"/>
   < taxon class="Actinopterygii" family="Acestrorhynchinae" genus="Acestrorhynchus" species="microlepis"/>
   < taxon class="Actinopterygii" family="Acestrorhynchinae" genus="Acnodon" species="normani"/>
   <taxon class="Actinopterygii" family="Acestrorhynchinae" genus="Knodus"/>
</taxaList>
```

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