



Track analysis of distribution patterns in Chironomidae (Insecta: Diptera): implications for conservation biogeography in southeastern Brazil

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Abstract. Chironomidae (Insecta: Diptera) are among the most diverse and widespread aquatic insects, with roughly 5,500 described species, inhabiting an enormous variety of aquatic ecosystems, ranging from moist soils to pools in tree-holes, and from low-oxygen lake sediments to fast-flowing mountain streams. Despite its ubiquity, the group remains underrepresented in studies addressing biogeographic patterns, particularly in South America. In this context, a panbiogeographic track analysis based on the distributional patterns of 80 Chironomidae genera was performed to predict conservation priorities for southeastern Brazil. In the track analysis approach, biogeographic nodes indicate the existence of compound or complex areas, resulting from terrain collision, docking or suturing. In this study, thirty-two biogeographic nodes corresponding to the priority areas for conservation were identified. The distribution of nodes showed that only 31% of the conceivable dispersion centers of Chironomidae were inside of presently established conservation units. Two priority areas indicated by the most important biogeographic nodes should be considered in future programs for biodiversity conservation in southeastern Brazil, since these areas may contain taxa from different ancestral biota. Identifying biotas and the processes that led to their evolution is essential for comprehend human induced changes in the global environment, and fundamental to elaborate new conservation strategies.

Keywords: Panbiogeography, conservation units, priority areas, Neotropical, Brazil

Resumo. Análise de traços de padrões de distribuição em Chironomidae (Insecta: Diptera): implicações para a biogeografia de conservação no sudeste do Brasil.

Chironomidae (Insecta: Diptera) estão entre os mais diversos e difundidos insetos aquáticos, com cerca de 5.500 espécies descritas, o grupo habita uma enorme variedade de ecossistemas aquáticos, tais como solos úmidos, buracos de árvores, sedimentos com baixo teor de oxigênio e riachos de montanha. Apesar de sua onipresença, o grupo continua sub-representado em estudos que abordam padrões biogeográficos, particularmente na América do Sul. Neste contexto, uma análise panbiogeográfica com base nos padrões de distribuição de 80 gêneros de Chironomidae foi realizada para predizer prioridades de conservação para o sudeste do Brasil. Neste método, os nós biogeográficos indicam a existência de áreas compostas ou complexas, resultantes da colisão do terreno, ancoragem ou sutura. Neste estudo, foram identificados 32 nós biogeográficos correspondentes às áreas prioritárias para conservação. A distribuição dos nós mostrou que apenas 31% dos centros de dispersão concebíveis para Chironomidae estavam dentro das unidades de conservação atualmente estabelecidas. Dessa forma, duas áreas

prioritárias indicadas pelos nós biogeográficos mais importantes devem ser consideradas em futuros programas de conservação da biodiversidade no sudeste do Brasil, uma vez que essas áreas podem conter taxa de biota ancestral diferente. Identificar as biotas e os processos que levaram à sua evolução é essencial para compreender as mudanças induzidas pelo homem no ambiente global e fundamental para elaborar novas estratégias de conservação.

Palavras chave: Panbiogeografia, unidades de conservação, áreas prioritárias, Neotropical, Brasil

Introduction

The state of São Paulo has 3,457 ha of remaining natural vegetation cover, which represent 13.9% of its surface, distributed according to the following percentages for each vegetation type: 5.8% forest, 5.9% secondary forest areas, 0.6% Cerrado (tropical savanna), 0.3% woodland, less than 0.1% of grassland, 0.6% of flooded forests, 0.1% mangrove and 0.6% sandbank. Kronka *et al.* (2005) evidenced that areas of Cerrado have suffered a drastic reduction in the state between 1962 and 2005 with the removal of 88.5% of its original cover, due to agricultural expansion and reforestation with exotic species to wood and cellulose industry. The coverage of the Atlantic rainforest in the state also has been significantly reduced due to a long process of exploitation and degradation which resulted in a reduction to only 11 to 16% of its original coverage throughout the country. The accelerated rate of conversion of natural areas into pastures and monocultures and the high degree of fragmentation of remaining natural state represent the two major problems faced in efforts for their conservation (Zaher *et al.* 2011).

In this context biogeographic knowledge is absolutely critical for determining where conservation areas should be established (Humphries *et al.* 1995), especially when limited resources force us to prioritize (Crisci *et al.* 2003). Several biogeographic methods are adopted for identifying the priority areas for conservation. Among them, panbiogeographic track analysis is a comprehensive approach to global biogeography that basically plots distributions of a particular taxon or group of taxa on maps and connects the disjunct distribution areas or collection localities together with lines called tracks (Crisci *et al.* 2003). The track analysis approach, as originally formulated by Leon Croizat, assumed that vicariance and range expansion are the only biogeographical processes needed to explain general biotic distributions (Craw *et al.* 1999, Crisci *et al.* 2000, Grehan 2011, Morrone 2015). This was in opposition to the prevailing paradigm at the time, known as dispersalism, which postulates that

organisms evolve in ‘centers of origin’ from pre-existing species and then randomly cross barriers to occupy new areas, where they adapt and evolve into new species (Morrone 2015). The areas elected by track analysis criteria are particularly important for the purposes of conservation (Morrone 1999) because they contain biotic elements from different origins and permit us to protect areas considering not solely the number of species, but the degree of differences between the biotas overlapping on them (Craw *et al.* 1999).

Numerous countries in South America have used panbiogeographic track analysis in the establishment of areas for conservation (Morrone & Lopretto 1994, Morrone 1999, Luna-Vega *et al.* 2000, Contreras-Medina & Eliosa-León 2001, Franco-Rosselli 2001, Morrone 2001a, Mondragón & Morrone 2004a). These studies were performed in different group of organisms such as coleopterans, birds and plants, and mostly conducted in terrestrial ecosystems. In Brazil few studies have employed track analysis tools (Franco-Rosselli & Berg 1997, Carvalho *et al.* 2003, Morrone 2004a, Nihei & de Carvalho 2005, Prevedello & Carvalho 2006, Maltchik *et al.* 2012), however, in the state of São Paulo, panbiogeographic track analysis methods have never been used for identify priorities areas for biodiversity conservation. Most protected areas are created to protect natural types and species of the terrestrial fauna and flora, but occasionally they also protect a considerable number of aquatic ecosystems, making them of great importance for the conservation of aquatic species (Agostinho *et al.* 2005, Nel *et al.* 2007). Within the aquatic fauna, macroinvertebrates have been widely used as biological indicators of water quality and anthropogenic impacts. In Brazil, few studies relate diversity of aquatic insects to prioritization and establishment of conservation units (Agostinho *et al.* 2005, Silva *et al.* 2007, 2011, Paz *et al.* 2008, Silva *et al.* 2011), however, all of them reaffirm the importance of using this fauna as bioindicators in environmental diagnoses and in selection of priorities areas for conservation.

The non-biting midges Chironomidae (Insecta: Diptera) are true flies, and the most widely distributed free-living holometabolous insects (Cranston 1982, Ferrington 2008). Species of Chironomidae inhabit an enormous variety of aquatic ecosystems, ranging from moist soils to pools in tree-holes, and from low-oxygen lake sediments to fast-flowing mountain streams (Ferrington *et al.* 2008). The countless species and habitat diversity makes this family a valuable indicator species for lentic and lotic aquatic ecosystems, but also particularly well suited for phylogenetic and biogeographical investigations (Silva & Ekrem 2016). Approximately 900 chironomid species are recognized from the Neotropical Region (Martin Spies, personal communication). This number has been increasing in recent years thanks to intense taxonomic work being done, particularly in Brazil and Argentina (e.g. Andersen & Pinho 2014, Andersen *et al.* 2015, Oliveira *et al.* 2013, Silva & Wiedenbrug 2015, Silva *et al.* 2014a,b, Siri *et al.* 2015, Trivinho-Strixino *et al.* 2013, 2015, Parise & Pinho 2016, Silva & Oliveira 2016, Silva & Ferrington 2018). When it comes to the state of São Paulo, the chironomid fauna is well-known. Several authors (e.g. Correia *et al.* 2005, 2006, 2013, Trivinho-Strixino *et al.* 2010, Trivinho-Strixino & Silva 2011, Oliveira *et al.* 2014, Silva *et al.* 2010, 2012) have addressed the group, which make the region suitable for biogeographic analyses. This study aimed to apply a track analysis to identify the distribution patterns of Chironomidae genera in the state of São Paulo, comparing the distribution of the biogeographic nodes with the presently conservation units of this area in order to predict conservation priorities for southeastern Brazil.

Material and methods

Study area: The state of São Paulo, located in southeastern Brazil, has an area of approximately 248,800 km². The climate of São Paulo is tropical to subtropical, the altitude is the largest contributor to what variation there is. The annual precipitation average is 1,454 mm. Rain is especially common in the warmer months averaging 219 mm, while the winter average is 47 mm. The average temperature varies between 10°C and 22°C at the coolest time of year, reaching around 33°C on the hottest days in the summer. The remaining patches of evergreen forest in the highlands are reminiscent of the wealth of vegetation in Brazil in days gone by. The vegetation

is greatly diversified and includes several kinds of hardwoods (such as rosewood), wild fruits, and plants that are used for medicinal and ornamental purposes or for making textiles.

Track analysis: Distributional data from 80 Chironomidae genera from 194 localities in the state of São Paulo (Fig. 1) were obtained from reliable published surveys and unpublished sources over three decades, between the years 1980 to 2010 (Appendix S1 and S2 in supporting information). In order to identify possible synonyms, the list was cautiously verified by checking the relevant literature and through communication with specialists. This study has gathered data generated with different sampling methods, however this fact should not affect the result, since panbiogeographic and track analyses reflect the presence or absence of specimens in a certain area. Thus, these analyses may utilize data from organism groups that require sampling with different methods. For this investigation, the genus level seemed to be the most appropriated, since in the Neotropical region the specific knowledge in Chironomidae is still incipient (Silva & Farrell 2017). Furthermore, larvae can be identified to genus level with reasonable level of certainty, literature exists for identification of male, pupa and larva and the genera are relatively well defined in all life stages. Finally, the genus level analysis offers a substantial advantage by allowing inclusion of a large amount of data from ecological studies. In this study, the taxa *Tanytarsus* gr. *ortoni* corresponds to the genus "Caladomyia" in previous literature, according to Lin *et al.* (2017).

The distributional patterns of Chironomidae genera were analysed through the track analysis approach, according to the methodology of Morrone & Crisci (1995) and Craw *et al.* (1999). The occurrence localities for each genus were plotted into maps and connected by their minimal geographical distance to obtain individual tracks. The generalized tracks for the genera was obtained by overlapping the individual tracks. The biogeographic nodes were recognized where two or more generalized tracks intersected or overlapped (Craw *et al.* 1999, Crisci *et al.* 2003). The most important generalized tracks and biogeographic nodes were identified by quantification of the number of individual and generalized tracks, respectively. Finally, the biogeographic nodes were superposed and compared with the map of conservation units existent in the state of São Paulo.

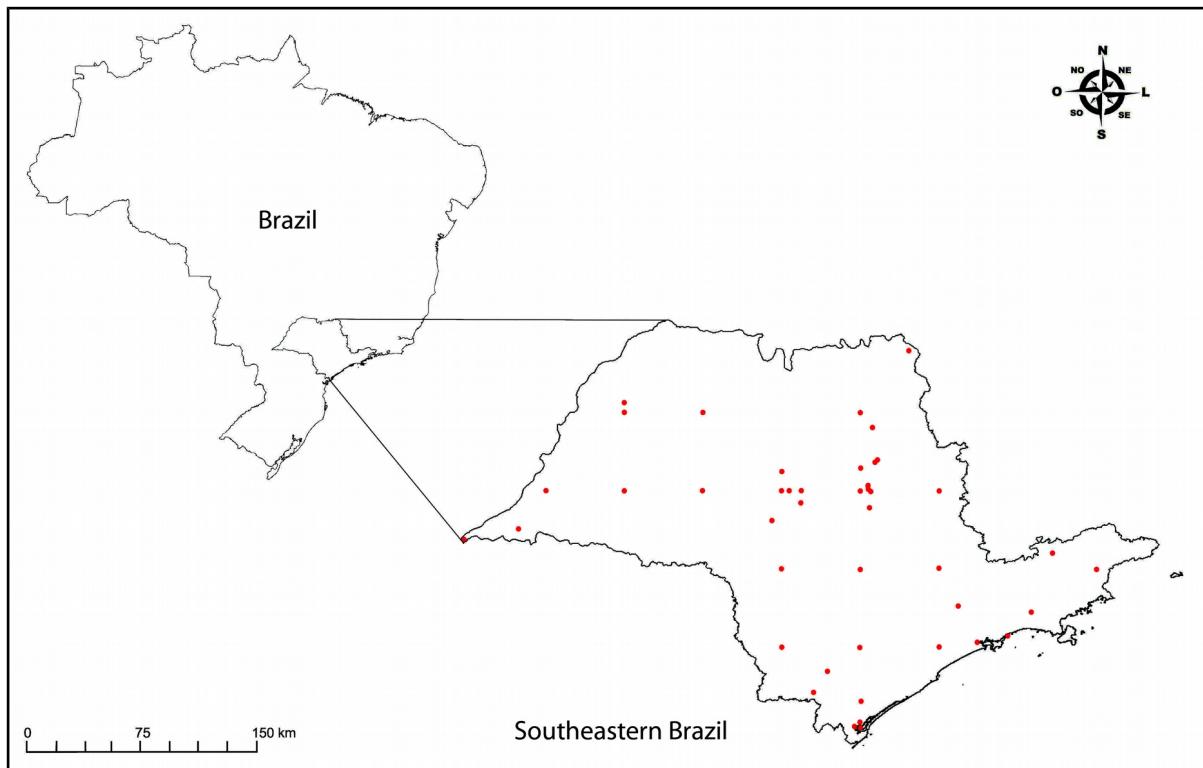


Figure 1. Map of the state of São Paulo showing the localities analyzed in southeastern Brazil (several localities are overlapped due to geographical proximity).

Results

In total, 80 genera of three subfamilies were sampled (Table I), which corresponded to 80 individual tracks obtained by geographical data available in the literature. Chironominae predominated followed by Tanypodinae and Orthocladiinae, respectively. The subfamily Podonominae was not recorded. Based on spatial congruence of the individual tracks (overlapping), 54 generalized tracks were generated (Table I, Fig. 2). *Ablabesmyia* Johannsen was the genus most present in the generalized tracks. This is a remarkably species-rich genus, composing one of the most distinctive and well-defined clades within the subfamily Tanypodinae (Silva & Ekrem 2016). The highest diversity of *Ablabesmyia* seems to be in the tropical and warm-temperate belts (Silva & Farrell 2017). Larvae of this genus inhabit small and large standing and flowing waters from cold temperate and arctic to warm tropical climatic zones. Late instar larvae are predatory, perhaps particularly on smaller chironomid larvae and oligochaetes which are engulfed (Cranston & Epler 2013). In this study, the group was involved in defining 23 generalized tracks. Another commonly found genus was *Tanytarsus* van der Wulp. This is a eurytopic genus, occurring in all types of freshwater, with

some marine and at least one terrestrial species. Larval *Tanytarsus* feed on microorganisms and detritus through filtering and gathering, a few species are scrapers. Herein, the genus participated in defining 20 generalized tracks. Finally, the third most common genus was *Labrundinia* Fittkau. This is a large group, predominantly Neotropical (Silva *et al.* 2015), with larvae inhabiting a variety of aquatic systems, from small streams and ponds to lakes and bays, usually associated with aquatic macrophytes or marginal vegetation in slow flowing streams or rivers (Silva *et al.* 2011, 2014c). *Labrundinia* species often have been reported as predators and have been recorded in many ecological studies. The group helped in defining 19 tracks.

The most important generalized tracks were the numbers 5 and 6, defined by 38 and 37 individual tracks, respectively. Both tracks are located in the center of the state of São Paulo, in an area of Cerrado (Fig. 2). The intersection or overlapping of generalized tracks permitted to identify 32 nodes for Chironomidae genera. The most important nodes were the 'o' defined by nine generalized tracks and the 'n', 'u', 'y' and 'α' defined by six generalized tracks (Table II).

Table I. Generalized tracks identified in the state of São Paulo, southeastern Brazil and genera which define them.

Generalized track	Total genera involved	Genera defining the generalized tracks
1	4	<i>Antillocladius, Corynoneura, Parametriocnemus, Pentaneura</i>
2	8	<i>Ablabesmyia, Antillocladius, Djalmabatista, Polypedilum, Procladius, Stenochironomus, Tanytarsus, Zavreliella</i>
3	16	<i>Ablabesmyia, Chironomus, Cladopelma, Clinotanypus, Dicrotendipes, Djalmabatista, Fissimentum, Fittkauimyia, Goeldichironomus, Harnischia, Labrundinia, Procladius, Pseudosmittia, Stenochironomus, Tanytarsus, Zavreliella</i>
4	25	<i>Ablabesmyia, Aedokritus, Beardius, Chironomus, Cladopelma, Clinotanypus, Coelotanypus, Cricotopus, Cryptochironomus, Dicrotendipes, Djalmabatista, Fissimentum, Fittkauimyia, Goeldichironomus, Harnischia, Labrundinia, Paratanytarsus, Polypedilum, Procladius, Pseudosmittia, Rheotanytarsus, Stenochironomus, Tanytarsus gr. ortonii, Thienemanniella, Zavreliella</i>
5	38	<i>Ablabesmyia, Alotanypus, Antillocladius, Clinotanypus, Corynoneura, Cricotopus, Cryptochironomus, Demicryptochironomus, Dicrotendipes, Djalmabatista, Endotribelos, Fissimentum, Fittkauimyia, Harnischia, Labrundinia, Larsia, Lopescladius, Macropelopia, Nilotanypus, Nanocladius, Onconeura, Parachironomus, Paralauterborniella, Parametriocnemus, Paratanytarsus, Paratendipes, Pentaneura, Phaenopsectra, Polypedilum, Rheotanytarsus, Saetheria, Stempellina, Stempellinella, Stenochironomus, Tanytarsus gr. ortonii, Thienemanniella, Zavreliella, Zavrelimyia</i>
6	37	<i>Ablabesmyia, Alotanypus, Antillocladius, Beardius, Chironomus, Clinotanypus, Corynoneura, Cryptochironomus, Cricotopus, Dicrotendipes, Djalmabatista, Endotribelos, Fissimentum, Fittkauimyia, Goeldichironomus, Harnischia, Labrundinia, Larsia, Lopescladius, Macropelopia, Nanocladius, Nilotanypus, Onconeura, Parachironomus, Parametriocnemus, Pentaneura, Phaenopsectra, Polypedilum, Rheotanytarsus, Stempellina, Stempellinella, Stenochironomus, Tanypus, Tanytarsus gr. ortonii, Zavreliella, Zavrelimyia</i>
7	6	<i>Ablabesmyia, Aedokritus, Chironomus, Fissimentum, Parachironomus, Tanytarsus.</i>
8	3	<i>Cladopelma, Demicryptochironomus, Saetheria</i>
9	7	<i>Microchironomus, Monopelopia, Nilothauma, Pelomus, Xestochironomus, Thienemannimyia, Tribelos</i>
10	2	<i>Riethia, Xenochironomus</i>
11	10	<i>Antillocladius, Corynoneura, Djalmabatista, Goeldichironomus, Labrundinia, Lopescladius, Nanocladius, Nilotanypus, Pentaneura, Stenochironomus</i>
12	9	<i>Ablabesmyia, Coelotanypus, Corynoneura, Goeldichironomus, Labrundinia, Lopescladius, Nanocladius, Pentaneura, Stenochironomus</i>
13	3	<i>Dicrotendipes, Parachironomus, Paralauterborniella</i>
14	14	<i>Ablabesmyia, Antillocladius, Corynoneura, Cryptochironomus, Endotribelos, Labrundinia, Larsia, Lopescladius, Nanocladius, Pentaneura, Polypedilum, Rheotanytarsus, Stenochironomus, Tanytarsus</i>
15	11	<i>Ablabesmyia, Cryptochironomus, Harnischia, Labrundinia, Lopescladius, Nanocladius, Parametriocnemus, Pentaneura, Polypedilum, Stenochironomus, Tanytarsus</i>
16	2	<i>Larsia, Rheotanytarsus</i>
17	15	<i>Cladopelma, Clinotanypus, Demicryptochironomus, Djalmabatista, Larsia, Macropelopia, Microchironomus, Monopelopia, Nilothauma, Pentaneura, Rheotanytarsus, Saetheria, Stempellina, Thienemanniella,</i>

Generalized track	Total genera involved	Genera defining the generalized tracks
		<i>Tribelos</i>
18	5	<i>Axarus, Chironomus, Clinotanypus, Procladius, Stempellina</i>
19	13	<i>Ablabesmyia, Antillocladius, Beardius, Corynoneura, Djalmabatista, Goeldichironomus, Nanocladius, Labrundinia, Larsia, Pentaneura, Saetheria, Tanytarsus, Tribelos,</i>
20	13	<i>Antillocladius, Beardius, Corynoneura, Demicryptochironomus, Djalmabatista, Endotribelos, Labrundinia, Nanocladius, Parachironomus, Paralauterborniella, Procladius, Stenochironomus, Thienemanniella</i>
21	12	<i>Ablabesmyia, Aedokritus, Cryptochironomus, Cricotopus, Metriocnemus, Parakiefferiella, Paratanytarsus, Phaenopsectra, Rheocricotopus, Saetheria, Stempellinella, Tanytarsus</i>
22	6	<i>Metriocnemus, Parakiefferiella, Paratanytarsus, Phaenopsectra, Rheocricotopus, Saetheria</i>
23	2	<i>Chironomus, Goeldichironomus</i>
24	4	<i>Ablabesmyia, Cricotopus, Cryptochironomus, Tanytarsus</i>
25	20	<i>Beardius, Cricotopus, Endotribelos, Fittkauimyia, Gymnometriocnemus, Lopescladius, Macropelopia, Monopelopia, Nandeva, Paratanytarsus, Pelomus, Phaenopsectra, Onconeura, Oukuriella, Rheocricotopus, Stempellinella, Tanypus, Tribelos, Xenochironomus, Zavreliomyia</i>
26	6	<i>Ablabesmyia, Larsia, Microtendipes, Rheotanytarsus, Tanytarsus, Thienemanniella</i>
27	7	<i>Clinotanypus, Ichthyocladius, Nilotanypus, Parachironomus, Parametriocnemus, Pseudosmittia, Zavreliella</i>
28	6	<i>Ichthyocladius, Parachironomus, Parametriocnemus, Pseudosmittia, Pentaneura, Tanytarsus gr. ortonii</i>
29	3	<i>Corynoneura, Glyptotendipes, Micropsectra</i>
30	5	<i>Gymnometriocnemus, Cladotanytarsus, Parametriocnemus, Pentaneura, Rheotanytarsus</i>
31	8	<i>Ablabesmyia, Cladotanytarsus, Gymnometriocnemus, Larsia, Parametriocnemus, Rheotanytarsus, Thienemanniella, Zavreliella</i>
32	29	<i>Ablabesmyia, Aedokritus, Brundiniella, Chironomus, Cladopelma, Cladotanytarsus, Clinotanypus, Cricotopus, Demicryptochironomus, Dicrotendipes, Djalmabatista, Fissimentum, Goeldichironomus, Harnischia, Labrundinia, Nanocladius, Nilothauma, Parachironomus, Paralauterborniella, Parapentaneura, Paratendipes, Pentaneura, Polypedilum, Riethia, Saetheria, Tanytarsus gr. ortonii, Thienemannimyia, Xestochironomus</i>
33	22	<i>Antillocladius, Coelotanypus, Clinotanypus, Cryptochironomus, Dicrotendipes, Djalmabatista, Fissimentum, Gymnometriocnemus, Goeldichironomus, Labrundinia, Nanocladius, Nilothauma, Oukuriella, Parachironomus, Paralauterborniella, Paratendipes, Pentaneura, Polypedilum, Saetheria, Stenochironomus, Xestochironomus, Thienemannimyia</i>
34	11	<i>Beardius, Corynoneura, Fissimentum, Gymnometriocnemus, Harnischia, Hudsonimyia, Nilothauma, Parachironomus, Oukuriella, Xenochironomus, Zavreliella</i>
35	2	<i>Beardius, Saetheria</i>
36	4	<i>Clinotanypus, Paralauterborniella, Thienemannimyia, Zavreliella</i>
37	12	<i>Ablabesmyia, Corynoneura, Endotribelos, Lopescladius, Nilotanypus, Parachironomus, Pentaneura, Polypedilum, Pseudosmittia, Rheotanytarsus, Saetherocladius, Tanytarsus gr. ortonii</i>

Generalized track	Total genera involved	Genera defining the generalized tracks
38	7	<i>Antillocladius, Djalmabatista, Labrundinia, Larsia, Nanocladius, Polypedilum, Tanytarsus,</i>
39	21	<i>Ablabesmyia, Antillocladius, Corynoneura, Djalmabatista, Endotribelos, Harnischia, Labrundinia, Larsia, Lopescladius, Microtendipes, Nanocladius, Onconeura, Parachironomus, Parametriocnemus, Pentaneura, Phaenopsectra, Rheotanytarsus, Stenochironomus, Tanytarsus gr. ortoni, Thienemannella</i>
40	20	<i>Ablabesmyia, Antillocladius, Endotribelos, Corynoneura, Cricotopus, Djalmabatista, Harnischia, Labrundinia, Larsia, Onconeura, Parachironomus, Parametriocnemus, Pentaneura, Phaenopsectra, Procladius, Rheotanytarsus, Stenochironomus, Tanytarsus gr. ortoni, Thienemannella</i>
41	3	<i>Cricotopus, Stempellina, Thienemannella</i>
42	4	<i>Aedokritus, Cryptochironomus, Nandeva, Xestochironomus</i>
43	2	<i>Gymnometriocnemus, Zavrelimyia</i>
44	3	<i>Antillocladius, Cladopelma, Nilotanypus</i>
45	5	<i>Cladotanytarsus, Cryptochironomus, Goeldichironomus, Fittkauimyia, Macropelopia</i>
46	27	<i>Ablabesmyia, Antillocladius, Chironomus, Coelotanypus, Corynoneura, Cricotopus, Cryptochironomus, Djalmabatista, Endotribelos, Fittkauimyia, Gymnometriocnemus, Goeldichironomus, Labrundinia, Larsia, Nanocladius, Paratendipes, Pentaneura, Polypedilum, Procladius, Rheocricotopus, Rheotanytarsus, Stenochironomus, Tanypus, Tanytarsus gr. ortoni, Thienemannella, Thienemannimyia, Zavrelimyia</i>
47	21	<i>Ablabesmyia, Chironomus, Coelotanypus, Cryptochironomus, Cricotopus, Djalmabatista, Endotribelos, Fittkauimyia, Goeldichironomus, Larsia, Lopescladius, Macropelopia, Pentaneura, Polypedilum, Rheocricotopus, Rheotanytarsus, Stempellina, Tanytarsus gr. ortoni, Tanypus, Thienemannella</i>
48	7	<i>Antillocladius, Corynoneura, Gymnometriocnemus, Labrundinia, Nanocladius, Stenochironomus, Zavrelimyia</i>
49	7	<i>Ablabesmyia, Coelotanypus, Larsia, Lopescladius, Paratendipes, Rheotanytarsus, Tanytarsus</i>
50	16	<i>Chironomus, Coelotanypus, Cryptochironomus, Djalmabatista, Endotribelos, Fissimentum, Goeldichironomus, Paratendipes, Polypedilum, Procladius, Saetheria, Stempellina, Stempellinella, Tanytarsus gr. ortoni, Thienemannella, Xestochironomus</i>
51	3	<i>Gymnometriocnemus, Microtendipes, Nanocladius</i>
52	14	<i>Ablabesmyia, Antillocladius Compterosmittia, Cricotopus, Larsia, Lopescladius, Onconeura, Parametriocnemus, Pelomus, Polypedilum, Rheotanytarsus, Saetherocladius, Stenochironomus, Tanytarsus</i>
53	11	<i>Antillocladius, Corynoneura, Cricotopus, Onconeura, Labrundinia, Lopescladius, Parametriocnemus, Pseudosmittia, Polypedilum, Saetherocladius, Stenochironomus</i>
54	29	<i>Ablabesmyia, Aedokritus, Asheum, Beardius, Chironomus, Cladopelma, Clinotanypus, Coelotanypus, Corynoneura, Cricotopus, Djalmabatista, Endotribelos, Fissimentum, Fittkauimyia, Goeldichironomus, Harnischia, Labrundinia, Larsia, Monopelopia, Nilothauma, Parachironomus, Paratendipes, Phaenopsectra, Polypedilum, Rheotanytarsus, Stempellina, Tanypus, Tanytarsus gr. ortoni</i>

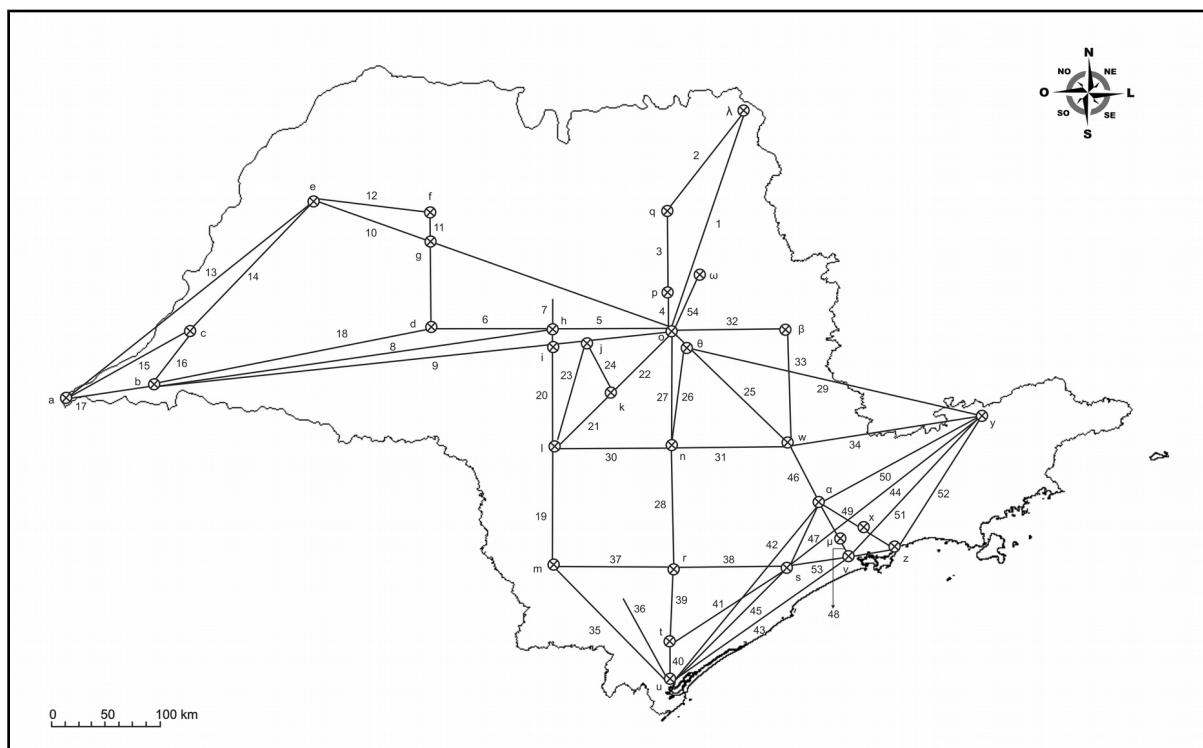


Figure 2. Generalized tracks and biogeographic nodes of Chironomidae (Insecta: Diptera) genera in the state of São Paulo, southeastern Brazil.

These biogeographic nodes conceivably consist in the priority areas for conservation of Chironomidae diversity in the state of São Paulo. In this study, only ten nodes (31%) were totally or partially inside of conservation units (Fig. 3). These nodes followed the following distribution: (1) a-node in the Morro do Diabo State Park, (2) r-node in the Carlos Botelho State Park, (3-5) s, v and z-nodes in the Serra do Mar State Park, (6) u-node in the Lagamar Cananéia State Park, (7) w-node in the Jataí State Ecological Station, (8) y-node in the Campos do Jordão State Park, (9) α-node in the Jaraguá State Park and (10) ω-node in the area of Valinhos State Ecological Station and Agrarian Reference Advice State Park (Figure 3). This investigation indicated two priority areas by the most important biogeographic nodes: (1) eastern of the state of São Paulo represented by o-node and (2) east-central of the state of São Paulo represented by n-node. The u, y and α-nodes areas although they were also identified as important biogeographic nodes they are already within conservation units in southeastern Brazil.

Discussion

Chironomidae

distribution

patterns:

Panbiogeographic track analysis is a biogeographical approach that emphasizes the importance of the spatial or geographical dimension of biodiversity in order to understand evolutionary patterns and processes (Craw *et al.* 1999). While phylogenetic analyses are applied extensively in comparative biology, the spatial component of evolution is generally neglected in the comprehension of the historical structure of biotic systems to identify priority areas for biodiversity conservation (Luna-Vega *et al.* 2000). In the track analysis approach, the determination of individual tracks is a useful tool, corresponding to the basic unit of this method. They represent the space where evolution occurs (Contreras-Medina *et al.* 2001) and indicate the distribution patterns of the studied organisms (Morrone 2001b). In this study, the spatial congruence of individual tracks (generalized tracks), may be considered as primary biogeographical homology. According to Morrone (2001a), panbiogeographic track analysis corresponds to the first stage in the recognition of primary biogeographical homologies, followed by confirmation of these cases in secondary homologies by analysis of cladistic biogeography (Morrone 2015). The primary biogeographical homologies

Table II. Biogeographic nodes identified in the state of São Paulo, southeastern Brazil and generalized tracks defining them.

Biogeographic Node	Generalized Tracks	Biogeographic Node	Generalized Tracks
a	13+14+15+17	q	2+3
b	8+9+16+17+18	r	28+37+38+39
c	14+15+16	s	38+53+41+45+47
d	11+6+18	t	39+40+41
e	10+12+13+14	u	35+36+40+42+43+45
f	11+12+13+14	v	43+48+51+3
g	10+11	w	25+31+33+34+6
h	5+6+7+20	x	44+49
i	9+20	y	29+34+44+50+51+52
j	9+23+24	z	49+52+53
k	21+22+24	α	42+46+47+48+49+50
l	19+20+21+23+30	β	32+33
m	19+35+37	θ	25+26+29
n	26+27+28+30+30+31	λ	1+2
o	1+4+5+9+10+22+27+32+54	μ	44+48
p	3+4	ω	54

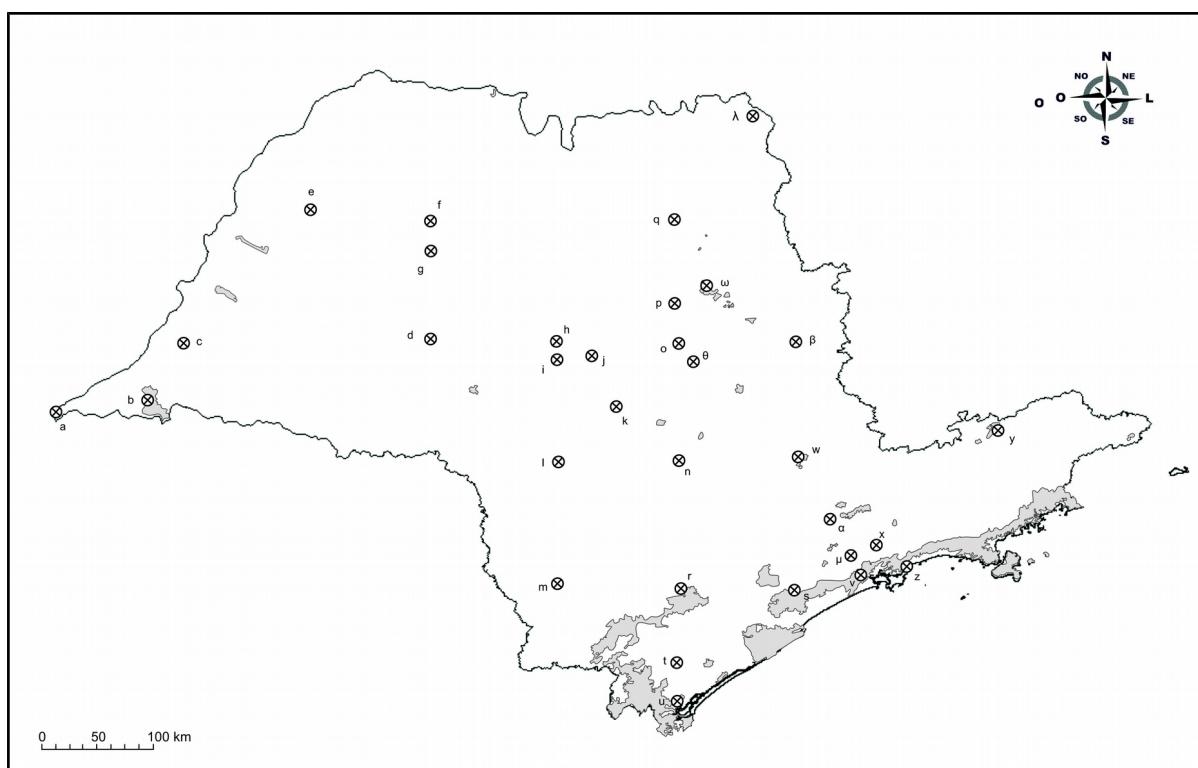


Figure 3 - Comparison between the distribution of the biogeographic nodes and the distribution of the conservation units (shaded gray regions) in the state of São Paulo, southeastern Brazil.

constitute in assumptions on common biogeographical history, inferred by corresponding patterns of distribution, which in track analysis correspond to the generalized tracks (Morrone 2001b, 2015).

Biogeographic nodes are complex areas that are recognized where two or more generalized tracks intersect or overlap (Craw *et al.* 1999). Nodes are particularly interesting from an evolutionary biogeographical viewpoint, because they allow us to

speculate on the existence of compound or complex areas. They may be characterized by the location of endemism, high diversity, distributional boundaries, disjunction, anomalous absence of taxa, incongruence and recombination of characters, and unusual hybrids (Morrone 2015); these features are found together only in the most important nodes (Heads 2004).. The distribution of biogeographic nodes determined in the state of São Paulo by the distribution patterns in Chironomidae may conceivably be explained based on fact that more studies and more sampling efforts were carried in these areas. However, the nodes recognized herein also may represent areas of great importance in the evolutionary context of the concerned taxa. The two priority areas identified in this investigation were located in the Cerrado, which is considered a biodiversity hot spot, and host an exceptional concentration of endemic plants. This area is reported to have lost more than 70% of its natural cover (Myers *et al.* 2000, Mittermeier *et al.* 2004) for firewood and growing crops, poor farming techniques, over-grazing, large-scale commercial logging, and depleting groundwater.

As aforementioned, panbiogeographic track analysis is aimed at recognizing primary biogeographical homology (Morrone 2001, 2004b), which represents a hypothesis about a common biotic history based on distributional congruence, and is formulated without any phylogenetic information. Therefore, even though Croizat's metaphor 'Earth and life evolve together' may be a valuable premise to comprehending general biogeographic patterns, the relationships between Earth history and life are more complex because biotic history is reticulate (Brooks 2004). To reduce our explanations entirely to vicariance or dispersal is misguided (Morrone 2015). Both processes should be integrated into a dispersal–vicariance model that permits us to understand the evolution of biological distribution patterns, integrating the dating of the lineages and the identification of the sets of taxa that share the same biogeographical history, which coexist within biotas. In the framework of this model, the panbiogeographic track analysis approach is a useful method for identifying biotas, and may constitute the first step of an evolutionary biogeographical analysis (Morrone 2015). Identifying biotas and the processes that led to their evolution is essential for comprehend human induced changes in the global environment, and fundamental to elaborate new conservation strategies.

Identifying biotas and the processes that led to their evolution is fundamental for more elaborate analyses. It has been previously proposed that track analysis is aimed at recognizing primary biogeographical homology, whereas cladistic biogeography is aimed at secondary biogeographical homology (Morrone, 2001, 2004a). Primary biogeographical homology represents a hypothesis about a common biotic history based on distributional congruence, which is formulated without any phylogenetic information. Secondary biogeographical homology refers to the cladistic biogeographical test of the previously recognized homology, thus requiring phylogenetic evidence (Morrone, 2009, 2014).

Conservation conclusions: The selection of priority areas is very problematic in biodiversity conservation programs (Sarkar & Margules 2002). In general, the methods for identifying biodiversity priority areas require great amount of data on the distribution and abundance patterns of the species richness, diversity and composition (Margules *et al.* 2002). In this context, the track analysis approach is an appropriate global perspective for developing a conservation science because it meets the requirement of homology, monophyly and empirical testability (Grehan 1989). According to Grehan (1993), the nodes are biodiversity hot spots in a historical context, and consequently they must be considered as conservation priority areas. These areas reproduce indirectly the long-term conservation of the biodiversity and spatial structure of the biota. They also include areas of high biogeographic diversity, since they are formed by different ancestral biotic or geologic fragments, qualifying them as priority areas for conservation (Prevedello & Carvalho 2006). On the other hand, when it comes to conservation biogeography, the track analysis approach presents the drawback of not dealing with endemic, rare or threatened species with higher conservation value, in addition to mainly focus entirely on the high-diversity sites.

Regarding the Neotropical region, there has been no regular conservation approach for tropical insects. Only for a minority of rare, threatened or exploited tropical taxa there are detailed ecological information that can assist in conservation programs (Lewis & Bassett 2007). This scenario may be attributed to the taxonomic impediment, which is perhaps at its greatest for tropical insects, where the mismatch between taxonomic effort and biological diversity is at its utmost, and it greatly inhibits tropical insect conservation biology by making even

the most taxonomically restrictive inventory a major undertaking (Lewis & Basset 2007). Probably only 7-10% of insect species are known to science. Of these, several are difficult to identify, yet many occupy significant ecological niches (Samways 1993). Therefore, meeting the taxonomic challenge will require the use of new strategies involving conservation biogeography, and the transfer of technologies and training to tropical countries, which harbor most biodiversity (Lewis & Basset 2007).

Chironomidae have been insufficient studied in relation to their need for protection. Considering the magnitude of the group, a reduced number of species are known to science. Of these, several are morphologically challenging to identify (Silva & Wiedenbrug 2014), yet many occupy significant ecological niches. In this context, there is a crucial need for a comprehensive biodiversity assessment tool to accelerate the pace at which biodiversity can be monitored and conserved (Mace 2004). This study indicates that the conservation units in southeastern Brazil do not encompass several priority areas for the historical and biogeographic conservation of Chironomidae. Numerous areas important for the biodiversity conservation are found outside the conservation units and are vulnerable to anthropic disturbance. The two priority areas indicated by the most important biogeographic nodes should be considered in the future for biodiversity conservation programs in southeastern Brazil, since these areas contain species from different ancestral biota. Additionally, the results obtained in this study demonstrate that the track analysis approach may be an important tool in the identification of priority areas for biodiversity conservation programs, as postulated by Grehan (1989).

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Track analysis of distribution patterns in Chironomidae (Insecta: Diptera): implications for conservation biogeography in southeastern Brazil

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Supplementary Material I

Table S-I. List of localities and type of biotopes in which chironomid distribution patterns in the state of São Paulo were based.

	Localities (Counties)	Biotope	Latitude	Longitude
1	Adrianópolis	Stream	-24.656944	-49.008889
2	Americana	Reservoir	-22.733333	-47.333333
3	Apiaí	River	-23.570278	-48.606389
4	Araraquara	Reservoir	-21.700000	-48.000000
5	Araraquara	Stream	-21.933333	-48.266667
6	Araraquara	Stream	-21.906944	-48.224722
7	Araraquara	Stream	-21.900000	-48.216667
8	Araraquara	Stream	-21.816944	-48.188056
9	Araraquara	Stream	-21.916667	-48.183333
10	Araraquara	Stream	-21.720556	-48.048056
11	Araraquara	Stream	-24.848889	-48.136111
12	Araraquara	Stream	-21.910556	-48.048056
13	Atibaia	Stream	-23.170700	-46.528400
14	Barra Bonita	Reservoir	-20.316667	-48.333333
15	Barra Bonita	Reservoir	-22.483333	-48.566667
16	Bariri	Reservoir	-22.163611	-48.739111
17	Bariri	Reservoir	-22.150000	-48.750000
18	Bariri	River	-22.257778	-48.796667
19	Bariri	River	-22.246667	-48.761389

	Localities (Counties)	Biotope	Latitude	Longitude
20	Bariri	River	-22.210833	-48.736389
21	Bariri	River	-22.190556	-48.690000
22	Bariri	River	-22.161944	-48.743056
23	Bauru	Reservoir	-22.333333	-49.000000
24	Bauru	River	-22.372500	-49.122500
25	Bauru	Stream	-22.321667	-49.070278
26	Bertioga	Stream	-23.822222	-46.150000
27	Bertioga	Stream	-23.800000	-46.166944
28	Boa Esperança do Sul	River	-22.305000	-48.433333
29	Boa Esperança do Sul	River	-22.077222	-48.433333
30	Boracéia	Stream	-23.652222	-45.895722
31	Boracéia	Stream	-23.653889	-45.891111
32	Brotas	Stream	-22.321181	-48.056300
33	Brotas	Lake	-22.193056	-47.917500
34	Cajamar	Stream	-23.418333	-46.773889
35	Cajamar	Stream	-23.324167	-46.850278
36	Cajamar	Stream	-23.353611	-46.890278
37	Cajati	Stream	-24.835000	-48.245278
38	Cajati	Stream	-24.837222	-48.248889
39	Cajuru	Stream	-21.200000	-47.150000
40	Campos de Jordão	Stream	-22.697500	-45.488889
41	Campos de Jordão	Stream	-22.697500	-45.488611
42	Campos de Jordão	Stream	-22.698889	-45.488611
43	Campos de Jordão	Stream	-22.692500	-45.465278
44	Campos de Jordão	Stream	-22.750000	-45.459167
45	Campos de Jordão	Stream	-22.692778	-45.460556
46	Campos de Jordão	Stream	-22.691389	-45.461667
47	Campos de Jordão	Stream	-22.693056	-45.489722
48	Campos de Jordão	Stream	-22.663611	-45.451111
49	Campos de Jordão	Stream	-22.697500	-45.488889
50	Campos de Jordão	Stream	-22.697500	-45.488889
51	Cananéia	Stream	-24.884167	-47.856111
52	Cananéia	Stream	-24.996667	-48.041944
53	Cananéia	Stream	-25.003056	-48.998056
54	Cananéia	Stream	-25.952222	-48.998056
55	Cananéia	Stream	-24.962222	-48.003889
56	Cananéia	Stream	-24.903333	-48.003611
57	Cananéia	Stream	-24.903333	-47.976667

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	Localities (Counties)	Biotope	Latitude	Longitude
58	Cananéia	Stream	-24.884167	-47.856111
59	Cananéia	Stream	-24.903500	-47.976917
60	Corumbataí	Stream	-22.303333	-47.670556
61	Corumbataí	Stream	-22.238611	-47.652500
62	Cubatão	Stream	-23.900000	-46.466667
63	Cubatão	Stream	-23.929167	-46.515278
64	Cubatão	Stream	-23.904167	-46.479444
65	Cubatão	Stream	-23.902222	-46.473056
66	Cubatão	Stream	-23.361944	-44.989444
67	Castilho	Reservoir	-20.871944	-51.487778
68	Descalvado	Stream	-22.037500	-47.780000
69	Dois Córregos	River	-22.366667	-48.366667
70	Dourado	Stream	-22.128889	-22.128889
71	Dourado	Stream	-22.128056	-48.267778
72	Eldorado Paulista	River	-24.688333	-47.995556
73	Eldorado Paulista	Stream	-24.919444	-48.218611
74	Eldorado Paulista	Stream	-24.300000	-48.416667
75	Eldorado Paulista	Stream	-24.884167	-47.856111
76	Eldorado Paulista	Stream	-24.903333	-47.976667
77	Gália	Reservoir	-22.386389	-49.686111
78	Gália	Stream	-22.386389	-49.686111
79	Garça	River	-22.582500	-49.659722
80	Guarapiranga	Stream	-21.950000	-48.250000
81	Guarapiranga	Stream	-21.983333	-48.250000
82	Ibaté	Stream	-21.886944	-47.966389
83	Ibitinga	Reservoir	-21.750000	-48.983333
84	Ibitinga	Reservoir	-22.433333	-48.166667
85	Ibitinga	Reservoir	-21.750000	-48.983333
86	Ibitinga	Reservoir	-22.433333	-48.166667
87	Ibitinga	Reservoir	-21.750000	-48.983333
88	Ibitinga	Reservoir	-22.400000	-46.800000
89	Ibitinga	River	-22.192500	-47.917222
90	Ibitinga	River	-21.683333	-48.350000
91	Ibitinga	River	-21.868611	-48.517222
92	Ibitinga	River	-21.925833	-48.907500
93	Ibitinga	River	-21.897222	-48.834444
94	Ibitinga	River	-21.874167	-48.902778
95	Ibitinga	River	-21.823333	-48.906111

	Localities (Counties)	Biotope	Latitude	Longitude
96	Ibitinga	River	-21.758056	-48.982500
97	Ibitinga	Stream	-21.866667	-48.275833
98	Itapeva	River	-23.570278	-48.209500
99	Itirapina	Reservoir	-22.215000	-47.890000
100	Itirapina	River	-22.215000	-47.890000
101	Itirapina	Stream	-22.274444	-47.962500
102	Ipeúna	Stream	-22.378333	-47.777778
103	Ipeúna	Stream	-22.390556	-47.752778
104	Iporanga	Stream	-24.585833	-48.592778
105	Itatinga	Stream	-23.101944	-48.615833
106	Itatinga	River	-23.033333	-48.566667
107	Jardinópolis	Stream	-21.017778	-47.763889
108	Jacupiranga	Stream	-24.860556	-48.091944
109	Jacupiranga	Stream	-24.857778	-48.091944
110	Jacupiranga	Stream	-24.866111	-48.110556
111	Jundiaí	Stream	-23.244722	-46.969444
112	Jundiaí	Stream	-23.243333	-46.935833
113	Jundiaí	Stream	-23.243333	-46.938611
114	Jundiaí	Stream	-23.245278	-46.948333
115	Lins	River	-21.413111	-51.423028
116	Luiz Antônio	Lake	-21.534500	-47.687222
117	Luiz Antônio	Lake	-21.623944	-47.806833
118	Luiz Antônio	Lake	-21.590806	-47.836667
119	Luiz Antônio	Lake	-21.608333	-47.816667
120	Luiz Antônio	Lake	-21.583333	-47.850000
121	Luiz Antônio	Reservoir	-21.608333	-47.783333
122	Luiz Antônio	Stream	-21.550000	-47.833333
123	Luiz Antônio	Stream	-21.566667	-47.833333
124	Luiz Antônio	Stream	-21.566667	-47.783333
125	Luiz Antônio	Stream	-21.600000	-47.833333
126	Luiz Antônio	Stream	-21.600000	-47.716667
127	Luiz Antônio	Stream	-21.616667	-47.800000
128	Mirassol	River	-22.537222	-50.029444
129	Novo Horizonte	Reservoir	-21.300000	-49.783333
130	Paraibuna	Reservoir	-22.750000	-44.750000
131	Paraíso	Stream	-21.534500	-47.687222
132	Paranapanema	Lake	-23.458333	-48.613889
133	Paranapanema	Lake	-21.608139	-47.830250

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	Localities (Counties)	Biotope	Latitude	Longitude
134	Paranapanema	Lake	-23.133333	-48.500000
135	Paranapanema	Reservoir	-22.580000	-53.058890
136	Paranapanema	River	-24.278194	-48.276778
137	Pedregulho	Stream	-20.201944	-47.416111
138	Pedregulho	Stream	-20.152778	-47.510556
139	Pedregulho	Stream	-20.229444	-47.460278
140	Peruibe	Stream	-24.283333	-47.000000
141	Piracicaba	River	-22.714167	-47.626667
142	Pirassununga	Reservoir	-21.931944	-47.376389
143	Pirassununga	Reservoir	-21.983333	-47.900000
144	Pirassununga	Reservoir	-23.550000	-45.833333
145	Ribeirão Bonito	River	-21.989722	-48.376111
146	Ribeirão Bonito	Stream	-22.000000	-48.200000
147	Ribeirão Grande	Stream	-24.296667	-48.417500
148	Ribeirão Grande	Stream	-24.272778	-48.455000
149	Ribeirão Grande	Stream	-24.272778	-48.423889
150	Ribeirão Preto	Reservoir	-21.183333	-47.850000
151	Rio Claro	Stream	-22.564167	-47.614167
152	Salesópolis	Reservoir	-23.599542	-48.968514
153	Salesópolis	Stream	-23.533333	-45.850000
154	São Bento do Sapucaí	Stream	-22.698889	-45.488611
155	São Carlos	Pond	-21.958333	-47.883333
156	São Carlos	Pond	-21.966667	-47.883806
157	São Carlos	Pond	-21.983333	-47.866667
158	São Carlos	Pond	-23.450000	-46.750000
159	São Carlos	Reservoir	-21.966667	-47.983333
160	São Carlos	Reservoir	-21.966667	-47.883333
161	São Carlos	Reservoir	-21.950000	-47.900000
162	São Carlos	Reservoir	-21.966667	-47.883333
163	São Carlos	Stream	-21.958611	-47.849444
164	São Carlos	Stream	-21.951944	-47.836667
165	São Carlos	Stream	-22.000000	-47.833333
166	São Carlos	Stream	-21.883333	-47.866667
167	São Carlos	Stream	-22.000000	-47.900000
168	São Carlos	Stream	-22.230556	-47.852778
169	São Carlos	Stream	-21.936667	-47.904167
170	São Carlos	Stream	-22.166944	-47.900278
171	São Paulo	Lake	-23.633333	-46.616667

	Localities (Counties)	Biotope	Latitude	Longitude
172	São Paulo	Lake	-23.650000	-46.616667
173	São Paulo	Reservoir	-23.888142	-46.560575
174	São Paulo	Stream	-23.466389	-46.766111
175	São Paulo	Stream	-23.455833	-46.760278
176	Teodoro Sampaio	Stream	-22.604444	-52.300556
177	Teodoro Sampaio	Stream	-22.598611	-52.233889
178	Teodoro Sampaio	Stream	-22.476111	-52.342778
179	Ubatuba	Stream	-23.512778	-45.183333
180	Ubatuba	Stream	-23.511111	-45.209444
181	Ubatuba	Stream	-23.500000	-45.245556
182	Ubatuba	Stream	-23.241667	-46.954444
183	Ubatuba	Stream	-23.472500	-46.762778
184	Ubatuba	Stream	-23.516667	-45.233333
185	Ubatuba	Stream	-23.511111	-45.209444
186	Ubatuba	Stream	-21.700000	-48.000000
187	Ubatuba	Stream	-23.243889	-6.950556
188	Ubatuba	Stream	-23.337500	-44.837222
189	Ubatuba	Stream	-23.455833	-46.760278
190	Ubatuba	Stream	-23.339167	-46.754722
191	Ubatuba	Stream	-23.522500	-45.250556
192	Vassununga	Stream	-21.633333	-47.666667
193	Vassununga	Stream	-21.666667	-47.700000
194	Vassununga	Stream	-20.201944	-47.416111



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Supplementary Material II

List of publications in which chironomid distribution patterns in the state of São Paulo were based.

1. Andersen, T. & Mendes, H. F. 2002. New species and records of *Axarus* "rogersi-group" from South and Central America (Diptera, Chironomidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 48(1): 35-40.
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5. Andrade, C. C. 2009. Macroinvertebrados bentônicos e análises físico-químicas indicadores de qualidade de água na bacia do rio Jacaré-Guaçu. **Master's Dissertation**. Universidade Federal de São Carlos, São Carlos, 92 p.
6. Barros, T. S. 2006. Padrões de diversidade e organização temporal de Chironomidae (Diptera) em um córrego tropical. **Master's Dissertation**. Universidade Federal de São Carlos, São Carlos, 75 p.
7. Barros, T. S. 2010. Integrando processos ambientais e espaciais na ecologia de comunidades aquáticas em escala regional. **PhD's Thesis**. Universidade Federal de São Carlos, São Carlos, 123 p.
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13. Corbi, J. J., Trivinho-Strixino, S. 2006. Ciclo de vida de duas espécies de *Goeldichironomus* (Diptera, Chironomidae). **Revista Brasileira de Entomologia**, 50(1): 72-75.
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