



Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais



**Padrões de distribuição de Drosofilídeos entre
Florestas/Bosques e Zonas de Mata
Paludosa/Banhados e entre os Biomas brasileiros
Pampa e Mata Atlântica**

Lucas Baptista Duarte

Orientador: Dr^a. Lizandra Jaqueline Robe
Co-orientador: Dr. Marco Silva Gottschalk

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Aluno: Lucas Baptista Duarte

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Dissertação apresentada ao Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais como requisito parcial para a obtenção do título de Mestre em Biologia de Ambientes Aquáticos Continentais.

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*Dedico esse trabalho à minha família
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apoio de vocês foi fundamental na construção e
conclusão de mais essa etapa.*

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RESUMO

O Brasil é considerado um país megadiverso, caracterizado por uma rica diversidade de fauna e flora. Toda essa biodiversidade distribui-se em seis biomas, cada um com suas características. Dois desses biomas, Pampa e Mata Atlântica, dividem o estado do Rio Grande do Sul em áreas com fitofisionomias distintas que vem sendo severamente impactados ao longo dos últimos anos. No entanto, os padrões de distribuição da biodiversidade dentro e entre esses biomas é ainda pouco compreendido. Essa dissertação propõe, pois, o uso de espécies de Drosophilidae, como modelos ecológicos para acessar os padrões de distribuição da biodiversidade no sul do Brasil, pela comparação da diversidade encontrada entre florestas/bosques e zonas de mata paludosa/banhados e entre os biomas Pampa e Mata Atlântica. Para tanto, foi utilizada uma estratégia baseada na realização de coletas pontuais, mas bem distribuídas ao longo do território alvo, em que drosofilídeos foram amostrados com o uso de armadilhas com isca de banana. Todos os indivíduos coletados foram identificados até o menor nível taxonômico possível. Neste sentido, o capítulo 1 desta dissertação compara as assembléias de Drosophilidae amostradas em áreas de mata paludosa/banhados com aquelas de florestas/bosques do RS, demonstrando a presença de padrões de abundância e composição diferenciados para os dois tipos de habitats, com menores níveis de diversidade no primeiro. Na comparação entre Biomas, apresentada no capítulo 2 desta dissertação, foi demonstrado que a diversidade gama de drosofilídeos encontrada na Mata Atlântica é maior do que aquela registrada para o Pampa, em consequência de sua maior diversidade beta. No entanto, muitas espécies apresentam uma maior associação com o último destes Biomas, demonstrando a importância da conservação das mais diferentes áreas.

Palavras-chave: diversidade alfa; diversidade beta; diversidade gamma; espécie bionindicadora; banhados; Pampa;

ABSTRACT

Brazil is considered a megadiverse country, characterized by a rich diversity of fauna and flora. All this biodiversity is distributed in six biomes, each with its own characteristics. Two of these biomes, Pampa and Mata Atlântica, divide the state of Rio Grande do Sul into areas with distinct phytophysiognomies that have been severely impacted during the last years. However, the patterns of biodiversity distribution within and between these biomes are still poorly understood. Thus, this dissertation proposes the use of Drosophilidae species as ecological models for accessing biodiversity distribution patterns in southern Brazil, by comparing the diversity found between flooded and nonflooded areas in RS and between the Pampa and Atlantic Forest Biomes. For this, punctual, but well distributed collections were performed throughout the target territory, where drosophilids were sampled with the use of banana baited traps. All individuals collected were identified to the lowest possible taxonomic level. In this sense, chapter 1 of this dissertation compares Drosophilidae assemblages sampled between flooded and nonflooded areas of RS, demonstrating the presence of differential patterns of abundance and composition of species for the two types of habitats, with lower levels diversity in the first. In the comparison between Biomes, presented in chapter 2 of this dissertation, it was shown that richness of drosophilids found in the Atlantic Forest is higher than that recorded for the Pampa, as a consequence of its higher beta diversity. However, many species also have a greater association with the last of these Biomes, demonstrating the importance of conserving the most different areas.

Key-words: alpha diversity; beta diversity; gamma diversity; bioindicator species; swamps; Pampa.

APRESENTAÇÃO

Esta dissertação apresenta em sua estrutura, introdução geral, capítulo 1, capítulo 2, referências bibliográficas e considerações finais e perspectivas, e seguem as normas da ABNT. O capítulo 1 segue as normas da revista RBE (Revista Brasileira de Entomologia) e apresenta resumo, introdução, material e métodos, resultados, discussão e referências. O capítulo determina a composição das assembléias de drosofilídeos presentes em áreas alagadas e comparando com as presentes em áreas não alagadas do extremo sul do Brasil. O capítulo 2 seguirá as normas da revista a ser submetido posteriormente e está estruturado em resumo, introdução, material e métodos, resultados, discussão e referências. Este capítulo faz comparação da diversidade (alfa, beta e gama) das comunidades de drosofilídeos entre os biomas brasileiros Pampa e Mata Atlântica.

Esta dissertação tem como objetivo contribuir com conhecimentos sobre as comunidades de drosofilídeos presentes em áreas alagadas do extremo sul do Brasil, bem como a diversidade presente nos biomas do estado do Rio Grande do Sul, somando ao conhecimento já existente.

SUMÁRIO

LISTA DE FIGURAS.....	x
LISTA DE TABELAS.....	xi
INTRODUÇÃO GERAL.....	13
1. Hotspots de diversidade: Brasil e seus Biomas meridionais.....	14
2. Espécies bioindicadores e drosofilídeos.....	16
REFERÊNCIAS BIBLIOGRÁFICAS.....	19

CAPÍTULO UM.....

Assemblage of drosophilids (Diptera, Drosophilidae) inhabiting flooded and nonflooded areas in the extreme South of Brazil.....	29
<i>Abstract</i>	30
INTRODUCTION.....	31
MATERIALS AND METHODS.....	
<i>Study area</i>	32
<i>Collections</i>	34
<i>Identification</i>	34
<i>Data analysis</i>	35
RESULTS.....	35
DISCUSSION.....	36
ACKNOWLEDGEMENTS.....	39
REFERENCES.....	39

CAPÍTULO DOIS.....

Comparison of alpha, beta and gamma-diversity patterns of drosophilids (Diptera) between the Brazilian Pampa and Atlantic Forest Biomes.....	51
<i>Abstract</i>	52
INTRODUCTION.....	53
MATERIALS AND METHODS.....	
<i>Collection and Identification of Specimens</i>	55
<i>Data analysis</i>	55
RESULTS.....	56

DISCUSSION.....	58
REFERENCES.....	59
CONSIDERAÇÕES FINAIS E PERSPECTIVAS.....	78
APENDICE: <i>Material Suplementar</i>	78

LISTA DE FIGURAS

CAPÍTULO UM

Figura 1: Rarefaction curves for flooded and nonflooded areas.....49

Figura 2: Principal Coordinates Analysis (PCoA) ordination of the set of sampling points, according to Bray-Curtis dissimilarity measures. The graphic presents the results obtained with the use of the first two coordinates, which explained 50% of the variability presented by the data. The plot presented in (A) was compacted in (B), in order to represent the 95% confidence ellipses.....50

CAPÍTULO DOIS

Figure 1: Gain in sample coverage as a function of the addition of individuals in Atlantic Forest (red) and Pampa (blue) samples. Solid lines = rarefaction by interpolation; dash lines = extrapolation.....74

Figure 2: Rarefaction curves of species richness for the Atlantic Forest (red) and Pampa (blue) Biomes. Solid lines = rarefaction by interpolation; dash lines = extrapolation; shaded area = 95% confidence interval as measured by 999 permutations.....75

Figure 3: Principal Coordinates Analysis (PCoA) ordination of the set of sampling points, according to Bray-Curtis dissimilarity measures in the two first coordinates, which explain 17.8% and 15.1% of the variation in the data. Crosses = Atlantic Forest sampling sites; squares = Pampa sampling sites.....76

LISTA DE TABELAS

CAPÍTULO UM

Table 1: List of sampling points, with their respective coordinates and sampling dates.....43

Table 2: List of species collected in flooded areas (points 1-8), with abundance and richness values recorded for each and for the total set of points.....44

Table 3: List of species collected in nonflooded areas (points 9-15), with abundance and richness values recorded for each and for the total set of points.....46

Table 4. Summary of the results provided by SIMPER Analysis, listing the ten species that are primarily responsible for the differences between flooded and nonflooded areas in decreasing order of contribution.....48

CAPÍTULO DOIS

Table 1: Biomes subdivision of the 42 sampling localities, with their respective geographical coordinates, dates and season of collection.....65

Table 2: List of sampled species, with their respective abundance (ni) and frequency (fi) values in each of the sampled Biomes, and in the total set of sampling points. Exotic species are demarked with an “*”. At the end of the table it is possible to find the comparative values of abundance (absolute and average $\pm$ standard deviation per sample), richness (absolute and average $\pm$ standard deviation per sample) and Pielou’s equitability index per biome, with the number of collections performed.....67

Table 3: List of species classified as generalist, or as Atlantic Forest or Pampa specialist by CLAM analysis.....71

Table 4: List of species with significant IndVals for the different Biomes.....	72
--	----

Table 5: List of the ten species that are primarily responsible for the differences between Pampa and Atlantic Forest according to SIMPER analysis in decreasing order of contribution.....	73
--	----

INTRODUÇÃO GERAL

A sobrevivência e a reprodução de um organismo em qualquer ambiente dependem de uma combinação de fatores bióticos e abióticos (Lara, 1995). Estes fatores condicionam o nicho da espécie. Neste sentido, Hutchinson (1957) cunhou o termo “nicho fundamental” para se referir ao conjunto de variáveis que condicionam a sobrevivência de uma espécie, diferenciando-o do “nicho realizado”, que se refere ao “espaço” efetivamente ocupado pela espécie, restringido pelas interações biológicas. Estas relações, no entanto, são dinâmicas, e as espécies também podem modificar o seu nicho pelos processos de perturbação e realocação (Odling-Smee *et al.*, 2003; Tidon 2006). Mesmo em condições ótimas, oscilações nas abundâncias das espécies ocorrem ao longo do tempo e do espaço (Poppe *et al.*, 2015).

Padrões globais de distribuição da diversidade e suas causas têm sido alvo de debates constantes na literatura ecológica ao longo do último século (MacArthur, 1965; Gaston, 2000; Hawkins *et al.*, 2003; Ricklefs *et al.*, 2004). Destes, o gradiente latitudinal de biodiversidade foi certamente um dos primeiros padrões ecológicos reconhecidos (Hawkins, 2003). No entanto, a compreensão dos padrões e processos atuando em escalas menores, com grupos específicos de organismos, ainda é, frequentemente, pouco compreendida.

Uma das primeiras avaliações necessárias para a compreensão dos padrões de distribuição da biodiversidade, e, desta forma, para o suporte a um argumento de conservação, diz respeito à inferências de riqueza de espécies e abundância de espécimes. Estes padrões podem ser avaliados em três escalas: diversidade alfa (α), beta (β) e gama (γ) (Whittaker, 1972). Neste caso, diversidade alfa (α) ou diversidade local é o número total de espécies em um habitat; diversidade gama (γ) ou diversidade regional é o número total de espécies observado em todos os habitats; e diversidade beta (β) é a mudança de espécies ao longo de um gradiente ambiental (Magurran, 2004). A diversidade, em geral, depende do esforço amostral do pesquisador, quanto mais exaustiva, maior as chances de conhecer a diversidade total do local (Gaston, 1996). No entanto, frequentemente, a distribuição das amostragens e dos estudos entre diferentes áreas ou habitats é bastante enviesada.

Dependendo da ênfase destes estudos, frequentemente são encontradas associações entre maiores níveis de interferência humana e menores níveis de diversidade (Gottschalk *et al.*, 2007). Isto ocorre porque o desenvolvimento humano vem causando mudanças nas paisagens naturais, transformando-os em paisagens fragmentadas e acarretando grande perda da biodiversidade, levando a alterações ecológicas importantes para a manutenção desses ambientes e das relações que nele ocorrem (Tabarelli *et al.*; 1999; Tabarelli & Gascon, 2005).

De fato, de acordo com diversos pesquisadores (Kolbert, 2014; WWF, 2016), estamos atualmente enfrentando a sexta extinção em massa, cuja extensão parece ser maior do que previamente pensado. Dentro desta perspectiva, conceitos ecológicos com uma base conservacionista vem recebendo cada vez mais destaque.

1. *Hotspots* de diversidade: Brasil e seus Biomas meridionais

O termo *Hotspots* foi introduzido em 1988 pelo ambientalista britânico Norman Myers e adotado em 1989 pela *União Internacional para a Conservação da Natureza* (IUCN) Para uma área ser classificada como um *hotspot*, ela deve: (1) abrigar no mínimo 1.500 espécies de plantas vasculares endêmicas e (2) ter 30% ou menos da sua vegetação original mantida (Mittermeier et al., 2004). Ao total existem 25 *hotspots* mundiais, dentre os quais duas ecoregiões brasileiras: Cerrado e Mata Atlântica. A Mata Atlântica encontra-se entre os *hotspots* que abrigam pelo menos 2% espécies de plantas endêmicas e vertebrados do mundo (Myers et al., 2000).

O Brasil engloba a maior cobertura de floresta tropical do mundo e constitui um dos principais detentores de megadiversidade do planeta, possuindo 10 a 13% do número total de espécies da Terra (Lewinsohn e Prado, 2005). Porém, uma pequena parcela destas florestas encontra-se em áreas de proteção ambiental ou é classificada como *hotspot*, o que torna o restante suscetível a degradação e a consequente perda de biodiversidade. O aumento constante do comércio agrícola e madeireiro, juntamente com o crescimento populacional são os principais causadores da destruição das florestas, e estes, por sua vez, afetam diretamente a biodiversidade, ocasionando a perda e até mesmo a extinção das espécies, que muitas vezes é fatal e irreversível (Mittermeier et al., 2004; IUCN, 2007). Desse modo, muitos estudos ecológicos vêm sendo realizados com objetivo de conhecer a riqueza presente em diversos habitats e assim demonstrar a importância da conservação desses locais (Develey et al. 2008; Leal et al. 2005; Tabarelli et al. 2005; Klink e Machado, 2005; Braga, 1979; Ferreira et al., 2005).

O Brasil tem seu território subdividido em seis Biomas de características distintas: Amazônia, Caatinga, Cerrado, Mata Atlântica, Pampa (ou Campos Sulinos) e Pantanal (Brasil, 2017). Cada um destes biomas apresenta uma diversidade animal e vegetal própria, como efeito do compartilhamento das condições geológicas ou climáticas, e da própria história de formação de paisagem (IBGE, 2017). Destes, o estado do Rio Grande do Sul apresenta áreas de Mata Atlântica (bioma compartilhado com outros 16 estados brasileiros: Alagoas, Bahia, Ceará, Espírito Santo, Goiás, Minas Gerais, Mato Grosso do Sul, Paraíba, Pernambuco, Piauí, Paraná, Rio de Janeiro, Rio Grande do Norte, Santa Catarina, Sergipe e São Paulo), e de Pampa (bioma exclusivo deste estado, do Uruguai e da Argentina - Pallarés et al., 2005).

Segundo o Instituto Brasileiro de Florestas (IBF, 2017), a Mata Atlântica é constituída principalmente por mata, distribuindo-se ao longo da costa litorânea do Brasil, desde o Rio Grande do Norte até o Rio Grande do Sul, e correspondendo a 13% do território nacional. A Mata Atlântica é considerada um dos maiores repositórios de biodiversidade do planeta, e abriga 35% das espécies vegetais do Brasil, além de 849 espécies de aves, 370 espécies de anfíbios, 200 espécies de répteis, 270 espécies de mamíferos e aproximadamente 350 espécies de peixes (Varjabedian, 2010; Brasil 2017). De fato, a Mata Atlântica constitui o Bioma brasileiro com a segunda maior riqueza de espécies, tanto em termos de flora como fauna. Na região sul do Brasil, este bioma apresenta temperaturas médias elevadas durante o ano todo e não apenas no verão; já no inverno a temperatura chega a cair abaixo de 0°. A alta pluviosidade nesse bioma (média de 1200 mm anuais) deve-se a barreira que a serra constitui para os ventos que sopram do mar. A Mata Atlântica apresenta uma variedade de fitofisionomias ao longo da sua abrangência, entre as quais destacam-se a Floresta Ombrófila Mista, com ocorrência no sul e sudeste do Brasil e com predominância de *Araucaria angustifolia*, e a Floresta Estacional Semidecidual, considerada uma transição entre a Floresta Tropical e o Cerrado (Oliveira-Filho & Fontes, 2000). Outra fitofisionomia da Mata Atlântica com destaque no Sul do Brasil é a Floresta Paludosa, também conhecida como Floresta Latifoliada Higrófila ou mesmo Mata de Brejo, caracterizada pela presença de solo permanentemente alagado (Marques et al., 2003). Por esta característica, estas áreas diferenciam-se da vegetação que se encontra no entorno, como é o caso das florestas ripárias (Ivanauskas et al., 1997). Essas matas ainda são pouco estudadas no Brasil e sua degradação é crescente, o que leva a aumento da fragmentação da Mata Atlântica (Toniato et al., 1998). Somando-se todos os danos, a Mata Atlântica apresenta, atualmente, apenas 8,5% da cobertura original (Brasil, 2014), e se encontra severamente ameaçado em vista desta perda de habitat.

Por outro lado, no Brasil, o Pampa ocorre apenas na metade Sul do Rio Grande do Sul, dividindo o estado com a Mata Atlântica. Este bioma ocupa 63% do território do estado (Suertegaray & da Silva, 2009) tem os campos como paisagem dominante (Boldrini et al., 2010). Neste caso, segundo Pillar et al. (2009), embora a vegetação dominante seja representada por gramíneas (Campos Limpos), existem muitas espécies herbáceas e arbustivas (Campos Sujos). Além disso, ao longo do manto de vegetação campestre, são encontradas manchas de matas densas, matas ciliares e matas de galeria localizadas em áreas úmidas, o que leva a constituição de um mosaico de paisagens (Boldrini et al., 2010) Estas áreas sofrem a influência de um clima temperado, com frentes frias periódicas no inverno, derrubando as temperaturas (Suertegaray & da Silva, 2009), e verões quentes e sem estações secas (Pillar et

al., 2009). O Pampa apresenta precipitação anual de 1200-1600 mm/ano e temperatura média anual de 13-17°C. Com uma biodiversidade vegetal estimada em 3000 espécies apenas para o RS, muito ainda se desconhece de sua diversidade total (Boldrini, 1997). De fato, segundo Binkowski (2009), o Pampa possui um papel importante na conservação da biodiversidade, por apresentar a riqueza de fauna e flora pouco pesquisada. Em 1996, este bioma apresentava uma área de 13,7 milhões ha, sendo 10,5 milhões ha no RS; porém essa área vem sendo perdida devido à crescente expansão agrícola (Pillar et al., 2009). O cultivo de *Pinus* sp. para produção de celulose é outro fator que vem diminuindo as áreas naturais, antes utilizadas com pecuária.

Uma formação que ocorre na Mata Atlântica, mas é especialmente comum nos Pampas gaúchos são os banhados, classificados como partes de terra parcial ou permanentemente alagadas, constituídas por uma vegetação característica de água doce ou salobra (Irgang & Gastal Jr., 1996) e consideradas uma área de transição entre os ecossistemas aquáticos e terrestres. Essas áreas são extremamente sensíveis ao regime hídrico e alterações no nível da água. Apresentam grande diversidade vegetal devido a alta produtividade do ambiente, o que atrai muitos animais que o utilizam para alimentação, nidificação, refúgio e reprodução (Irgang & Gastal Jr., 1996). Apresentam grande importância no armazenamento do excesso de água proveniente das chuvas, característica essa denominada de efeito esponja (Dorst, 1973). Entre os principais impactos sofridos por esses ambientes, destacam-se a expansão urbana e suas consequências, como depósito de lixo, descarga de efluentes domésticos, caça e drenagem para irrigação (Burger, 1999). Devido a esses fatores, a degradação dos banhados vem aumentando, e, como consequência, a diversidade a eles associada vem diminuindo. É, pois, cada vez mais necessário a criação de planos de manejo e conservação dessas áreas, devido a sua importância e fundamental função no ecossistema.

2. Espécies bioindicadores e drosofilídeos

O termo “bioindicador” se refere a uma espécie ou grupo de espécies que refletem o estado abiótico ou biótico do meio em que se encontram e o impacto produzido sobre o mesmo (Parmar et al., 2016). Embora Platão tenha sugerido algo semelhante ao se referir às alterações humanas impactando a colheita de frutos (Rapport, 1992), foi somente no século XVI que os primeiros conceitos se referindo as comunidades de plantas e animais surgiram com os estudos de Clements (1920). Dessa forma, descobriu-se a característica bioindicadora de muitos táxons (Parmar et al., 2016) e diversos estudos vem sendo realizados para verificar a resposta destes organismos frente a mudanças que ocorrem no ambiente (Pimentel et al. 2011; Kumari et al., 2008; Koskimies, 1989; Young et al. 2014; Brown Jr. & Freitas, 2000). Neste caso, embora as relações entre espécies e ambiente sejam em grande parte incompreendidas, diferentes táxons

vem sendo utilizados como bioindicadores na análise das condições gerais do ambiente ou de um componente da biodiversidade (McGeoch, 1998). Entre eles, os insetos constituem um grupo comumente empregado como bioindicador (Andersen, 1997; Brown Jr., 1997; Andersen *et al.*, 2001; Oliveira *et al.* 2014), devido a sua grande diversidade, abundância e sensibilidade às alterações ambientais (Wink *et al.*, 2005). Segundo Brown Jr. (1997) os insetos das ordens Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepdoptera e Orthoptera são os principais indicadores do monitoramento ambiental.

Nesta linha, o uso potencial de diferentes espécies de Drosophilidae como bioindicadores vem sendo sugerido (Parsons, 1991) e, mais recentemente, demonstrado (Ferreira & Tidon, 2005; Mata *et al.*, 2008; Penariol & Madi-Ravazzi, 2013). Estas moscas são candidatas ao monitoramento do grau de perturbação ambiental devido ao conhecido impacto que mudanças de temperatura, luz, umidade e precipitação causam na sua sobrevivência, fertilidade e taxa de desenvolvimento (Pavan, 1959; Torres & Madi-Ravazzi, 2006; Poppe *et al.*, 2013) e também por sua íntima relação com diferentes espécies de plantas (Pavan, 1959; Carson, 1971; Leão & Tidon, 2004; Vaz *et al.*, 2014), fungos (Gottschalk *et al.*, 2009; Naranjo-Lázaro *et al.*, 2014), ácaros (Poinar & Grimaldi, 1990) e vespas parasitóides (Guimarães *et al.*, 1999) em diferentes etapas do seu ciclo de vida.

Drosophilidae constitui uma família de insetos bastante diversa e amplamente distribuída, com representantes encontrados em todos ambientes a partir do nível do mar, com exceção das regiões árticas (Throckmorton, 1975). Apresenta mais de 4.300 espécies distribuídas em 77 gêneros e duas subfamílias (Steganinae e Drosophilinae) (Bächli, 2017). Esta família é bastante conhecida pelo amplo impacto de uma de suas espécies, *Drosophila melanogaster*, nas pesquisas científicas das mais diversas áreas da biologia, mas principalmente na genética e na evolução. De fato, esta espécie é tida como o organismo modelo *premier* da biologia de eucariotos multicelulares (Markow & O'Grady, 2007; Markow & O'Grady, 2008). O tamanho pequeno, o ciclo de vida curto, e a facilidade de coleta e manuseio são algumas das características que proporcionam à família uma crescente utilização no meio científico.

Ecologicamente, a maior parte das espécies de drosofilídeos oviposita e se alimenta de microorganismos, especialmente leveduras, que se desenvolvem sobre a matéria orgânica em decomposição. No entanto, o tipo de substrato explorado varia, e existem espécies frugívoras, antofílicas, micofílicas e, até mesmo, parasitas e predadoras (Carson, 1971). Em cada caso, a amplitude do nicho tende a variar. Se levarmos em conta os substratos de oviposição e alimentação dos adultos, enquanto algumas espécies exploram uma ampla variedade de substratos, outras são extremamente especializadas (Powell, 1997). A extensão de distribuição

também varia amplamente, e ao mesmo tempo em que existem espécies cosmopolitas (comensais humanas) (Parsons & McDonald, 1978), existem espécies altamente endêmicas (Lachaise & Silvain, 2004).

No Brasil, pouco mais de 300 espécies de Drosophilidae são conhecidas até o momento (Gottschalk et al., 2008), porém estima-se que esse número possa ser bem maior devido ao grande viés geográfico e metodológico associado a estes estudos. Uma importante fonte de tendenciosidades é proporcionada pelo delineamento amostral mais comumente empregado, que se baseia no emprego de amonstragens repetidas em uma única ou em poucas localidades (Mata et al., 2008; Cavasini et al., 2014; Mendes et al., 2017). Neste sentido, pode-se dizer que as comunidades de drosofilídeos no Brasil são ainda pouco conhecidas, e esta situação se agrava em alguns de seus estados e biomas (Gottschalk et al., 2008). Por exemplo, enquanto diversos estudos ecológicos ou de inventariamento de Drosophilidae vem sendo realizados na região sul e sudeste, em especial no bioma Mata Atlântica (Medeiros & Klaczko, 2004; Ferreira & Tidon, 2005; De Toni et al., 2007; Gottschalk et al., 2007; Cavasini et al. 2014; Garcia et al., 2014; Rohde et al., 2014; Gustani et al., 2015), pouco se sabe sobre a composição, a ecologia, ou a diversidade desses organismos em outras regiões, em especial para o Bioma Pampa (Hochmüller et al., 2010; Poppe et al., 2012; Poppe et al., 2013; Mendes et al., 2017). Além disso, não há registro de trabalhos voltados para a caracterização das assembleias de drosofilídeos em áreas alagadas de água doce destes biomas.

Embora a ocorrência de Drosophilidae já tenha sido registrada em áreas alagadas (Keiper et al., 2002), a composição de suas assembleias em regiões de banhados e brejos, ou mesmo em zonas de mata paludosa, é ainda pouco conhecida. Até o momento, poucas espécies são conhecidas para essas áreas, entre elas *D. quinaria* e *D. tripunctata*, que emergiram de larvas que se alimentavam de repolho-de-gambá (*Symplocarpus foetidus*) em decomposição (Grimaldi & Jaenike, 1983); *D. deflecta*, em Nenúfar amarillo (*Nuphar lútea*); e *D. palustris* e *D. subpalustris*, que se alimentam de folhas e galhos em decomposição (Keiper et al. 2002). Essa baixa diversidade em áreas alagadas de água doce contrasta com aquela encontrada em manguezais (Schmitz et al., 2010), onde pelo menos 69 espécies já foram registradas. Em suma, existem inúmeras lacunas amostrais no conhecimento das assembleias de drosofilídeos neotropicais, e o preenchimento destas é fundamental para a adequada compreensão dos fatores que afetam ou limitam a distribuição das diferentes espécies. Somente o conjunto destas informações, tomadas em um âmbito comparativo, tem, pois, o potencial de propor espécies bioindicadoras para os diferentes biomas e habitats e caracterizar efetivamente a sua diversidade, o que pode, por fim, auxiliar na definição de áreas e estratégias de conservação.

Dadas as circunstâncias acima mencionadas, o objetivo geral desta dissertação é avaliar os padrões de distribuição de drosofilídeos no sul do Brasil, pela comparação da diversidade encontrada entre florestas/bosques e zonas de mata paludosa/banhados e entre os biomas Pampa e Mata Atlântica. Para tanto, são propostos os seguintes objetivos específicos:

- Investigar a composição, a abundância e a riqueza de espécies em assembleias de drosofilídeos distribuídas em áreas florestais e bosques ao longo dos biomas Mata Atlântica e Pampa, na região sul do Brasil;
- Investigar a composição, a abundância e a riqueza de espécies em assembleias de drosofilídeos distribuídas em zonas de mata paludosa e banhados ao longo dos biomas Mata Atlântica e Pampa, na região sul do Brasil;
- Examinar as diferenças de composição nas assembleias de drosofilídeos de áreas florestais/bosques com relação a zonas de mata paludosa/banhados, avaliando o valor indicador de diferentes espécies com relação a estes habitats;
- Examinar as diferenças de composição nas assembleias de drosofilídeos da Mata Atlântica e do Pampa, avaliando o valor indicador de diferentes espécies com relação a estes biomas.

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CAPÍTULO 1

Assemblage of drosophilids (Diptera, Drosophilidae) inhabiting flooded and nonflooded areas
in the extreme South of Brazil

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Assemblage of drosophilids (Diptera, Drosophilidae) inhabiting flooded and nonflooded areas in the extreme South of Brazil

Duarte, L. B.^a; Robe, L. J.^{a,b}; Gottschalk, M. S.^c

a - Universidade Federal do Rio Grande (FURG), Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais (PPGBAC), Av. Itália, km 08 Campus Carreiros, CEP 96203-900 - Rio Grande, RS – Brasil, Phone: +55 53 3293-5128

b - Universidade Federal de Santa Maria (UFSM), Programa de Pós Graduação em Biodiversidade Animal (PPGBA), Avenida Roraima 1000, CEP 97105-900 - Santa Maria, RS - Brazil, Phone: +55 55 3220-8912

c - Universidade Federal de Pelotas (UFPel), Instituto de Biologia, Departamento de Ecologia, Zoologia e Genética, Campus Capão do Leão, Programa de Pós Graduação em Biologia Animal (PPGBA), Programa de Pós Graduação em Entomologia (PPGEnt), Mail Box 354, CEP 96010-900 - Capão do Leão, RS – Brazil, Phone: +55 53 3275-7340

Corresponding author.

E-mail: marco.gottschalk@yahoo.com.br (M.S. Gottschalk)

Abstract:

Several studies on the potential use of drosophilid assemblages as bioindicator systems have been carried out in the last years. Nevertheless, the successful application of these organisms in these systems requires adequate filling of several knowledge gaps. In this sense, little is known about drosophilid assemblages in wetlands and flooded areas. The present study provides the first survey of drosophilid species inhabiting such environments in the extreme South of Brazil and compares general beta-diversity patterns between assemblages of flooded versus nonflooded areas. The specimens were collected with banana-baited traps during 2010-2016, and the assemblages recovered in eight wetlands of the southernmost coast of Brazil were compared to those recovered from seven non-flooded areas of the Pampa and Atlantic Forest biomes. A total of 5,028 individuals were collected in the flooded areas, and these represented four genera and 27 species. These numbers contrast with those

recovered from nonflooded wooded areas, in which four genera and 37 species were determined among the 2,571 individuals caught. The lower diversity and the differential species composition patterns presented by flooded areas was statistically supported, a result that might be related to the higher climatic variations and the lower resource availability faced by drosophilids species inhabiting these habitats. The higher abundance of exotic Drosophilidae species (as *Drosophila simulans* and *Zaprionus indianus*), added to the complete absence of species considered as indicators of environmental quality (as *Drosophila ornatifrons*) in flooded habitats suggests that even wetlands located within conservation units may be yet somewhat threatened.

Key-words: alfa-diversity; beta-diversity; bioindicator species; swamps; wetlands.

Introduction

According to Keddy (2010), wetlands are ecosystems of transition between aquatic and terrestrial environments, whose biota is particularly adapted to flooded conditions. These areas may support and incubate significant parts of current biodiversity, serving as habitat even for predominantly terrestrial groups, like Insects. For Diptera, for example, aquatic or semi-aquatic larval stages are encountered in at least 32 of the 155 families (Williams and Feltmate, 1992; Sundermann *et al.*, 2007). In fact, Diptera species are important components of these ecosystems, where they act on the energy flow and nutrient cycling, serving also as bioindicators of water quality (Moulton, 1998; Sankarperumal and Pandian, 1992).

Drosophilidae is one of the most diverse and widely distributed Diptera families, encompassing more than 4.300 species (Bächli, 2016), encountered throughout different environments above the sea level, with the exception of Antarctic regions (Throckmorton, 1975). Almost all species in this family present terrestrial life cycles, without any aquatic or semi-aquatic stage across development (Tsacas and Legrand, 1979). Nevertheless, different species present different ecological requirements, and some taxa are specially adapted to wet conditions, as observed by Robe *et al.* (2014) and more recently by Freitas *et al.* (personal communication) with correlational niche

inference methods. These patterns highlight the importance of these organisms as bioindicators for the impact of climatic changes.

Although the occurrence of Drosophilidae has already been recorded in freshwater wetlands (Keipter *et al.*, 2002), the composition of their assemblages in these habitats is still poorly understood. Until now, few species were registered in these environments, among which we may detach: *Drosophila quinaria* Loew (1866) and *D. tripunctata* Loew (1862), which emerged from larvae eating *Symplocarpus foetidus* in decomposition (Grimaldi and Jaenike, 1983); *D. deflecta* Malloch (1924) in *Nuphar lutea*; and *D. palustris* Spencer (1942) and *D. subpalustris* Spancer (1942), which feed on decaying leaves and twigs (Keiper *et al.*, 2002). Another species discovered in wetlands is *D. aguape*, collected in *Eichhornia azurea* flowers collected along the Paraguay River, in the Brazilian Pantanal Biome, state of Mato Grosso (Val & Marques, 1996). This apparent low diversity in limnic wetlands contrasts with that found in mangroves (Schmitz *et al.*, 2010), where at least 69 species have been recorded. However, most species observed by Schmitz *et al.* (2010) are probably transient in mangroves, once the authors did not found rearing sites in this environment.

Considering the increasing degradation of wetlands and flooded areas (Finlayson, 2007), the search for an understanding of the ecological patterns and processes operating in these areas urges. So, this study aims to provide a first step towards a better knowledge of the presence and ecological influence of Drosophilidae species in wetlands and flooded areas, supplying an inventory of the assemblages of drosophilids inhabiting such environments in the extreme South of Brazil and comparing beta-diversity patterns between flooded versus nonflooded areas. This region is especially profitable for such studies since it presents almost 39% of its surface covered by lakes and lagoons (Schwarzbold & Schäfer, 1984), whose water regime depends exclusively on the pluviometry regime (Vieira, 1983).

Materials and methods

Study area

Drosophilids were collected between 2010 and 2016 in wetlands or flooded areas in the municipalities of Rio Grande, Osório and Três Cachoeiras and in nonflooded

environments in the municipalities of Santa Maria, São Nicolau, Pelotas, Canguçu, Horizontina, Cruz Alta and Chapecó (Table 1, Supplementary Material – Fig. S1). Samplings in wetlands were performed in eight flooded areas distributed along the Rio Grande do Sul (RS) Coastal Plain, characterized as swamps in virtue of the dominance of trees that are rooted in hydric soils, but not in peat (Keddy, 2010), and including tropical mangroves swamps and bottomland forests in floodplains. Samplings in nonflooded points encompassed mainly wooded areas, distributed along the interior of the state of Rio Grande do Sul and South of Santa Catarina (SC). The areas differed by their kind or level of anthropic influences and the eight swamp sampling points covered a heterogeneous set of environments:

- 1) Ecological Station of Taim (TA), in Rio Grande – RS, a flooding area with more than 34,000 hectares, that shelters several animal and plant taxa, including some endangered species, and encompasses a large area of protected swamps (Gomes *et al.*, 1996). Nevertheless, despite the conservation efforts, the ecological station is still impacted by livestock farming, forestry, nearby use of agrochemicals and by a road that crosses the region.
- 2) Environmental Protection Area of Estrada Velha (EV), in Rio Grande – RS, encompassing 18 hectares of woods that are periodically flooded. This area is impacted not only by high levels of atmospheric pollution related to the intense vehicle flow of BR392 and to nearby industries but also by cattle raising and agricultural practices.
- 3) Environmental Protection Area of Lagoa Verde (LV), in Rio Grande – RS, that covers 510 hectares of protected area inside the urban portion of Rio Grande. Among the main threats faced by this area, it is possible to highlight housing anthropic presence and the atmospheric pollution from the highway located in the vicinities.
- 4) Biguás Lake (LB), in Rio Grande – RS, that encompasses a lake with an extension of approximately 1.5 hectares and a maximum of 2 meters of depth, located inside the *Campus* of Universidade Federal do Rio Grande (FURG). The lake is periodically enriched by organic matter from domestic effluents that contributes to the outcrop of aquatic macrophytes and phytoplankton, alternating the trophic state of the lake between eutrophy and hypereutrophy.

5) Ilha dos Marinheiros (IM), in Rio Grande – RS, an island of 39 km², located at the Southern margin of the Patos Lagoon, which embraces a swamp with less than 1m depth. It is mostly explored by agricultural practices, and, as a consequence, is mostly impacted by the use of agrochemicals.

6) A particular property, in Osório (OS) – RS, located between two lakes (Emboaba and Emboabinha). It is mostly impacted by the breeding of domestic animals, and by the inadequate disposal of materials near the Lagoon.

7) Waterfall Poço das Andorinhas (TCPA), in Três Cachoeiras – RS, characterized by a natural and locally conserved landscape, with low anthropic interference, mainly related to touristic practices.

8) Bridge of the Well (TCPA), in Três Cachoeiras – RS, located approximately 7 km of the waterfall Poço das Andorinhas (point 7). It is crossed by a local road, with low vehicle flow.

Collections

The flies were collected with banana-baited traps sprinkled with baker's yeast (*Saccharomyces cerevisiae*), constructed according to Tidon and Sene (1988). Ten baits were distributed in each of the sampling points, where they were left for 2-3 days. In the flooded areas, the baits were tied in trees or in riparian vegetation close to the water surface, with a distance of 1-4m from each other, according to the size of the flooded area, whereas in nonflooded areas, baits were randomly suspended at a height of approximately 1.5m within more or less dense forest areas, with a distance of about 10m from each other. After collections, the flies were preserved in ethanol 100%.

Identification

First, the specimens were screened and identified based on their external morphology, and after, the terminalia of the males was dissected and prepared to proceed the identifications (Bächli *et al.*, 2004). So, with the help of identification keys and aedeagus illustrations available in the literature (Freire-Maia and Pavan, 1949; Grimaldi, 1990; Vilela and Bächli, 1990), males could be identified to the species level,

whereas females of cryptic groups were only identified at the group level, and later proportionally distributed according to the identity of the males of the same group collected at the same point for analysis purposes. After determination, each slide was fixed with Canada balsam, tagged according to the identification and precedence, and added to the lab's collection.

Data analysis

Abundance and richness were measured for each of the sampling points, as well as for flooded and nonflooded areas taken as a whole. Sample rarefaction curves were constructed for each studied environments, with confidence intervals measured through 1,000 randomizations, as implemented in PAST 2.17 c (Hammer et al., 2001). The differences between assemblages encountered in flooded and nonflooded areas were also evaluated through a Principal Coordinates Analysis (PCoA), in PAST 2.17c (Legendre and Legendre, 1983; Abdi & Williams, 2010), using Log(n+1) transformed abundance values and Bray-Curtis dissimilarity measures. Raw abundance data was also employed in a one-way Analysis of Similarities (ANOSIM) (Clarke, 1993) performed in PAST 2.17c, with Bray-Curtis similarity measures. A Similarity Percentage analysis (SIMPER) (Clarke, 1993) was also performed in this software using Bray-Curtis, in order to assess the contribution of each species to the observed patterns. The indicator value (*IndVal*) (Dufrene and Legendre, 1997) of each species to flooded or nonflooded environments was finally measured with the use Labdsv 1.8-0 package (Roberts, 2016) in R version 3.3.3 (R Core Team, 2013).

Results

We collected 5.028 specimens along the eight flooded sampling points, and these encompassed 27 species of four Drosophilidae genera and, in *Drosophila*, 13 species groups (Table 2). Among these samples, abundance varied from 6 to 2.167 (in TA and LV, respectively), whereas richness ranged from 1 to 17 (in TA and EV, respectively).

These values contrast with those found for nonflooded areas, where a total of 2.571 specimens comprising 37 species of four genera and also 13 *Drosophila* groups were sampled (Table 3). In these localities, abundance varied from 41 to 1.200 (in SM and

SN, respectively), whereas richness ranged from 7 to 21 (in SM and CHAP, respectively).

Although in both cases, sample rarefaction curves do not suggest equilibrium in species representativeness was reached, they clearly support a smaller richness for flooded in comparison with nonflooded areas (Fig. 1). The PCoA also supported this difference, and both environments presented non-overlapping patterns in regard to coordinate 1, which explained almost 30% of the variability (Fig. 2A). Moreover, considering the 95% ellipses of the two first coordinates, none wood point fell inside the confidence interval of flooded areas (Fig. 2B). The ANOSIM also supported a significant difference in species composition patterns between flooded and nonflooded areas, with values of 45.18 for mean rank within and 59.84 for mean rank between ($R = 0.2792$ and $p = 0.016$).

SIMPER analysis revealed that the greater abundance of *D. simulans* Sturtevant (1919) in flooded areas explained almost 11% of the dissimilarity between the two set of areas (Table 4). Summed to this, the different patterns of presence/absence of *D. sukii* Matsumura (1931) (detected only in swamps), *D. ornatifrons* Duda (1927) and *D. mediopunctata* Dobzhansky and Pavan (1943) (detected only in nonflooded woods), and the greater abundance of *D. onca* Dobzhansky and Pavan (1943) in nonflooded areas explained more than 36% of the difference. In fact, *D. ornatifrons* (indval = 1.00, freq = 7), *D. mediopunctata* (indval = 0.71, freq = 5) and *D. onca* (indval = 0.63, freq = 8) presented significant indval estimates for nonflooded woods. Although *D. sukii* recovered a significant indval estimate for swamps (indval = 0.87, freq = 7), this result is probably an artifact of the temporal difference between samplings (see below).

Discussion

This study provides the first attempt to address the dissimilarities in Drosophilidae species composition between flooded and non-flooded wooded areas, and despite shortages related to the temporal and spatial distribution of the sampling points, it clearly showed lower diversity values for swamps. In this sense, richness values ranged from 1 to 17 and 7 to 21 in flooded and nonflooded areas, respectively, and the sample rarefaction curves do not overlap even when confidence values are

considered. This difference can be attributed to the low plasticity presented by several drosophilid species against environmental variations such as humidity, temperature, precipitation, etc., as demonstrated by Freitas *et al.* (personal communication). In this sense, as nonflooded areas present a more closed environment, species inhabiting these environments generally face a lower variation in climatic conditions, added to a wider protection against intense precipitation. Moreover, swamps are much more homogeneous in regard to resource availability, presenting lower abundance and richness of plant species, which could restrict attractiveness for several frugivorous drosophilid species. After all, the more plants, the more potential niches to be colonized (Cuevas-Reyes *et al.* 2004)

Multivariate analyses of PCoA and ANOSIM corroborated the different composition patterns presented by flooded and nonflooded areas, and none of the second set of points fell inside the 95% ellipses of flooded areas when the first two coordinates of the PCoA ordination were taken into account. Interestingly, the collection point with the lower similarity to the others was just Taim (average Bray-Curtis similarity of 0.03 to nonflooded areas), which encompasses a large area of protected swamps (Gomes *et al.*, 1987). So, in agreement with the hypothesis depicted above, the higher homogeneity in vegetation and the climatic variability presented by larger swamp areas also presented a negative impact on frugivorous species diversity. This contrasts with the patterns detected for mangroves, which were suggested to act as sink habitats for drosophilids populations (Schmitz *et al.*, 2010).

According to SIMPER analysis, qualitative or quantitative differences related to only ten species explained more than 61% of the differences between flooded and nonflooded areas. Among these, *D. simulans*, *D. mercatorum* Patterson and Wheeler (1942), *D. buzzatti* Patterson and Wheeler (1942) and *Z. indianus* Gupta (1960) were encountered in flooded and nonflooded areas but presented larger abundance values in swamps. *Drosophila simulans* was by far the most abundant species in both habitats, representing 72% of the Drosophilidae species sampled in this study, which is in agreement with the high abundance presented by this species in different environments, from mangroves (Schmitz *et al.*, 2010), to forest (Hochmüller *et al.* 2010, Poppe *et al.* 2012) and urban habitats (Gottschalk *et al.* 2007; Hochmüller *et al.* 2010). This species is generally associated with disturbed environments, and thus considered a bioindicator of anthropic alterations, together with *Zaprionus indianus*

(Ferreira and Tidon, 2005), another exotic species sampled in our study. Among native Neotropical species, *D. mercatorum* was usually sampled in areas with open vegetation or anthropic actions (Ferreira and Tidon 2005; Gottschalk *et al.* 2007), explaining the higher abundance in flooded environments. As concerns *D. buzzatti*, the higher abundance in flooded areas may also be explained by the distribution of flooded points in coastal areas, where the cactophylic resources explored by this species may be especially profitable (Franco *et al.* 2006).

Despite the abundance differences depicted above, the sole species to present a significant bioindicator value for flooded areas was *D. suzukii*. Nevertheless, this result is probably an artifact of temporal differences between samplings in flooded (2015-2016) and nonflooded areas (2010-2011), once since the first record of this species in the south of Brazil in 2013, it rapidly spread across the area (Deprá *et al.* 2014). Moreover, recent studies have suggested that this species presents high environmental suitability for temperate and subtropical areas in the continents of Asia, Europe and North and South America (Santos *et al.*, 2017), including the entire area focused in this study.

At contrast with these patterns, *D. onca*, *D. immigrans* Sturtevant (1921) and *D. polymorpha* Dobzhansky and Pavan (1943) presented larger abundance and fidelity values to nonflooded areas, whereas *D. ornatifrons* and *D. mediopunctata* were exclusive and presented significant indicator values for such environments. Among these, *D. polymorpha* was previously suggested as tolerant in regard to urbanization levels (Gottschalk *et al.* 2007), which might also be the case for variation in humidity levels, although intermediate values are probably preferred. Conversely, *D. mediopunctata* seems to be more restricted, being collected only in nonflooded environments, especially in the points sampled during autumn and winter, confirming the patterns found by several authors in other environments (Franck and Valente 1985; De Toni *et al.* 2007; Cavasini *et al.* 2014). The other species exclusive to nonflooded woods was *D. ornatifrons*, which is considered an indicator of the quality of the environment, being easily found in forest remnants with low anthropogenic action, mainly in the Atlantic Forest (Gottschalk *et al.*, 2007; Cavasini *et al.*, 2014). In this sense, the absence of this species in flooded areas, added by the straightforward prevalence of exotic species in these habitats, suggests that the target environments

may be already somewhat threatened, despite the fact that several of them are located within Brazilian conservation units.

So, although the results suggest a lower diversity for swamps in comparison to nonflooded woods, the diversity in composition patterns presented by these areas even for Drosophilidae species reinforces the need to conserve these habitats. In fact, this study suggests drosophilids might be useful as bioindicators of habitat quality in swamps, and signs of environmental degradation were detected for these environments even within conservation units.

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Tables

Table 1: List of sampling points, with their respective coordinates and sampling dates.

Code	Sampling Cities	Sampling Date	Latitude	Longitude
1	Taim (TA)	28/12/2015	-32.49	-52.58
2	APP Estrada Velha (EV)	20/04/2016	-32.12	-52.15
3	APA Lagoa Verde (LV)	25/11/2015	-32.16	-52.18
4	Lago dos Biguás – FURG (LB)	20/04/2016	-32.07	-52.16
5	Ilha dos Marinheiros (IM)	21/12/2015	-31.99	-52.15
6	Osório (OS)	22/11/2016	-29.97	-50.23
	Três Cachoeiras - Poço And.			
7	(TCPA)	23/11/2016	-29.44	-50.05
	Três Cachoeiras - Ponte do Poço			
8	(TCPPA)	23/11/2016	-29.44	-50.05
9	Santa Maria (SM)	24/08/2010	-29.68	-53.81
10	São Nicolau (SN)	08/09/2010	-28.21	-55.24
11	Pelotas (PEL)	26/08/2011	-31.76	-52.33
12	Canguçu (CAN)	26/08/2011	-31.39	-52.67
13	Horizontina (HOR)	13/10/2010	-27.62	-54.31
14	Cruz Alta (CA)	28/05/2011	-28.64	-53.6
15	Chapecó (CHAP)	30/08/2010	-27.09	-52.61

Notes: Points 1-8 represent flooded swamps, whereas points 9-15 represent nonflooded woods.

Table 2: List of species collected in flooded areas (points 1-8), with abundance and richness values recorded for each and for the total set of points.

Group	Species	1. TA	2. EV	3. LV	4. LB	5. IM	6. OS	7. TCPA	8. TCPPA	Total
<i>annulimana</i>	<i>D. schineri</i>	0	0	2	0	0	0	0	0	2
<i>busckii</i>	<i>D. busckii</i>	0	0	0	5	1	0	0	0	6
<i>bromeliae</i>	<i>D. bromelioides</i>	0	35	0	0	0	0	0	0	35
<i>calloptera</i>	<i>D. atrata</i>	0	8	0	0	0	0	0	0	8
<i>cardini</i>	<i>D. cardini</i>	0	25	0	0	0	0	0	0	25
	<i>D. polymorpha</i>	0	4	12	0	14	0	0	0	30
<i>dreyfusi</i>	<i>g.dreyfusi</i> (NI)*	0	0	0	0	2	0	1	0	3
<i>guarani</i>	<i>D. griseolineata</i>	0	5	0	0	0	1	0	0	6
<i>immigrans</i>	<i>D. immigrans</i>	0	0	0	23	8	0	3	0	34
<i>melanogaster</i>	<i>D. simulans</i>	6	283	1814	630	848	42	87	30	3740
	<i>D. suzukii</i>	0	44	13	9	6	12	23	6	113
<i>repleta</i>	<i>D. hydei</i>	0	4	14	73	6	3	0	0	100
	<i>D. mercatorum</i>	0	49	25	12	17	3	0	1	107
	<i>D. onca</i>	0	0	0	0	0	0	21	4	25
	<i>D. repleta</i>	0	0	0	0	3	0	0	0	3
	<i>D. serido</i>	0	0	2	0	0	15	0	0	17
	<i>D.buzzatii</i>	0	12	118	2	3	62	0	0	197
<i>saltans</i>	<i>D. sturtevanti</i>	0	0	0	0	0	0	1	0	1
<i>tripunctata</i>	<i>D. bandeirantorum</i>	0	2	0	0	0	0	0	0	2

	<i>D. mediosignata</i>	0	52	0	0	0	0	0	0	52
	<i>D. paraguayensis</i>	0	7	0	0	0	0	0	0	7
	<i>D. roehrae</i>	0	2	0	0	0	0	0	0	2
<i>willistoni</i>	<i>sg. willistoni</i>	0	2	0	0	39	0	0	0	41
	<i>Leucophenga</i> sp.	0	24	0	0	0	1	0	0	25
	<i>R. punctuloides</i>	0	0	11	0	0	0	0	0	11
	<i>R. obesa</i>	0	0	0	2	0	0	0	0	2
<i>armatus</i>	<i>Z. indianus</i>	0	204	156	72	2	0	0	0	434
Abundance		6	762	2167	828	949	139	136	41	5028
Richness		1	17	10	9	12	7	6	4	27

Table 3: List of species collected in nonflooded areas (points 9-15), with abundance and richness values recorded for each and for the total set of points.

Groups	Species	9. SM	10. SN	11. PEL	12. CAN	13. HOR	14. CA	15. CHAP	Abund.
<i>busckii</i>	<i>D. busckii</i>	0	0	2	0	1	0	0	3
<i>canalineia</i>	<i>D. piratininga</i>	0	0	1	0	0	0	0	1
<i>cardini</i>	<i>D. cardini</i>	0	0	0	0	0	4	0	4
	<i>D. neocardini</i>	0	0	0	0	0	0	4	4
	<i>D. polymorpha</i>	6	9	5	1	6	2	28	57
<i>coffeata</i>	<i>D. fuscolineata</i>	0	1	0	0	0	2	1	4
<i>guarani</i>	<i>D. maculifrons</i>	0	0	0	0	1	1	0	2
	<i>D. ornatifrons</i>	1	2	4	40	2	22	8	79
<i>immigrans</i>	<i>D. immigrans</i>	0	5	8	0	71	1	147	232
<i>melanogaster</i>	<i>D. kikkawai</i>	0	0	0	0	1	0	0	1
	<i>D. simulans</i>	0	1138	13	1	49	0	541	1742
<i>mesophragmatica</i>	<i>D. mesophragmatica</i>	1	1	0	0	0	0	0	2
<i>pallidipenis</i>	<i>D. pallidipennis</i>	0	0	0	0	1	0	3	4
<i>repleta</i>	<i>D. hydei</i>	2	0	0	0	0	0	3	5
	<i>sg. fasciola</i> sp.1	0	0	0	2	0	0	0	2
	<i>D. mercatorum</i>	0	24	0	0	5	0	57	86
	<i>D. onca</i>	21	8	10	0	10	4	6	59
	<i>D. papei</i>	0	0	0	0	3	0	0	3

	<i>D. buzzatii</i>	2	0	0	3	0	0	0	5
<i>saltans</i>	<i>D. neosaltans</i>	0	0	0	0	0	0	9	9
	<i>D. prosaltans</i>	8	0	0	0	0	0	0	8
<i>tripunctata</i>	<i>D. bandeirantorum</i>	0	0	0	0	0	0	3	3
	<i>D. cuaso</i>	0	0	0	0	0	0	2	2
	<i>D. fragilis</i>	0	0	0	0	0	0	2	2
	<i>D. mediopicta</i>	0	2	0	0	0	3	0	5
	<i>D. mediopunctata</i>	0	5	14	25	0	24	2	70
	<i>D. nappae</i> AFF	0	0	0	2	0	0	0	2
	<i>D. paraguayensis</i>	0	5	63	0	0	5	22	95
	<i>D. sp.M4</i>	0	0	0	0	0	0	2	2
	<i>D. trifilum</i>	0	0	0	0	0	0	2	2
	<i>D. roehrae</i> AFF	0	0	0	0	0	3	0	3
	<i>D. bocainensis</i>	0	0	5	0	0	0	0	5
<i>willistoni</i>	<i>sg. willistoni</i>	0	0	4	0	0	0	28	32
	<i>Leucophenga</i> sp.	0	0	0	2	0	0	0	2
<i>armatus</i>	<i>Z. indianus</i>	0	0	0	0	0	2	7	9
<i>orbitalis</i>	<i>Z. orbitalis</i>	0	0	1	0	0	0	0	1
<i>vittimaculosa</i>	<i>Z. vittimaculosa</i>	0	0	0	0	0	6	18	24
Abundance		41	1200	130	76	150	79	895	2571
Richness		7	11	12	8	11	13	21	37

Table 4. Summary of the results provided by SIMPER Analysis, listing the ten species that are primarily responsible for the differences between flooded and nonflooded areas in decreasing order of contribution.

Taxon	Average dissimilarity	Contribution (%)	Cumulative contribution (%)	Mean abundance in flooded areas	Mean abundance in nonflooded areas
<i>D. simulans</i>	8.338	10.790	10.790	2.170	1.280
<i>D. suzukii</i>	5.320	6.884	17.670	0.998	0.000
<i>D. ornatifrons</i>	5.177	6.699	24.370	0.000	0.840
<i>D. mediopunctata</i>	4.577	5.923	30.300	0.000	0.749
<i>D. onca</i>	4.443	5.750	36.040	0.255	0.846
<i>D. immigrans</i>	4.362	5.644	41.690	0.367	0.866
<i>D. polymorpha</i>	4.082	5.282	46.970	0.374	0.816
<i>D. mercatorum</i>	3.986	5.157	52.130	0.798	0.563
<i>D. buzzatii</i>	3.779	4.890	57.020	0.759	0.154
<i>Z. indianus</i>	3.771	4.880	61.900	0.856	0.197

Figures

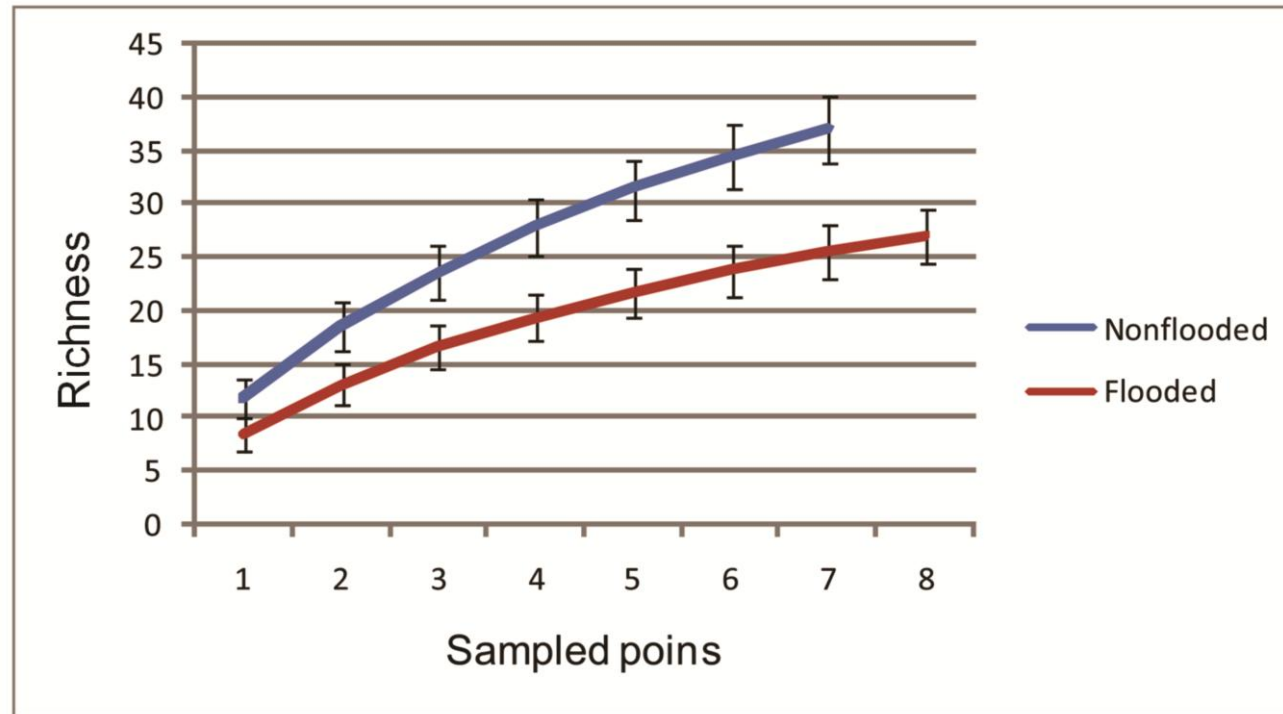


Fig. 1: Rarefaction curves for flooded and nonflooded areas.

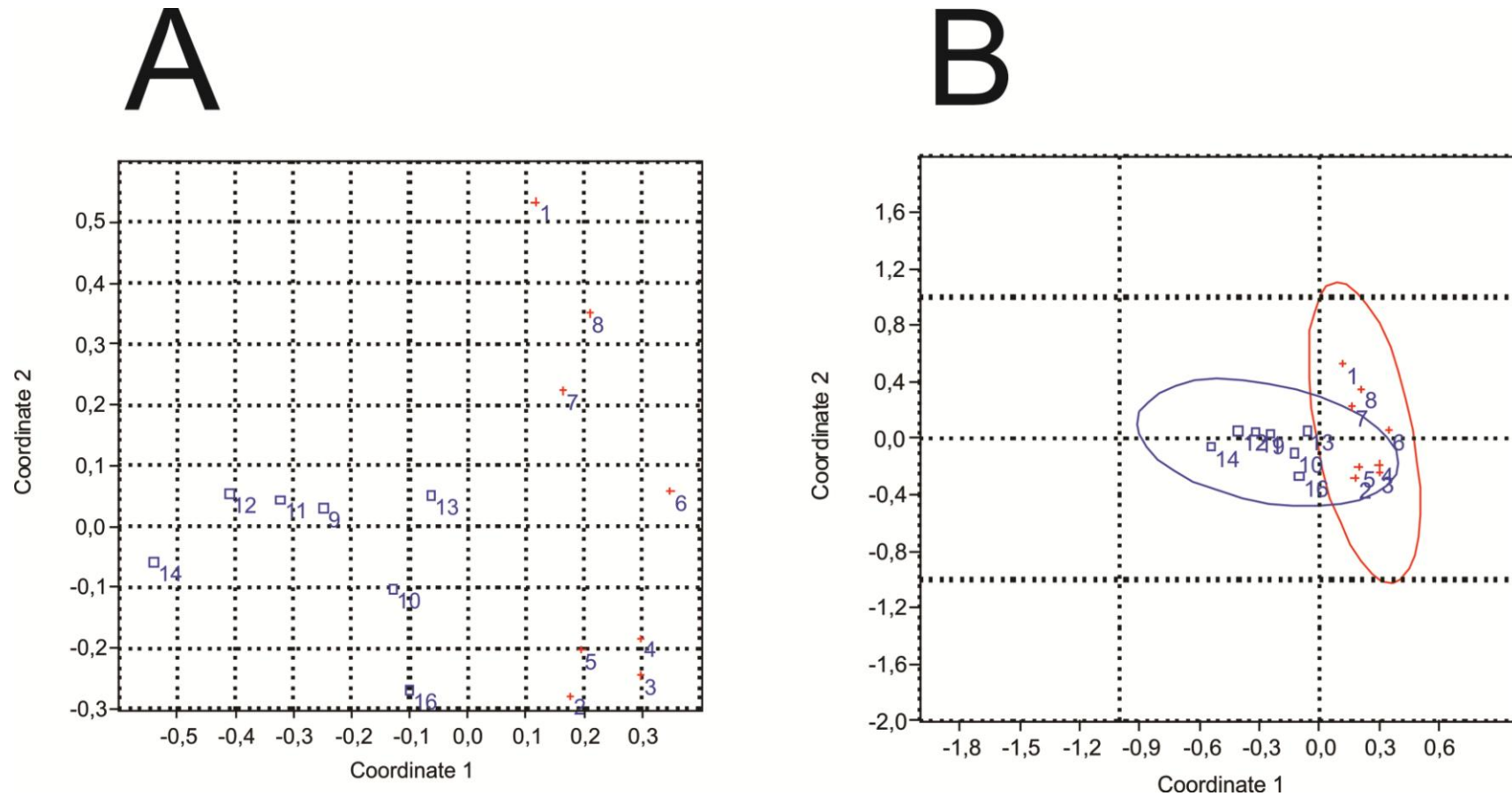


Fig. 2: Principal Coordinates Analysis (PCoA) ordination of the set of sampling points, according to Bray-Curtis dissimilarity measures. The graphic presents the results obtained with the use of the first two coordinates, which explained 50% of the variability presented by the data. The plot presented in (A) was compacted in (B), in order to represent the 95% confidence ellipses.

CAPÍTULO 2

Comparison of alpha, beta and gamma-diversity patterns of drosophilids (Diptera)
between the Brazilian Pampa and Atlantic Forest Biomes

Comparison of alpha, beta and gamma-diversity patterns of drosophilids (Diptera) between the Brazilian Pampa and Atlantic Forest Biomes

Duarte, L. B.¹; Cenzi de Ré, F.², Poppe, J. L.³, Deprá, M.⁴; Robe, L. J.^{1,2}, Gottschalk, M. S.⁵

1 - Universidade Federal do Rio Grande (FURG), Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais (PPBGAC), Av. Itália, km 08 Campus Carreiros, CEP 96203-900 - Rio Grande, RS – Brasil, Phone: +55 53 3293-5128

2 - Universidade Federal de Santa Maria (UFSM), Programa de Pós Graduação em Biodiversidade Animal (PPGBA), Avenida Roraima 1000, CEP 97105-900 - Santa Maria, RS - Brazil, Phone: +55 55 3220-8912

3 - Universidade Regional Integrada do Alto Uruguai e das Missões (URI), Rua José Bonifácio, 3149, São Luiz Gonzaga, RS, Brazil, Phone: +55 55 3352-8150.

4 – Universidade Federal do Rio Grande do Sul (UFRGS), Instituto de Biociências, Agronomia, CP 15053, Porto Alegre, RS, Brazil, Phone: +55 51 3308-6713.

5 - Universidade Federal de Pelotas (UFPel), Instituto de Biologia, Departamento de Ecologia, Zoologia e Genética, Campus Capão do Leão, Programa de Pós-Graduação em Biologia Animal (PPGBA), Programa de Pós-Graduação em Entomologia (PPGEnt), Mail Box 354, CEP 96010-900 - Capão do Leão, RS – Brazil, Phone: +55 53 3275-7340

Abstract:

Although Brazil is considered a megadiverse country, with about 13% of global biodiversity, many aspects related to differences in species composition over its area are still poorly understood. This is particularly damaging because understanding the patterns of species and diversity distribution are key to conservation. In the extreme south of Brazil two distinct but highly impacted biomes can be encountered: the Pampa Biome, characterized by the predominance of natural fields and shrub vegetation, and the Atlantic Forest, which harbours dense forests. Flies of Drosophilidae are abundant across both phytophysionomies, although the differences in assemblage composition have

not yet been accessed. Thus, this study aims to compare alpha, beta and gamma-diversity patterns of Drosophilidae assemblages between the Pampa and Atlantic Forest Biomes. For this, short-term samplings were performed in a wide area, encompassing 37 localities, during 2010 and 2013. In each of these sites, flies were captured with the use of 10 banana-baited traps, with the collected specimens identified by external morphology and male genitalia patterns. We obtained a total of 17.044 individuals subdivided in 66 species, of which eight are exotic. Of these, 14.679 individuals and 55 species were collected in the Atlantic Forest, and 2.365 individuals and 37 species were sampled in Pampa. A rarefaction curve confirmed a smaller richness for the Pampa, despite the similarities in species richness and equitability index per sample between both biomes. This pattern suggests that the higher γ -diversity in the Atlantic Forest is a consequence of its higher β -diversity. Moreover, although a PCoA did not detect significant differences in the patterns of species abundance/composition between the two major sampling areas, at least 24 species were supported by CLAM as specialists to a major Biome, four of which presented significant indicator values. Such a pattern suggests that several Drosophilidae species present some kind of preference to one of the two different Biomes, which certainly store a significant portion of the Brazilian biodiversity, and have to be urgently protected.

Key-Words: diversity indices; assemblage; Southern Brazil; Hotspot; natural fields

Introduction

Global-scale diversity gradients and its causes have been a trend topic in ecological and biogeographical studies along the last century (MacArthur, 1965; Rex et al., 1993; Pausas and Ribeiro, 2017), although comprehension of the patterns and processes acting on smaller scales is still frequently vaguer. In this sense, although Brazil is usually considered a megadiverse country (Mittermeier et al., 1997; Mittermeier, 1988), harboring 10 to 13% of the global biodiversity (Lewinsohn e Prado, 2005), many aspects related to the compositional differences along the country area are yet poorly understood. This is particularly damaging because the comprehension of the patterns of distribution of species

diversity and their causes are fundamental to developing effective conservation strategies (Ferrier et al., 2002).

The state of Rio Grande do Sul, southern Brazil, is divided by a large ecotone between two distinct Biomes: the Pampa, encompassing mainly natural fields distributed from its southern half to Uruguay and Argentina; and the Brazilian Atlantic Forest, composed mainly of dense, open and mixed ombrophilous forests and semideciduous and deciduous seasonal forests distributed from the north of the state to Northeast of the country, encompassing 16 Brazilian states (Boldrini et al., 2010; IBGE, 2004). The Atlantic Forest is usually considered one of the 25 main hotspots of the world, containing about 2% of the endemic species of plants and vertebrates from around the world (Myers, et al., 2000). Although the Pampa is being increasingly studied, its diversity is yet considered poorly assessed (Lewihnsen, 2006). Both Biomes are undergoing a wide degradation of its original area due to human expansion: the Atlantic Forest currently covers less than 22% of its original area (Brasil, 2017), being represented by archipelagos of forest remnants surrounded by open pasture or agricultural areas (Ribeiro et al., 2009); the Pampa Biome preserves less than 36% of its native vegetation (CSR / IBAMA, 2011a; 2011b), due to the progressive introduction and expansion of monocultures and pastures with exotic species (Brasil, 2017).

As spatial patterns of biodiversity are commonly regular across different taxonomic groups (MacArthur, 1965), assessments with model species can improve the comprehension of the subjacent processes, helping in the establishment of conservation endeavors. Insects are widely considered good model organisms for conservation, since they have different tolerances to environmental disturbances, responding quickly to these changes (Samways, 2015, Akeboshi et al., 2015). Among the insects used as bioindicators, flies of Drosophilidae are effective models of environmental variations, being frequently used in environmental conservation studies (Cavasini et al., 2008; Leblanc et al., 2013).

Drosophilidae encompasses more than 4,300 species, distributed in 77 genera and two subfamilies (Steganinae and Drosophilinae) (Bächli, 2017), which are found in different environments, to the exception of the Arctic regions (Toda, 2017). According to Throckmorton (1975), the areas with higher diversity

and abundance of Drosophilidae generally comprise woods or forests. In Brazil, there are more than 300 species, most of which belong to the genus *Drosophila* (Gottschalk et al., 2008), although this number is probably underestimated, given the geographical and methodological bias associated with these studies.

Drosophilidae assemblages of the Atlantic Forest have been target of several studies, but especially with mid or long-term samplings in the same locality (Ferreira & Tidon, 2005; De Toni et al., 2007; Gottschalk et al. 2007; Döge et al., 2008; Santos et al., 2010; Cavasini et al., 2014). At the other hand, Drosophilidae assemblages of the Pampa were addressed by only four punctual studies (Hochmüller et al., 2010; Poppe et al., 2012; Poppe et al., 2014; Mendes et al., 2017). In this way, the present study aims to compare alpha, beta and gamma-diversity patterns of Drosophilidae assemblage between Pampa and Atlantic Forest Biomes using short-term sampling in a wide area.

Material and Methods

Collection and Identification of Specimens

The flies were sampled in 37 locations covering areas of the Pampa and Atlantic Forest Biomes (12 and 25 points, respectively), between 2010 and 2013 (Tab. 1). In some locations, the samples were collected more than once, totaling 42 sampling events. The specimens were captured in bottle traps with fermented banana baits, following the model proposed by Tidon & Sene (1988). Ten traps were tied to the trees about 1m from the ground, with a distance of about 10m from each other, and remained in the field for 72h.

The collected specimens were identified by their external morphology and species of cryptic groups were identified through dissection of the male terminalia using specialized bibliography (Freire-Maia & Pavan, 1949; Grimaldi, 1990; Vilela & Bächli, 1990). The cryptic females were first identified up to group level, and later proportionally distributed according to the identity of males collected at the same point in the same date. All specimens were carefully labeled and stored in 100% alcohol and deposited in Drosophilidae Collection of Museu de História Natural Carlos Ritter (MHNCR).

Data analysis

Average and standard deviation of absolute abundance, species richness and Pielou's equitability index were estimated for each sample and compared between biomes. Sample rarefaction curves were constructed for each of the studied environments, as suggested by Chao et al. (2016), using interpolation and extrapolation to compare species richness with unbalanced abundance.

A Principal Coordinate Analysis (PCoA) was performed in order to evaluate the similarities in patterns of species abundance/composition between the two major sampling areas, with significance tested through an Analysis of Similarity (ANOSIM). These analyzes were performed with the Bray-Curtis coefficient of similarity in PAST v.2.17 c (Hammer et al., 2001). The same parameters were also used to measure the contribution of each species to the observed patterns, as determined by the Similarity Percentage analysis (SIMPER).

Finally, the Multinomial Species Classification Method (CLAM) was performed based on the absolute abundances of each species in each of the sampling points, with $p = 0.005$ and $k = 0.5$, as described and suggested by Chao & Lin (2011). This analysis evaluates the association of species to each of the studied biomes, classifying the species based on frequency data into four categories: Generalists, Atlantic Forest Specialists, Pampa Specialists, and Too Rare to Classify. Additionally, the indicator value (IndVal) of each species to either Pampa or Atlantic Forest was measured with the package Labdsv v. 1.8-0 (Roberts, 2016) in R software v.3.4.1 (R Core Team, 2017).

Results

In total, 17.044 individuals were collected, and these encompassed 66 species, of which 56 (85%) belonged to the genus *Drosophila stricto sensu* (Tab. 2). Disregarding differences in sampling effort, 14.679 individuals subdivided in 55 species were collected in the Atlantic Forest, and 2.365 individuals encompassing 37 species were sampled in Pampa. Nevertheless, these differences do not influence species richness estimations, once the sample coverage reached 0.99 between 600 and 1.000 individuals for both kinds of samples (Fig. 1). Thus, sample rarefaction curves in fact support a smaller richness for Pampa in comparison with Atlantic Forest (Fig. 2). Interestingly, this occurs despite the presence of similar values of species

richness per sample in both biomes (Tab. 2), pointing out that the higher γ -diversity in the Atlantic Forest is a consequence of its higher β -diversity. Moreover, although there are more individuals collected in the Atlantic Forest in each collection, the dominance in both biomes is the same, as evidenced by the similar Evenness index recovered for both Biomes (Tab. 2). This reinforces the idea that the greater diversity of the Atlantic Forest is due to a higher β -diversity between the sampling points.

Regarding exotic species, a total of eight species were encountered in our sample (five of the *melanogaster* group, *D. busckii*, *D. immigrans* and *Z. indianus*). *Drosophila simulans* and *D. immigrans* were very abundant and presented high incidence in our collections, being the two more-dominant species (Tab. 2). *Drosophila busckii* and *Z. indianus* were less abundant, but both have high incidence ($f_i > 25\%$). *Drosophila ananassae*, *D. kikkawai* and *D. melanogaster* were rarer and mainly associated to areas of the Atlantic Forest. *Drosophila suzukii* was encountered in only three of our samples (two in Atlantic Forest and one in Pampa), all of them occurring in 2013.

Some species occurred exclusively in one of the studied Biomes. This is the case of *D. neocardini*, *D. fuscolineata*, *D. repleta*, *D. prosaltans*, *D. mediosignata*, *Z. vittimaculosa* and *Zygothrica* sp., native species that were collected only in the Atlantic Forest with an abundance of less than 100 individuals. On the other hand, *D. griseolineata*, *D. gaucha*, *D. loewi*, *Leucophenga* sp. and *Z. orbitalis* were found only in the Pampa Biome, with an abundance of less than 50 individuals. These records of occurrence suggest a preference of some species to colonize one of the studied Biomes, but probably do not represent a real restriction in species distributions, since to the exception of *D. fuscolineata*, all species were previously sampled at least occasionally in both biomes (Bächli, 2017). In fact, after performing a Multinomial Species Classification Method, as suggested by Chazdon et al. (2011), seven species were classified as generalist (all Neotropical species), eight species were associated to the Atlantic Forest (four of them exotic to the Neotropics) and 16 species were associated to the Pampa Biome (three of them exotic to the Neotropics) (Tab. 3). More than half of the sampled species (35) could not be classified to either category due to their low abundance and frequency.

Complementarily, we also evaluated the Indicator Values (IndVal) of each species in regard to the Atlantic Forest or Pampa Biomes. This index indicated low specificity and/or fidelity of most of the species to the studied areas. In fact, only five species showed IndVal values that differed significantly from chance, of which four showed a significant association with Pampa and only one was associated to the Atlantic Forest (Tab. 4). Although significant, the observed IndVal values were too low to be considered as indicative of a strict relationship of these species to the biomes.

In regard to the general species composition patterns, the Principal Coordinate Analysis (PCoA) performed with the Bray-Curtis index was not able to discriminate Atlantic Forest and Pampa Biomes sampling sites (Fig. 3). The Analysis of Similarity (ANOSIM) also pointed a high similarity between sampling points of both biomes, and the composition of species based on Bray-Curtis similarity index was not different between them ($R = 0.03681$, $p = 0.2433$). Even so, some degree of dissimilarity was observed, and this was mainly attributed by SIMPER to *D. simulans* (responsible for 11% of the dissimilarity), *D. immigrans* (8%) and *D. mediopunctata* (6,8%) (Tab. 5).

Discussion

This study contributes as a first approach to the knowledge about the differential patterns of Drosophilidae species composition between sites, since it covers a wide area of the Southern Atlantic Forest and Northern Pampa Biomes, differing from other studies that are usually punctual. In fact, most of the recent studies carried out in these biomes used mid- to long-term sampling effort in only one locality (Poppe et al. (2012), Cavasini et al., (2014); Gottschalk et al. (2007); Poppe et al., (2014); Mendes et al., (2017)). In this sense, Poppe et al. (2012) and Mendes et al. (2017) evaluated the diversity of Drosophilidae in punctual localities of the Pampa Biome during at least 12 months and registered between 26 to 46 species. Our study, with a short-term photographic sampling effort in 14 Pampa localities, resulted in 37 species. In the same way, De Toni et al. (2007) and Cavasini et al. (2014) performed surveys of Drosophilidae in the Atlantic Forest over different seasons, during at least one year, and obtained richness values ranging from 58 to 78, a number of species similar to the 66 species registered in this study for this Biome. This similarity

suggests the effectiveness of our sampling strategy in capturing the general patterns, encouraging us to continue using this sample design in order to address beta and gamma compositional differences.

Our comparisons between the Atlantic Forest and Pampa Biomes sampling sites did not show differences in species richness patterns, when only α -diversity is taken into account. However, species richness was significantly higher in the Atlantic Forest when the samples were pooled, evidencing a higher γ -diversity as a consequence of a higher β -diversity. This result cannot be explained by differences in sample effort between Biomes, as suggested by the sample coverage evaluations. So, this result is probably related to the greater homogeneity presented by the Pampa Biome, which is dominated by natural fields and open areas with a lower floristic diversity characterized in great part by herbaceous and shrub species (Pillar et al., 2009). In fact, according to Tidon (2006), floristic diversity offers a larger range of microhabitats used for feeding, oviposition and protection against environmental factors that influence the abundance of the specimens.

Regarding the species recorded in our survey, *D. simulans* was the most abundant, being recorded in 75% of the sampling sites of the Atlantic Forest and 93% of the Pampa. Such a pattern has been recurrently observed in other studies (Gottschalk et al., 2007; Hochmüller et al., 2010; Poppe et al. 2012; Mendes et al. 2017). Nevertheless, SIMPER analysis revealed that this species is especially abundant in the Atlantic Forest, and that it explains 11% of the dissimilarity between the studied Biomes. *Drosophila immigrans* is another exotic species that seems to be more abundant in the Atlantic Forest, although its frequency was higher in Pampa sampling sites. Conversely, although *Drosophila mediopunctata* is reported as strictly associated with forests and non-anthropized areas, being therefore considered an excellent bioindicator of nondisturbed areas (Cavasini, 2009), its abundance was somewhat higher in the Pampas.

Considering the distribution patterns, we did not find strong evidences of species strictly related to one of the studied Biomes, although several species seem to present some level of specialization. In this sense, both CLAM and IndVal suggested *D. mercatorum* as preferentially associated to the Atlantic Forest, and *D. griseolineata*, *D. buzzatii* and *Z. orbitalis* as better adapted to the

Pampas. Such a pattern shows that despite the lower gamma-diversity presented by the Pampa Biome, and its general compositional similarity to the Atlantic Forest, it probably stores a significant portion of Drosophilidae diversity. Expanding these findings to other taxons, which possibly present similar patterns (Bolzan et al., 2016), it is possible to emphasize the urge of adopting effective strategies to conserve this Biome, that is being severely impacted during the last century (Pillar et al., 2009)

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Tables

Table 1. Biomes subdivision of the 42 sampling localities, with their respective geographical coordinates, dates and season of collection

Biome	Sample	Locality	Date	Season	Latitude	Longitude
Atlantic Forest	1	Aratiba, RS	February 18, 2012	Summer	-27.29	-52.34
	2	Caibaté, RS - point 1	October 13, 2010	Autumn	-28.17	-54.38
	3	Caibaté, RS - point 2	April 9, 2010	Autumn	-28.32	-54.63
	4		April 4, 2010	Autumn	-28.32	-54.63
	5	Catuípe, RS	June 10, 2012	Winter	-28.15	-54.04
	6	Caxias do Sul, RS	June 29, 2011	Winter	-29.09	-51.1
	7	Chapecó, SC	August 30, 2010	Winter	-27.04	-52.37
	8		October 10, 2011	Spring	-27.04	-52.39
	9	Concórdia, SC	August 15, 2011	Winter	-27.02	-52.02
	10	Constantina, RS	August 15, 2011	Winter	-27.43	-52.59
	11	Cruz Alta, RS	May 28, 2011	Autumn	-28.34	-53.37
	12	Erechim, RS	May 23, 2013	Autumn	-27.71	-52.17
	13		March 28, 2013	Autumn	-27.71	-52.17
	14	Foz do Iguaçu, PR	November 30, 2011	Spring	-25.46	-53.81
	15	Guarujá, SP	September 14, 2010	Spring	-23.59	-46.15
	16	Horizontina, RS	October 13, 2010	Spring	-27.37	-54.18
	17	Ijuí, RS	June 10, 2012	Winter	-28.23	-53.55
	18	Jacutinga, RS - point 1	June 6, 2010	Winter	-27.79	-52.54
	19	Jacutinga, RS - point 2	August 15, 2011	Winter	-27.44	-52.3
	20	Parque Estadual do Turvo, Derrubadas, RS	November 15, 2012	Spring	-27.63	-53.87

	21	Santa Maria, RS	August 24, 2010	Winter	-29.66	-53.72
	22	Santiago, RS	July 18, 2010	Winter	-29.41	-53.48
	23	São Francisco de Paula, RS	July 20, 2012	Winter	-29.42	-50.39
	24	São Luiz Gonzaga, RS	May 22, 2012	Autumn	-28.24	-54.57
	25	São Nicolau, RS	September 8, 2010	Spring	-28.1	-55.15
	26	Silveira Martins, RS	June 1, 2012	Winter	-29.63	-53.6
	27	Vale do Veneto, RS	July 3, 2010	winter	-29.68	-53.51
	28	Vila Maria	May 23, 2013	Autumn	-28.61	-52.09
Pampa	29	Canguçu, RS	August 26, 2011	Winter	-31.39	-52.67
	30	Chuí, RS	August 25, 2011	Winter	-33.68	-53.44
	31	Osório, RS	May 24, 2013	Autumn	-29.88	-50.27
	32	Pelotas, RS	August 26, 2011	Winter	-31.46	-52.26
	33		August 30, 2010	Winter	-31.46	-52.26
	34	Porto Alegre, RS - point 1	August 2, 2012	Winter	-30.06	-51.12
	35	Porto Alegre, RS - point 2	August 30, 2010	Winter	-30.04	-51.07
	36	Quaraí, RS	November 16, 2011	Spring	-30.23	-56.26
	37		September 8, 2010	Spring	-30.23	-56.26
	38	Rio Grande, RS	August 30, 2010	Winter	-32.03	-52.05
	39	Rosário do Sul, RS	July 11, 2011	Winter	-30.14	-54.55
	40	Santa Maria, RS	June 9, 2010	Winter	-29.68	-53.8
	41	Taim, RS	August 25, 2011	Winter	-32.49	-52.58
	42	Uruguaiana, RS	July 2, 2011	Winter	-29.44	-57.04

Table 2. List of sampled species, with their respective abundance (ni) and frequency (fi) values in each of the sampled Biomes, and in the total set of sampling points. Exotic species are demarked with an “*”. At the end of the table it is possible to find the comparative values of abundance (absolute and average $\pm$ standard deviation per sample), richness (absolute and average $\pm$ standard deviation per sample) and Pielou’s equitability index per biome, with the number of collections performed.

Subfamily	Genus	Subgenus	species group	species	Biomes				TOTAL	
					Atlantic Forest		Pampa		ni	fi
					ni	fi	ni	fi		
Drosophilinae	<i>Drosophila</i>	<i>Dorsilopha</i>	<i>busckii</i>	<i>D. busckii*</i>	40	7	75	7	115	14
		<i>Drosophila</i>	<i>annulimana</i>	<i>D. annulimana</i>	-	-	6	1	6	1
			<i>canalineia</i>	<i>D. piratininga</i>	-	-	1	1	1	1
			<i>cardini</i>	<i>D. cardini</i>	150	7	32	3	182	10
				<i>D. cardinoides</i>	18	1	7	1	25	2
				<i>D. neocardini</i>	36	2	-	-	36	2
				<i>D. polymorpha</i>	396	22	223	10	619	32
			<i>coffeata</i>	<i>D. coffeata</i>	1	1	-	-	1	1
				<i>D. fuscolineata</i>	5	4	-	-	5	4
			<i>dreyfusi</i>	<i>D. briergeri</i>	2	1	-	-	2	1
			<i>guarani</i>	<i>D. griseolineata</i>	-	-	33	6	33	6
				<i>D. maculifrons</i>	210	13	35	6	245	19
				<i>D. ornatifrons</i>	177	20	69	6	246	26
			<i>immigrans</i>	<i>D. immigrans*</i>	2105	17	257	12	2362	29
			<i>mesophragmatica</i>	<i>D. gaucha</i>	-	-	20	2	20	2

	<i>D. mesophragmatica</i>	2	2	4	1	6	3
<i>pallidipennis</i>	<i>D. pallidipennis</i>	18	17	15	1	33	18
<i>repleta</i>	<i>D. antonietae</i>	2	1	-	-	2	1
	<i>D. buzzatii</i>	25	3	87	6	112	9
	<i>D. hydei</i>	17	5	15	2	32	7
	<i>D. mercatorum</i>	846	16	15	6	861	22
	<i>D. nigricuria</i>	1	1	-	-	1	1
	<i>D. onca</i>	78	8	23	4	101	12
	<i>D. papei</i>	2	1	-	-	2	1
	<i>D. paranaensis</i>	8	1	-	-	8	1
	<i>D. repleta</i>	17	3	-	-	17	3
	<i>D. senei</i>	8	1	-	-	8	1
	<i>D. serido</i>	4	1	2	1	6	2
	<i>D. zottii</i>	3	1	-	-	3	1
	<i>g.1</i>	3	1	-	-	3	1
	<i>sg. fasciola sp.1</i>	-	-	2	1	2	1
<i>tripunctata</i>	<i>D. bandeirantorum</i>	23	7	44	2	67	9
	<i>D. cuaso</i>	2	1	-	-	2	1
	<i>D. fragilis</i>	2	1	-	-	2	1
	<i>D. loewi</i>	-	-	27	1	27	1
	<i>D. mediopicta</i>	16	4	6	2	22	6
	<i>D. mediopunctata</i>	373	13	304	8	677	21
	<i>D. mediosignata</i>	10	1	-	-	10	1
	<i>D. montevidensis</i>	-	-	3	1	3	1
	<i>D. nappae</i>	24	4	11	2	35	6

		<i>D. paraguayensis</i>	108	13	301	7	409	20
		<i>D. roehrae</i> AFF	3	1	-	-	3	1
		<i>D. sp.M4</i>	1	1	-	-	1	1
		<i>D. trifilum</i>	1	1	-	-	1	1
		<i>Sg.1</i>	2	2	-	-	2	2
<i>Sophophora</i>	<i>melanogaster</i>	<i>D. ananassae</i> *	63	1	-	-	63	1
		<i>D. kikkawai</i> *	4	3	1	1	5	4
		<i>D. melanogaster</i> *	56	4	-	-	56	4
		<i>D. simulans</i> *	7321	22	450	13	7771	35
		<i>D. suzukii</i> *	42	2	68	1	110	3
	<i>saltans</i>	<i>D. neosaltans</i>	9	1	-	-	9	1
		<i>D. prosaltans</i>	24	3	-	-	24	3
		<i>D. sturtevanti</i>	63	3	6	1	69	4
	<i>willistoni</i>	<i>D. bocainensis</i> complex	9	3	10	2	19	5
		<i>D. nebulosa</i>	4	2	2	1	6	3
		<i>D. willistoni</i> subgroup	2076	17	83	5	2159	22
<i>Hirtodrosophila</i>	<i>magnarcus</i>	<i>H. magnarcus</i>	-	-	1	1	1	1
<i>Zaprionus</i>	<i>vittiger</i>	<i>Z. indianus</i> *	224	10	103	3	327	13
<i>Zygothrica</i>		<i>Z. hypandriata</i>	-	-	2	1	2	1
		<i>Z. orbitalis</i>	-	-	17	4	17	4
		<i>Z. vittimaculosa</i>	30	4	-	-	30	4
		<i>Zygothrica</i> sp.	11	2	-	-	11	2
Steganinae	?	?	<i>Steganinae</i>	1	1	-	1	1
		<i>Amiota</i>	<i>Amiota</i> sp.	1	1	-	1	1
		<i>Leucophenga</i>	<i>Leucophenga</i> sp.	-	-	5	5	4

<i>Rhinoleucophenga</i>	<i>Rhinoleucophenga</i> sp.	2	1	-	-	2	1
Total abundance		14679		2365		17044	
Total species richness		55		37		66	
Average ($\pm$ standard deviation) of abundance in samples		524 ($\pm$ 811)		169 ($\pm$ 219)		-	
Average ($\pm$ standard deviation) of species richness in samples		9.8 ($\pm$ 5.67)		9.7 ($\pm$ 5.28)		-	
Average ($\pm$ standard deviation) of equitability in samples		0.57 ($\pm$ 0.23)		0.66 ($\pm$ 0.11)		-	
Number of samples		28		14		42	

Table 3. List of species classified as generalist, or as Atlantic Forest or Pampa specialist by CLAM analysis.

Generalist species	Atlantic Forest specialist species	Pampa specialist species
<i>D. cardini</i>	<i>D. neocardini</i>	<i>D. busckii</i> *
<i>D. cardinoides</i>	<i>D. immigrans</i> *	<i>D. polymorpha</i>
<i>D. maculifrons</i>	<i>D. ananassae</i> *	<i>D. griseolineata</i>
<i>D. onca</i>	<i>D. melanogaster</i> *	<i>D. ornatifrons</i>
<i>D. sturtevantii</i>	<i>D. simulans</i> *	<i>D. suzukii</i> *
<i>D. mediopicta</i>	<i>D. mercatorum</i>	<i>D. gaucha</i>
<i>D. nappae</i>	<i>D. willistoni</i> subgroup	<i>D. lowei</i>
	<i>Z. vittimaculosa</i>	<i>D. pallidipennis</i>
		<i>D. hydei</i>
		<i>D. buzzatii</i>
		<i>D. bandeirantorum</i>
		<i>D. mediopunctata</i>
		<i>D. paraguayensis</i>
		<i>D. bocainensis</i> complex
		<i>Z. indianus</i> *
		<i>Z. orbitalis</i>

Exotic species are demarked with an “*”.

Table 4. List of species with significant IndVals for the different Biomes.

Species	Biome	IndVal	p-value
<i>D. mercatorum</i>	Atlantic Forest	0.55	0.031
<i>D. griseolineata</i>	Pampa	0.43	0.002
<i>D. buzzatii</i>	Pampa	0.37	0.011
<i>Leucophengasp.</i>	Pampa	0.29	0.010
<i>Z. orbitalis</i>	Pampa	0.21	0.038

Table 5. List of the ten species that are primarily responsible for the differences between Pampa and Atlantic Forest according to SIMPER analysis in decreasing order of contribution

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean abund. 1	Mean abund. 2
<i>D._simulans</i>	7,648	10,61	10,61	1,49	1,06
<i>D._immigrans</i>	5,818	8,07	18,68	0,849	0,664
<i>D._mediopunctata</i>	4,918	6,822	25,5	0,504	0,698
<i>D._mercatorum</i>	4,634	6,427	31,93	0,845	0,215
<i>D._paraguayensis</i>	4,62	6,408	38,34	0,388	0,665
<i>D._polymorpha</i>	4,121	5,716	44,05	0,774	0,541
<i>sg._willistoni</i>	4,093	5,678	49,73	0,679	0,359
<i>D._ornatifrons</i>	3,741	5,189	54,92	0,556	0,357
<i>D.buzzatii</i>	3,308	4,589	59,51	0,082	0,433
<i>D._busckii</i>	3,075	4,266	63,77	0,161	0,376

Figures

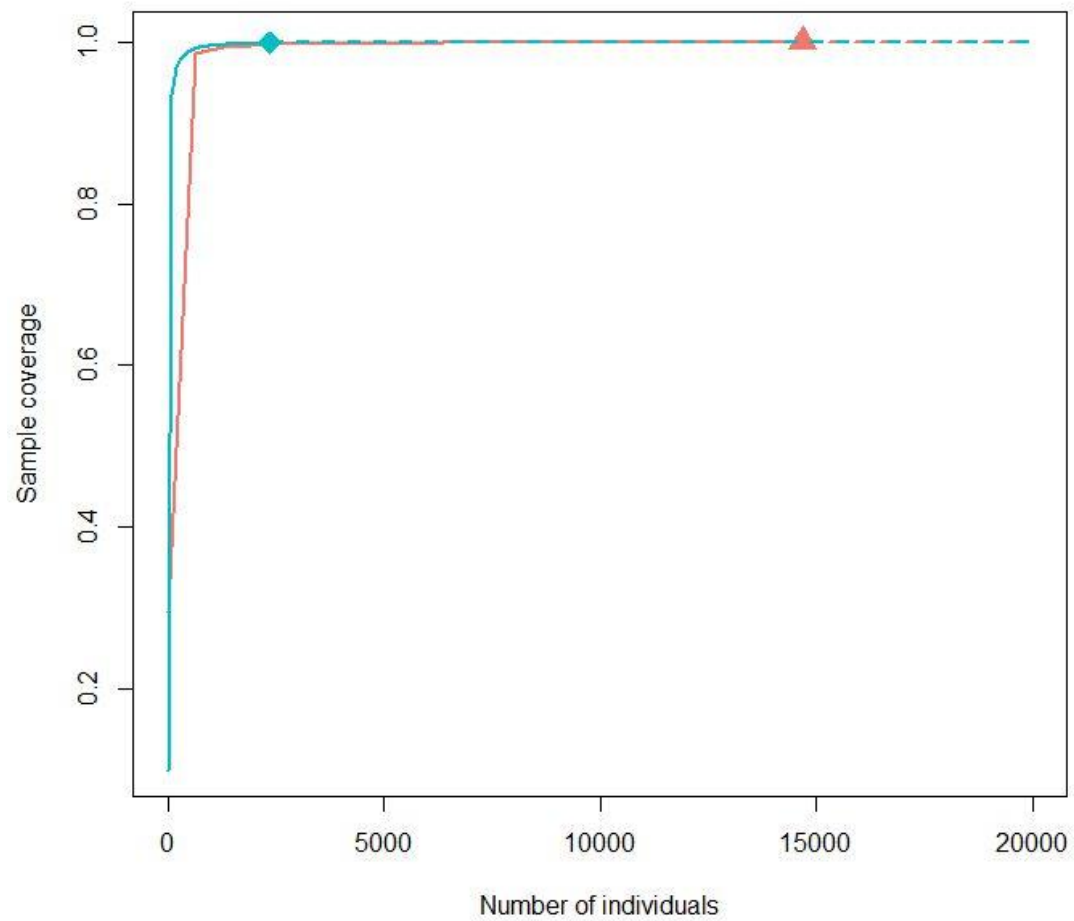


Fig. 1: Gain in sample coverage as a function of the addition of individuals in Atlantic Forest (red) and Pampa (blue) samples. Solid lines = rarefaction by interpolation; dash lines = extrapolation.

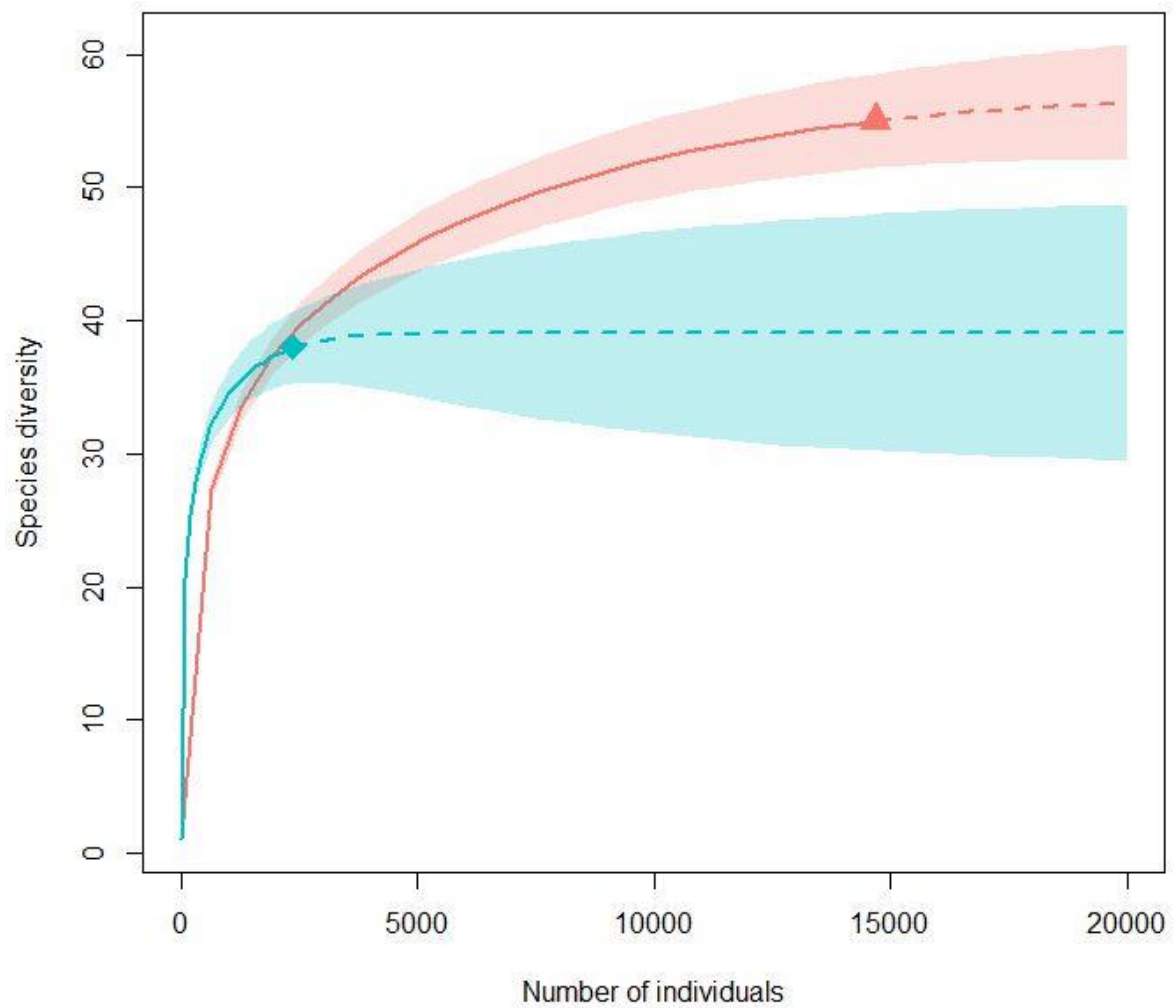


Fig. 2: Rarefaction curves of species richness for the Atlantic Forest (red) and Pampa (blue) Biomes. Solid lines = rarefaction by interpolation; dash lines = extrapolation; shaded area = 95% confidence interval as measured by 999 permutations.

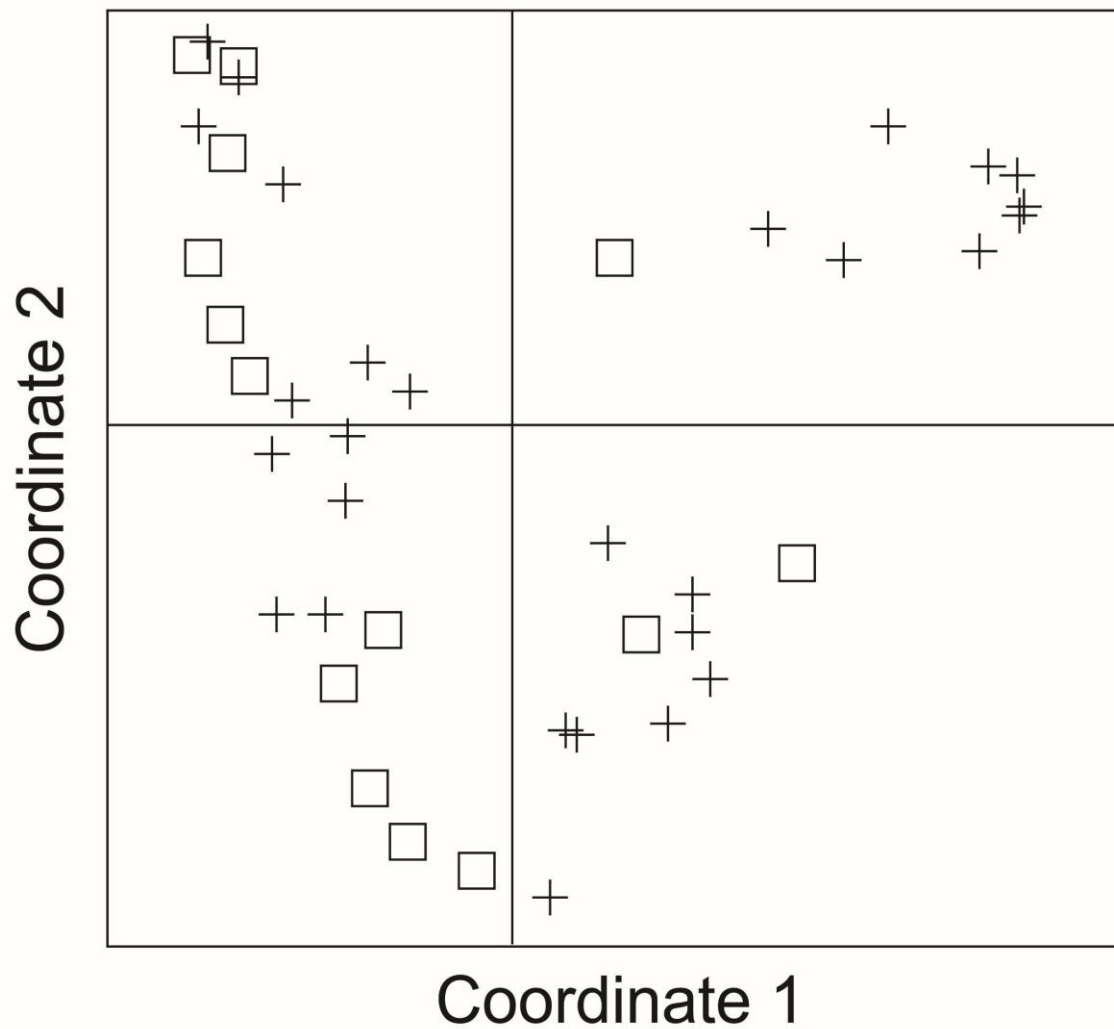


Fig. 3: Principal Coordinates Analysis (PCoA) ordination of the set of sampling points, according to Bray-Curtis dissimilarity measures in the two first coordinates, which explain 17.8% and 15.1% of the variation in the data. Crosses = Atlantic Forest sampling sites; squares = Pampa sampling sites.

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

O presente estudo mostrou diferenças nos padrões de distribuição de drosofilídeos entre áreas alagadas e matas, e entre os Biomas Pampa e Mata Atlântica no Sul do Brasil. Embora tanto as áreas alagadas quanto o Bioma Pampa tenham demonstrado menor riqueza de espécies, os resultados apresentados demonstram a importância da conservação dos diferentes habitats. Neste sentido, os estudos aqui realizados permitiram não apenas uma melhor compreensão destes habitats, como também dos fatores que influenciam a distribuição de drosofilídeos. Também demonstrou-se que a utilização de estratégias amostrais espacialmente e temporalmente dispersas pode ter uma grande utilidade na compreensão destes padrões. Estudos futuros devem ser realizados com a mesma base de dados, para incluir a análise do impacto dos diferentes fatores abióticos na distribuição e na composição diferencial de espécies. Este conjunto de informações é especialmente importante frente ao crescente uso de drosofilídeos como bioindicadores de alteração ambiental.

ANEXOS

CAPÍTULO UM

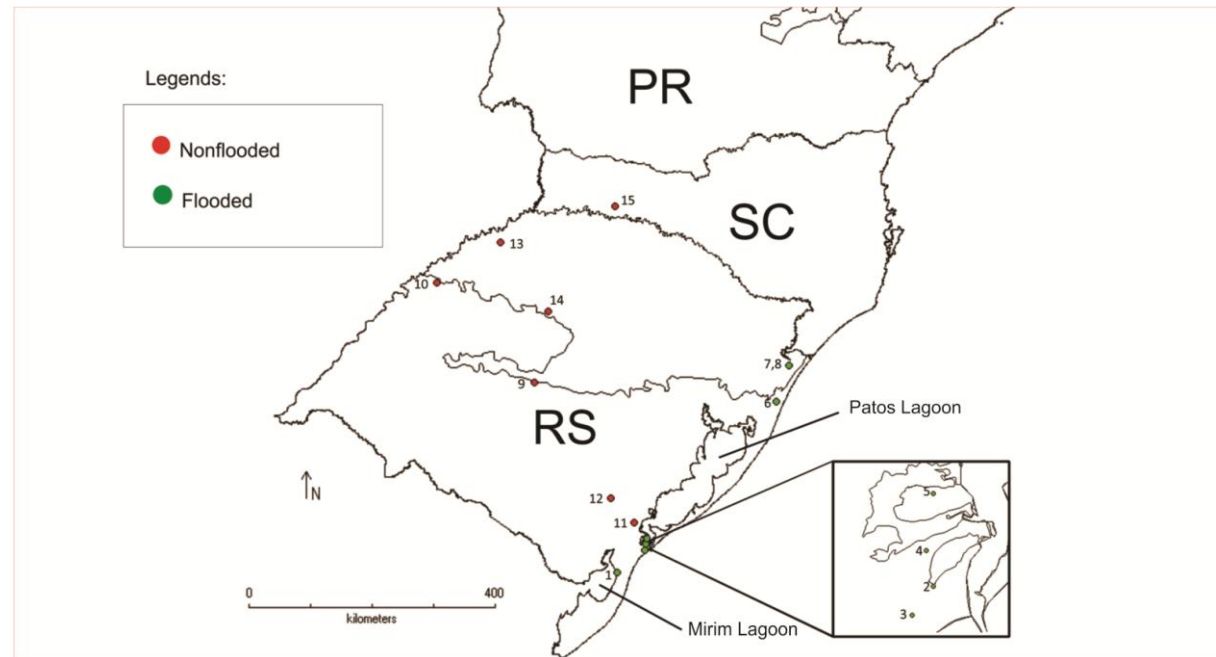


Fig. S1: Southern Brazil map, showing the distribution of the 15 collection points (1-8 representing flooded swamps, 9-15 representing nonflooded woods). Most collections were performed in the Rio Grande do Sul Brazilian state (RS in the map), across the Pampa and Mata Atlantica biomes (distinguished by distinct colors in the map). The RS coastal plain embraces the two of the Brazilian largest lagoons (Patos and Mirim Lagoons)

