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Chironomidae (Diptera) em córregos de baixa ordem em áreas florestadas do Estado de São Paulo, Brasil

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Orientadora:

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Profa. Dra. Susana Trivinho-Strixino

"Enquanto nos diferimos pelos detalhes que conhecemos
sobre o mundo, em nossa infinita ignorância
nos tornamos todos iguais"
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RESUMO

Visando ao melhor entendimento da distribuição espacial dos Chironomidae (Diptera) em córregos na Mata Atlântica (Brasil) foi desenvolvido um estudo envolvendo três aspectos apresentados nesta tese na forma de capítulos: 1) avaliação da riqueza de espécies; 2) distribuição das larvas considerando múltiplas escalas espaciais; 3) exploração de recursos, particularmente o uso de frutos caídos nos córregos por larvas de Chironomidae. Foram selecionadas 5 áreas no Estado de São Paulo e, para avaliar a diversidade de Chironomidae, planejamos um desenho amostral estratificado, incorporando variação entre áreas, entre córregos e entre mesohabitats. Foram utilizados métodos complementares para coletar larvas, exúvias e adultos. No geral, os resultados indicam que: 1) córregos de baixa ordem da Mata Atlântica estão entre as áreas de maior riqueza de espécies de Chironomidae do mundo; 2) a taxocenose de Chironomidae de córregos de baixa ordem florestados é caracterizada por elevado número de espécies concentradas em alguns gêneros (*Tanytarsus, Caladomyia, Polypedilum* e *Stenochironomus*); 3) a importância de cada escala espacial depende do descritor de taxocenose de Chironomidae e da resolução taxonômica considerada; 4) que estudos focados em apenas um habitat ou escala não são apropriados para entender a riqueza e distribuição da taxocenose de Chironomidae em córregos; 5) características morfo-comportamentais de alguns táxons podem representar um dos principais fatores para explicar os padrões encontrados em pequenas escalas espaciais; 6) a entrada de matéria orgânica, particularmente frutos, proveniente da mata ripária constitui um importante recurso e habitat para larvas de Chironomidae.

ABSTRACT

With the aim of understanding the distribution of Chironomidae (Diptera) in Brazilian Atlantic Forest streams at multiple spatial scales, we carried out three complementary studies, which are presented here as chapters: 1) we focus on Chironomidae species richness; 2) we assess the Chironomidae larvae distribution attempting to explore some aspects that could be most influential in determining the chironomid spatial distribution; 3) we report the occurrence of chironomid larvae in fallen-fruits in Atlantic Forest streams. We selected 5 sites in the State of São Paulo and we designed a stratified sampling design incorporating environmental characteristics that potentially may influence chironomid distribution in the different scales (variation among sites – streams – mesohabitats). We used different sampling methods for collecting larvae, exuviae and adults of Chironomidae. As a whole, our results allow us to point out: 1) low order streams from Atlantic Forest as one of the most chironomid speciose areas in the world; 2) the chironomid assemblage is taxonomically deep, with some genera being represented by a large number of species (*Tanytarsus, Caladomyia, Polypedilum*, and *Stenochironomus*); 3) the identification of the scale importance depends on the chironomid assemblage descriptor and the taxonomic resolution considered; 4) studies focusing on one scale or habitat (e.g. riffles) are not appropriate for studying Chironomidae distribution patterns and richness in low order streams; 5) biological traits of some groups may underlie most evident in-stream chironomid distribution pattern; 5) the input of allochthonous matter from riparian vegetation, particularly fallen-fruits, represents an important habitat and food resource for chironomids in Atlantic Forest streams.

ÍNDICE

1. INTRODUÇÃO GERAL

A distribuição espacial e temporal dos seres vivos tem sido um tema amplamente estudado em ecologia, remontando ao início da mesma como ciência (MCINTOSH, 1985). Parte da importância do tema deve-se à relevância teórica e prática que o mesmo oferece, abrangendo perspectivas evolutivas e ecossistêmicas (CALLICOTT et al., 1998).

Em ambientes aquáticos, o estudo da distribuição dos macroinvertebrados de ambientes lóticos tem despertado grande interesse e tem gerado muitos dos modelos gerais de funcionamento de córregos e rios. Como exemplos podemos citar o "conceito do contínuo fluvial" (VANNOTE et al., 1980); o "conceito da descontinuidade serial" (CDS) (STANFORD & WARD, 1983) e a "hipótese da hidrologia do córrego como determinante para distribuição dos organismos" (STATZNER & HIGLER, 1986). Estes estudos também têm auxiliado em avaliações da qualidade ambiental (ROSENBERG & RESH, 1993; RESH & JACKSON, 1993; MOULTON, 1998), conservação da biodiversidade (KIRBY, 1992; ZWICK, 1992; NEW, 1995; SAMWAYS, 1995) e projetos de manejo e recuperação ambiental (O' NEILL, 1999).

Historicamente, os trabalhos sobre distribuição de macroinvertebrados em córregos e rios se restringiram à dimensão longitudinal destes ambientes (CORKUM, 1989) e de forma geral, duas grandes vertentes podem ser identificadas: uma direcionada para pequenas escalas e considerando variáveis dentro do córrego, como velocidade da água, substrato, profundidade, entre outras (HYNES, 1970; MINSHALL & MINSHALL, 1977; LOGAN & BROOKER, 1983) e, em alguns casos, interações bióticas como determinantes da distribuição dos organismos (PECKARSKY, 1979); a outra direcionada para largas escalas, na qual a maioria dos trabalhos tem se voltado para discussão da

distribuição longitudinal em rios, testando similaridades de modelos gerais de funcionamento de ecossistemas e enfatizando a importância do entorno e de variáveis abióticas para a distribuição dos macroinvertebrados (PERRY & SCHEFFER, 1987; DUDGEON, 1989, 1994; CORKUM, 1991; BATISTA et al., 1998, entre outros). Segundo DOWNES et al. (1993), a maioria dos trabalhos realizados em largas escalas tem usado a ordem do rio como a menor unidade de replicação. Estes implicitamente assumem que as variações em escalas menores não são importantes, resultando em generalizações pouco consistentes. Além disso, de acordo com MINSHALL et al. (1983); CORKUM (1989, 1991) existem poucos trabalhos comparando a distribuição da macrofauna em córregos e rios localizados em paisagens relativamente uniformes ou biomas. Há pouca síntese entre as abordagens, em parte, provavelmente, devido à falta de conhecimento relativo a importância das variações em diferentes escalas (DOWNES et al., 1993)

Alguns autores têm discutido a importância de se considerar múltiplas escalas hierárquicas (FRISSEL, et al., 1986; PICKETT et al., 1989; RICHARDS et al., 1996.), incorporando variações características de cada escala e de diferentes dimensões como longitudinal, lateral e vertical (WARD, 1984) ao papel dos distúrbios naturais e artificiais nos estudos de ambientes lóticos (RESH et al, 1988; GILLER et al., 1992). Esta abordagem vem trazendo contribuições práticas importantes para a conservação (LEWIS et al., 1996), avaliações ambientais (WOHL et al., 1995; CARTER et al., 1996; LEWIS et al., 1996; RICHARDS et al., 1997) e também tem contribuído para o incremento e melhoria das ferramentas analíticas (JONHSON & GAGE, 1997).

No Brasil, foram desenvolvidos vários trabalhos que tratam direta ou indiretamente da distribuição dos macroinvertebrados em ambientes lóticos. Dentre os núcleos de pesquisa que atualmente trabalham com o tema destacam-se os situados nas seguintes instituições (pesquisadores que atuam na instituição): Universidade de São Paulo – Ribeirão Preto (Dr. Claudio G. Froehlich), Universidade Federal de São Carlos (Dra. Susana Trivinho-Strixino, Dr. Giovanni Strixino e Dra. Alaíde Fonseca Gessner), Universidade de São Paulo - São Paulo (Dra. Gisela Y. Shimizu e Dra. Ana Lúcia Brandimarte), Universidade Estadual Paulista - Assis (Dr. Pitágoras da Conceição Bispo),

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Embora o número de pesquisadores e publicações sobre macroinvertebrados aquáticos tenha crescido no Brasil nos últimos anos, uma recente publicação do BIOTA-FAPESP (JOLY & BICUDO, 1999) aponta a necessidade de maior conhecimento para a maioria dos grupos de macroinvertebrados no Estado de São Paulo e, provavelmente, para as demais regiões do Brasil a situação não seja diferente.

Considerações sobre os Chironomidae

Os Chironomidae são um grupo de insetos pertencentes à ordem Diptera subordem Nematocera. Esta família apresenta distribuição cosmopolita (ASHE et al., 1987) e estimativas grosseiras apontam para a existência de 10000 a 20000 espécies (COFFMAN, 1995).

O grupo vem sendo amplamente estudado no mundo (ARMITAGE et al., 1995). Este interesse, em parte, deve-se à importância dos Chironomidae nos ambientes aquáticos e terrestres (PINDER, 1986), monitoramento e avaliações ambientais (ROSENBERG, 1993; ARMITAGE et al.,

1995), pesquisas paleoecológicas (WALKER, 1995), agricultura (FERRARESE, 1993) e saúde pública (CRANSTON, 1995).

No Brasil, embora muitos trabalhos citem a fauna de Chironomidae, a maioria deles os tratam ao nível taxonômico de família ou subfamília (SANSEVERINO, 1998). Parte desta problemática deve-se a dificuldades de identificação e ausência de manuais regionais que tratem desta família. Com exceção do "Guia de identificação e diagnose de larvas de Chironomidae do Estado de São Paulo" (TRIVINHO-STRIXINO & STRIXINO, 1995) e algumas revisões de gêneros (por ex.: *Stenochironomus*, *Cricotopus*, *Dicrotendipes*, *Parachironomu*s, *Oukuriella* e *Antillocladius*) não existem manuais que contemplem os diferentes estágios de vida dos Chironomidae neotropicais.

Atualmente, as seguintes instituições com seus respectivos coordenadores de pesquisa focam seus trabalhos em espécies de Chironomidae do Brasil: Instituto Oswaldo Cruz (Dr. Sebastião de Oliveira, Dr. Arlindo Serpa Filho e Dra. Maria Conceição Messias), Universidade Federal do Rio de Janeiro (Dr. Jorge Nessimian), Universidade Federal de São Carlos (Dra. Susana Trivinho-Strixino, Dr. Giovanni Strixino e Dra. Alaíde Fonseca Gessner), Universidade de São Paulo (Dra. Gisela Y. Shimizu), Universidade Federal de Minas Gerais (Dr. Marcos Callisto), Universidade Federal do Rio Grande do Sul (Dr. Gilberto G. Rodrigues), Museu de Zoologia de Munich - Alemanha (Dr. E. Fittkau), Museu de Bergen - Noruega (Dr. Ole Sæther e Dr. Trond Andersen), além dos estudantes que desenvolvem trabalhos de pós-graduação e iniciação científica no Brasil e no exterior, como Humberto Mendes, Guilherme Abbad Silveira, Sheyla R. M. Couceiro e Ângela Sanseverino.

Recentes publicações a respeito de Chironomidae neotropicais indicam o total de 155 gêneros e 709 espécies (SPIES & REISS, 1996 e TRIVINHO-STRIXINO & STRIXINO, 1999). No Brasil, estão registradas 168 espécies distribuídas em 32 gêneros (TRIVINHO-STRIXINO & STRIXINO, 1999). Entretanto, o conhecimento taxonômico ainda é escasso, o que pode ser exemplificado pela descrição de 26 novas espécies no Brasil após a publicação do catálogo de SPIES & REISS (1996).

Particularmente no Estado de São Paulo, o conhecimento sobre os Chironomidae de ambientes lóticos ainda é incipiente (TRIVINHO-STRIXINO & STRIXINO, 1999) e, de acordo com ROQUE et al. (2000), os poucos estudos publicados estão concentrados na região centro oeste.

Segundo FITTKAU (2000), desde 1805 quando Fabricius descreveu o primeiro Chironomidae da América do Sul, muitos estudos foram realizados, entretanto a maior parte da fauna neotropical ainda não foi cientificamente descrita, sendo fundamental para isso, uma intensiva cooperação nacional e internacional.

A importância e a diversidade de Chironomidae, aliada à escassez de informações a respeito do grupo em ambientes lóticos do Estado de São Paulo, estimulou a elaboração desta tese, integrada ao Programa BIOTA-FAPESP (Fundação de Amparo à Pesquisa de São Paulo), e anexo ao Projeto "Levantamento e biologia de crustáceos, insetos e moluscos de água doce do Estado de São Paulo", que apresentava como objetivo maior inventariar e caracterizar a biodiversidade do Estado de São Paulo, definindo mecanismos para sua conservação, seu potencial econômico e sua utilização sustentável.

Neste contexto, o principal objetivo no desenvolvimento deste doutoramento e elaboração desta tese foi entender a distribuição de Chironomidae (Diptera) em córregos de baixa ordem florestados do Estado de São Paulo, considerando diferentes escalas espaciais. Ainda, considerando o referencial teórico metodológico clássico da ciência ecologia (para uma introdução sobre o assunto ver FORD, 2000), os estudos apresentados aqui podem ser classificados como exploratórios e descritivos, visando basicamente a identificação de possíveis padrões ecológicos e descrição de aspectos da história natural dos Chironomidae. Embora o trabalho apresente limitações no que diz respeito ao entendimento e teste de hipóteses sobre processos e mecanismos que geram os possíveis padrões de distribuição de Chironomidae, esta fase de ecologia descritiva ainda é um passo essencial para o entendimento e formulação de hipóteses mais consistentes sobre a biodiversidade de Chironomidae na região Neotropical.

Ao longo da tese, três temas complementares são apresentados, sendo os dois primeiros relacionados diretamente a temática da distribuição espacial dos Chironomidae e o terceiro representa um desdobramento de observações de campo não previamente planejadas, envolvendo a temática da exploração de recurso provenientes da mata ripária, particularmente frutos. Os temas foram organizados em capítulos independentes para facilitar a leitura e cópia completa isolada dos mesmos. Além disso, estão elaborados em formato de artigos e escritos em inglês. Reconhecendo a deficiência na divulgação da tese para leitores brasileiros e não especialistas, apresento a seguir um resumo contendo os principais aspectos tratados em cada capítulo e, no final da tese, um glossário com a definição de algumas palavras chaves para facilitar o entendimento do texto.

Riqueza de espécies de Chironomidae em córregos de baixa ordem na Mata Atlântica do sudeste brasileiro: uma primeira aproximação usando abordagem bayesiana.

Neste capítulo é avaliada a riqueza de espécies de Chironomidae em 15 córregos de baixa ordem na Mata Atlântica do Estado de São Paulo, considerando uma abordagem quantitativa e múltiplas escalas espaciais. Foram identificadas 191 morfoespécies de Chironomidae (125 Chironominae, 38 Orthocladiinae e 28 Tanypodinae). O número de espécies foi estimado através de uma abordagem Bayesiana e os resultados variaram de 200 (195-207) a 230 (218-244) espécies. Os resultados indicam que córregos da Mata Atlântica apresentam riqueza de espécies tão elevada quanto à apresentada em regiões do mundo consideradas mais ricas em espécies.

Distribuição de larvas de Chironomidae em córregos de baixa ordem da Mata Atlântica (Brasil), considerando múltiplas escalas espaciais.

Neste capítulo são explorados aspectos relacionados à distribuição espacial das larvas de Chironomidae em 15 córregos da Mata Atlântica do Estado de São Paulo, considerando múltiplas escalas espaciais. No geral, os resultados indicaram: 1) a importância da escala na distribuição das larvas depende do descritor de taxocenose e da resolução taxonômica considerada; 2) características biológicas, como aspectos

morfo-comportamentais, podem ser importantes fatores explicativos da distribuição das larvas em pequenas escalas espaciais; 3) múltiplos fatores atuando em diferentes escalas podem influenciar sinergeticamente a distribuição das larvas em múltiplas escalas.

Chironomidae (Diptera) em frutos caídos em córregos da Mata Atlântica, São Paulo, Brazil

Neste capítulo é reportada a ocorrência de larvas de Chironomidae vivendo dentro de frutos de 12 espécies vegetais caídos em córregos na Mata Atlântica. Larvas de várias espécies de *Endotribelos* foram as mais abundantes e freqüentemente encontradas nestes habitats. Os resultados apontam para a importância de frutos como habitat e recurso alimentar para larvas de Chironomidae em córregos da Mata Atlântica.

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2. CHIRONOMID SPECIES RICHNESS IN LOW ORDER STREAMS IN SOUTHEASTERN BRAZILIAN ATLANTIC FOREST: A FIRST APPROXIMATION THROUGH A BAYESIAN APPROACH

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Introduction

Although Chironomidae often represent the most abundant invertebrate taxon in any freshwater environment and are recognized as one of the most speciose freshwater groups, currently, the estimation of chironomid species richness remains imprecise in all spatial scales. The estimated Chironomidae fauna in the world ranges from 10,000-12,000 (ASHE et al., 1987) to 8,000 – 20,000 (COFFMAN, 1995). However, there are pitfalls and difficulties with these estimates, among them: lack of information from some areas (e.g. Neotropical), non-standard sampling effort, and lack of taxonomic review for many taxa.

The Neotropical region is exemplary for discussing the chironomid species richness because it probably represents one of the most species-rich areas in the world. REISS (1982) speculated that the Central American region may have 1,500-2,000 species and according to FITTKAU (2001), we can expect a total far exceeding 1,000 chironomid species in Amazonia alone. However, the scarce knowledge on chironomid taxonomy and few attempts to examine chironomid richness in a quantitative analytical manner introduce many uncertainties into calculations that estimate biodiversity

based on species numbers, compromising discussions on zoogeographical patterns, environmental assessment, and conservation programs.

Following most comprehensive studies of taxonomic composition and species richness in low order streams in a historical perspective, although long expected that streams in tropical rainforest could have a high chironomid species number (FITTKAU, 1971), only recently has this been documented quantitatively. COFFMAN (1989) reviewed 152 studies of Chironomidae species richness, of which only three had been carried out in low latitudes. The number of taxa occurring in second-order streams varied from 13 to 144. Based mainly in the studies of LEHMANN (1979; 1981) and HARRISON & RANKIN (1976) in Zaire and St. Vincent respectively, Coffman hypothesized that lotic chironomids do not show increasing species richness in sub-tropical and tropical regions. FERRINGTON et al. (1993), studying a stream in Puerto Rico found richness similar to Lehmann and Harrison & Rankin's studies, but suggested that the richness in Quebrada Prieta (Puerto Rico) could relate to insularity and not reflect the richness in mainland rainforest streams. In other studies, elevated richness of chironomids in tropical low order streams was demonstrated, and some mechanisms of origin and maintenance of the species richness were discussed (COFFMAN et al., 1992; COFFMAN & DE LA ROSA, 1998). These works resulted in some important predictions and characteristics of stream tropical chironomid fauna: 1) low latitude and low order, continental streams have as many chironomid species as do similar temperate ones; 2) they are taxonomically narrow, restrict to few subfamilies and tribes and relatively few genera; 3) taxonomically deep, with many genera being represented by a moderately large to a very large number of similar species; 4) high alpha and beta diversities.

We address here chironomid richness in a low order forested stream in the Atlantic rainforest within a quantitative framework and estimate total richness using a Bayesian statistic approach. We discuss also some of the predictions of COFFMAN et al. (1992) and COFFMAN & DE LA ROSA (1998) and comment on some ecological aspects related to the Brazilian Atlantic chironomid fauna.

Methods

The study area

With a high concentration of endemic taxa and vulnerability to processes that threaten this unique biodiversity, the Atlantic Forest has been identified as a biodiversity hotspot of global significance (MYERS et al., 2000).
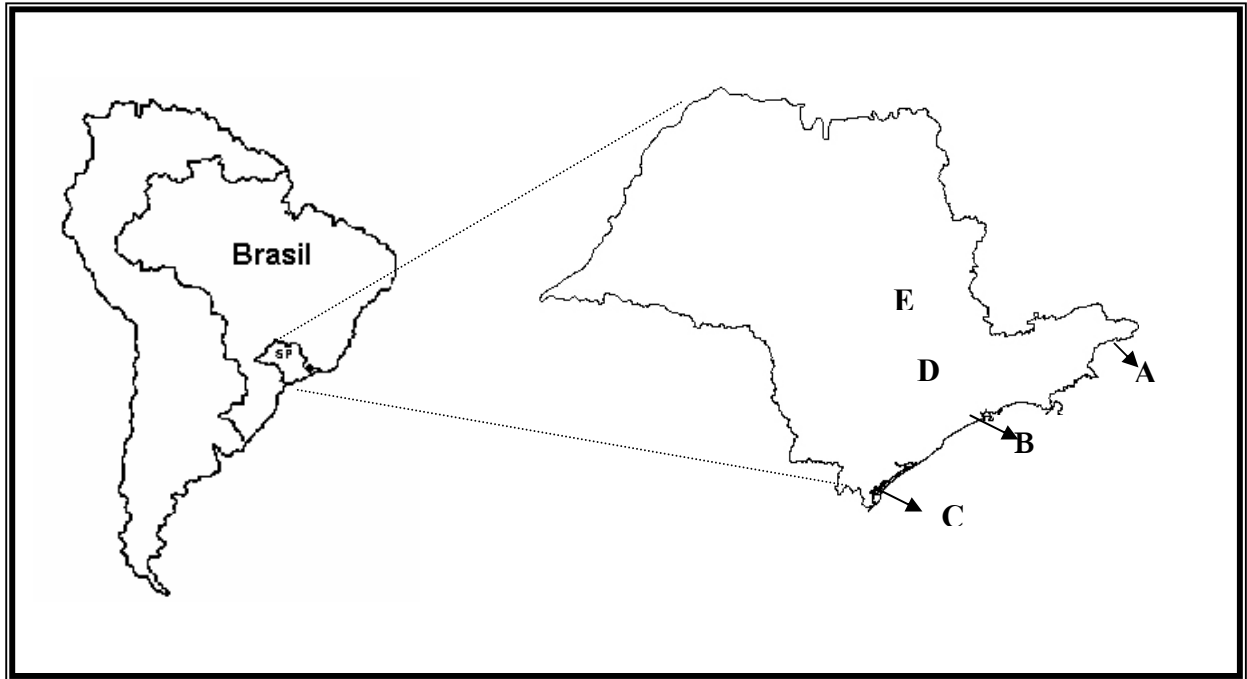
Figure 1. Sampling sites in the State of São Paulo. A – Ubatuba, B – Cubatão, C – Cananéia, D – Jaraguá, E – São Carlos.
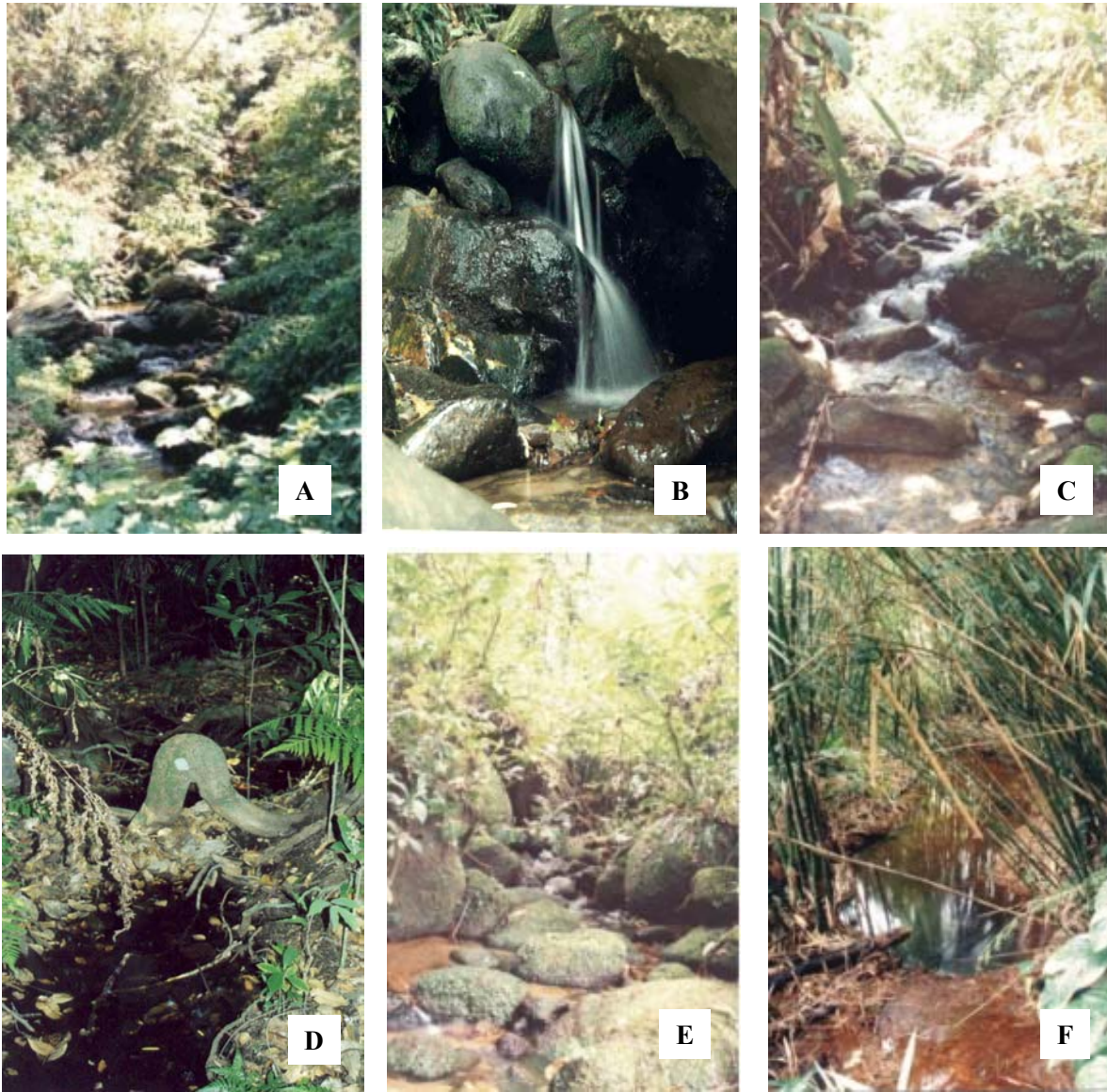
Figure 2. Brazilian Atlantic Forest streams. A. Stream 1, Parque Estadual da Serra do Mar – Núcleo Cubatão; B. Stream 1, Parque Estadual do Jaraguá; C. Stream 2, Parque Estadual da Serra do Mar – Núcleo Cubatão; D. Stream 3, São Carlos City; E. Stream 1, Parque Estadual da Serra do Mar – Núcleo Picinguaba; F. Stream 3, Parque Estadual da Serra do Mar – Núcleo Picinguaba.

The Atlantic Forest comprises two major vegetation types: the coastal forest or Atlantic Rain Forest and the tropical seasonal forest or Atlantic semi-deciduous forest (MORELLATO & HADDAD, 2000). The Atlantic Rain Forest covers mostly the low to medium elevation (< 1000 m a.s.l.) of the eastern slopes of mountain chain that runs along the coastline from southern to northeastern Brazil; the Atlantic-deciduous Forest extends across the plateau (usually > 600 m) in the center and southeastern interior of the country. The Atlantic Rain Forest experiences warm and wet climate without dry season; a seasonal climate with a relatively severe dry season (generally from April to September) predominates over the distribution of the Atlantic Semi-deciduous Forest. Here we used a comprehensive definition of Atlantic Forest (OLIVEIRA-FILHO & FONTES, 2000) that includes coastal rain forest, semi-deciduous forests, subtropical Araucaria, and riparian-forested formations.

We designed a stratified sampling design regarding a multiple spatial scale approach to assess chironomid richness. We incorporated environmental characteristics that potentially may influence chironomid richness in the different scales (variation among sites – streams – mesohabitats). A total of 15 low order (1-2) forested streams in the State of São Paulo were analyzed (Fig. 1 and Fig. 2). We selected 5 sites: A. Parque Estadual da Serra do Mar – Núcleo Picinguaba (Picinguaba, Ubatuba), B. Parque Estadual da Serra do Mar – Núcleo Cubatão (Cubatão), C. Parque Estadual da Serra do Mar – Cananéia (Cananéia), D. Parque Estadual do Jaraguá (Jaraguá) and E. São Carlos City (São Carlos) (Fig. 1). At each site 3 streams with different gradient level (high, medium and low) were chosen, and within each stream, riffles and pools were sampled in two periods (dry season, 2001 and wet season, 2002).

Table 1. General features of the studied streams in Atlantic forest, São Paulo, Brazil.

Site/stream	Gradient	Oxygen (mg.l⁻¹)	Conductivity (µS cm⁻¹)	pH	Geographic coordinates
Cananéia					
Stream 1	high	8.0	32-34	7.2-7.3	S 24º54'12" W 47º58'36"
Stream 2	medium	6.31	43-46	6.9-7.1	S 24º53'03" W 47º51'22"
Stream 3	low	8.1	50	7.5	-
Cubatão					
Stream 1	high	8.6-8.9	28-33	7.1-7.3	S 23º55'45" W 46º30'55"
Stream 2	medium	8.5-8.9	40-47	7.2	S 23º54'15" W 46º28'46"
Stream 3	low	6.6	52	7.5	S 23º54'08" W 46º28'23"
Picinguaba					
Stream 1	high	8.4-8.6	15-26	6.5-7.5	S 23º20'15" W 44º50'14"
Stream 2	medium	8.8-8.9	17-28	6.8-7.3	near S 2320'15" W 44º50'14"
Stream 3	low	6.5	18	6.5	-
Jaraguá					
Stream 1	high	8.8-8.9	79-77	7.4	S 23º27'59" W 46º45'58"
Stream 2	medium	6.5-6.9	30-67	6.9	near S 23º27'59" W 46º45'58"
Stream 3	low	6.81	30	6.81	-
São Carlos					
Stream 1	high	11.7	5	5.6	S 21º56'12" W 47º54'15"
Stream 2	medium	7.9	10	5.4	S 21º57'07" W 47º50'12"
Stream 3	low	7.2-9.0	13-15	6.9-7.2	S 21º58'07" W 47º53'08"

All the streams studied are in conservation areas, are shallow deep (< 50 cm), the tree canopy covering more than 70% of their channel, absence of macrophytes, water with a high level of dissolved oxygen, low conductivity, and slightly alkaline or acid, temperature ranging from 15-23ºC. The substrates of the high gradient streams are characterized by predominance of pebbles while the low ones by great abundance of organic material (wood and leaves). Some general information about the streams is given in table 1.

We used several different sampling methods for chironomids:

Larvae: in each stream samples of different mesohabitats (3 riffles and 3 pools in each season) were collected, using a Surber collector. The use of mesohabitat as an appropriate scale to collect macroinvertebrates followed PARDO & ARMITAGE (1997). We also reared larvae to obtain adults.

Pupae: Accumulation of foam along the stream margins and associated with debris dams indicated where exuviae were likely to have accumulated. A 20 cm diameter, fine-meshed net was inserted under the foam and gently lifted clear of the water. The contents were then washed into a container. Further samples were added to the first over a period of thirty minutes.

Adults: samples were obtained daily in a condensed manner during three days of the rainy and dry season. Three Malaise traps were employed at each site placed above the streams.

The specimens were mounted on slides, and identified, bearing in mind the limited knowledge of the Neotropical fauna. The Chironomidae specimens are deposited in the collection of the Laboratório de Entomologia Aquática da Universidade Federal de São Carlos (SP). We illustrated all the morphospecies and the illustrations can be obtained from the author. Because the knowledge of Neotropical region is in its infancy (see SPIES & REISS, 1996) statements regarding chironomid richness are necessarily preliminary.

Statistical analysis

We established the criterion of "maximum richness within any chironomid stage per site", where the site species pool (three streams per site) represents the sum of the richness found within a taxon independently from the sampling methods or developmental stages, considering the following aspects: 1) for many genera, one life stage appears to be better for the discrimination of

species than do the others (e.g. in *Endotribelos* – larvae, in *Stenochironomus* – adults, in *Corynoneura* group - pupae), 2) the sample of all chironomid stages in an area can maximize the survey of rare species, 3) data of larvae, pupae and adults came from different spatial scale and methods.

The use of statistical methods for estimating species richness is a very controversial issue (see BUNGE & FITZPATRICK, 1993; COLWELL & CODDINGTON, 1994; MELO & FROEHLICH, 2001). Recently, Bayesian estimate methods have been proposed for estimating biodiversity and they seem particularly appropriate for cases in which studies cannot be replicated and for assessment of the risk and safety in various environmental settings involving biodiversity in which "expert opinion is sought" (RECKHOW, 1990; ELLISON, 1996; HILBORN & MARGEL, 1997; PIGLIUCCI, 2002, but see DENNIS, 1996). Here we used a Bayesian estimation method through multinominal incomplete distribution (LEITE et al., manuscript attached to this thesis), adapted from Derenzo-Hildebrand model (SANATHANAN, 1972). Among the assumptions, the model considers that each species has a different probability of being sampled at a site. More details on the statistics and the assumptions are given in LEITE et al. (manuscript attached to this thesis). Although we note that extrapolative methods cannot be a substitute for any survey with high spatial and temporal sampling effort, they can be important tool for incorporating an uncertain number of species into the assessment of biodiversity.
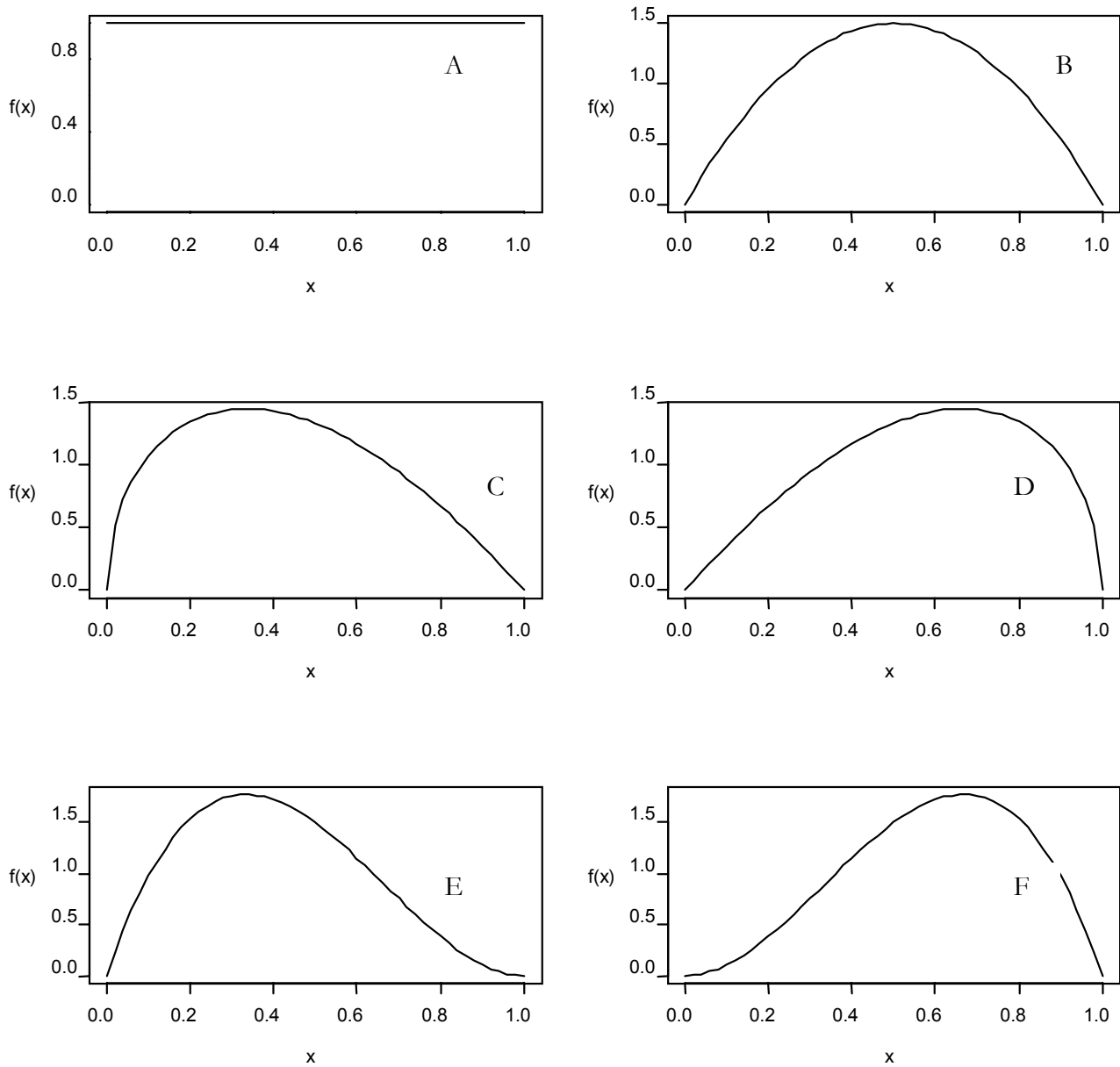
Figure 3. Priors used for estimating Chironomidae richness through a Bayesian approach.

We chose different priors to exemplify the possible scenarios on Chironomidae assemblages in Brazilian Atlantic Forest streams (Fig. 3).

Distribution a priori A is non-informative and assumes equal probability of finding different species in the streams studied.

Distribution a priori B represents a chironomid assemblage characterized by most species with intermediate probability of being sampled.

Distribution a priori C represents a chironomid assemblage characterized by the predominance of species with low probability of being sampled.

Distribution a priori D represents a chironomid assemblage with the predominance of species characterized by high probability of being sampled.

Distribution a priori E represents a chironomid assemblage characterized by the predominance of species (more than the priori C) with low probability of being sampled.

Distribution a priori F represents a chironomid assemblage characterized by the predominance of species (more than the priori D) with high probability of being sampled.

Results

A total of 191 species has been recognized (Table 1). The largest number of species occurs in the subfamily Chironominae (125 spp), followed by Orthocladiinae (38 spp) and Tanypodinae (28 spp).

Only 21 species could be identified into named species: *Antillocladius folia* Mendes; *Caladomyia riotarumensis* Reiff; *Chironomus reissi* Correia, Trivinho-Strixino & Michaelova; *Corytibacladius gercinoi* Oliveira, Messias & Santos; *Endotribelos albatum* Sublette & Sasa; *E. grodhausi* Sublette & Sasa; *Guassutanypus oliverai* Roque & Trivinho-Strixino; *Larsia fittkaui* Sublette & Sasa; *Larsia berneri* Beck & Beck; *Monopelopia caraguata* Mendes, Marcondes & Pinho*; Nandeva gaucha* Wiedenbrug, Reiss & Fittkau*; N. latiloba* Sæther & Roque*, N. strixinorum* Sæther & Roque*; Parakiefferiella strixinorum* Wiedenbrug & Andersen*; Rheotanytarsus c.f. pantanalensis* Kyerematen & Andersen; *Stenochironomus impendens* Borkent; *Tanytarsus impar* Trivinho-Strixino & Strixino; *T. ligulatus* Reiss; *T. magnus* Trivinho-Strixino & Strixino; *T. fastigatus* Reiss*; Xenochironomus xenolabis* Kieffer. Many probably are new species, with many being similar to already described species.

Table 2. List of Chironomidae sampled in 15 low order streams in Atlantic forest, São Paulo, Brazil. L –
Larva, P – pupa, and A – adult.

Taxa	Number of mophospecies	Stage
Tanypodinae		
Ablabesmyia Johannsen, 1905	4	L,P
Coelotanypus Kieffer, 1913	1	L,P
aff. *Denopelopia* Roback & Rutter, 1988	1	A
Djalmabatista Fittkau, 1968	1	L,P
Fittkauimyia Karunakaran, 1969	1	L,P
Guassutanypus Roque & Trivinho-Strixino, 2003	1	L,P,A
Larsia Fittkau, 1962	4	L,P
Labrundinia Fittkau, 1962	3	L,P
Monopelopia Fittkau, 1962	1	L,P
Pentaneura Philippi, 1865	6	L,P
Genus Stur, Fittkau & Serrano (in press)	1	L
Procladius Skuse, 1889	1	L,P
Zavrelimyia Fittkau, 1962	1	L,P
Pentaneurini	2	L,P
Chironominae		
Beardius Reiss & Sublette, 1985	4	A
Caladomyia Säwedal, 1981	18	A
Chironomus Meigen, 1803	3	A
Constempellina Brundin, 1947	1	L
Cryptochironomus Kieffer, 1918	1	L
Dicrotendipes Kieffer, 1913	4	A
Endotribelos Grodhaus, 1987	6	L,P,A
Fissimentum Cranston & Nolte	2	L
Goeldichironomus Fittkau, 1965	1	A
Harnischia complex Kieffer, 1921	5	L,P,A
Nandeva Wiedenbrug, Reiss & Fittkau, 1998	3	P,A
Neelamyia Soponis, 1987	2	A
Nilothauma Kieffer, 1921	2	A
Oukuriella Epler, 1986	1	L,P,A
Paratendipes Kieffer, 1911	3	A
Parachironomus Lenz, 1920	1	A
Paralautherboniella Lenz, 1941	1	L,P,A
Paratanytarsus Thienemann & Bause in Bause, 1913	1	A
Polypedilum Kieffer, 1912	13	A
Pseudochironomini	2	A
Rheotanytarsus Thienemann & Bause in Bause, 1913	3	A
Stenochironomus Kieffer, 1919	10	L,P,A
Stempellina Thienemann & Bause in Bause, 1913	3	A
Stempellinella Brundin, 1974	2	A
Tanytarsus van der Vulp, 1874	26	A
Xenochironomus Kieffer, 1921	1	P
Xestochironomus Sublette & Wirth, 1972	6	A
Orthocladiinae		
Antilocladius Saether, 1981	1	A
cf. *Boreosmittia* Tuiskunen, 1986	1	A

Bryophaenocladius Thienemann, 1934	1	A
Cardiocladius Kieffer, 1912	1	P
gr. *Corynoneura* Winnertz, 1846	8	P
Cricotopus van der Vulp, 1874	3	A
Corytibacladius Oliveira, 2001	1	A
Diplosmittia Saether, 1981	1	A
cf . *Gymnometriocnemus* Goetghebuer, 1932	1	A
aff. *Limnophyes* Eaton, 1875	4	A
Lopescladius Oliveira, 1967	3	P
Metriocnemus van der Wulp, 1874	1	A
Parakiefferiella Thienemann, 1936	1	P,A
Parametriocnemus Goerghebuer, 1932	3	L,P,A
Pseudosmittia Goerghebuer, 1932	1	A
Pseudorthocladius gr. (?*Psectrocladius*?) Goetghebuer, 1932	2	A
Rheocricotopus Thienemann & Harnisch, 1932	1	P
aff. *Stackelbergina* Shilova & Zelentsov, 1978	1	L
Orthocladiinae n. det.	2	A
Orthocladiinae genus 4 (Wiedenbrug, 2000)	1	P

Tanytarsus, Stenochironomus, Caladomyia, Polypedilum were the richest genera. Within Orthocladiinae, the *Corynoneura* group was represented by a high number of species. Of the total recognized species 75 belong to these 5 taxa (40 %). No Diamesinae, Prodiamesinae and Podonominae were collected.

Most chironomids collected have aquatic larvae, except some Orthocladiinae that probably have semi-aquatic and terrestrial immature stages (ex. *Antillocladius*, cf. *Boreosmittia*).

The Bayesian estimation method through multinominal incomplete distribution produced the chironomid richness estimations showed in Table 3.

Table 3. Estimation of chironomid species richness through Bayesian approach using different priories.

Priori (parameters α, β)	Chironomid richness (Mean)	Mode	Credibility interval	Probability of credibility interval
A (1, 1)	229	229	217-243	0.95
B (2, 2)	214	213	205-224	0.95
C (1.5, 2)	230	230	218-244	0.95
D (2, 1.5)	207	206	199-215	0.96
E (2, 3)	229	229	217-243	0.96
F (3, 2)	200	200	195-207	0.96

Discussion

The results, from observed as well as the estimated species number, show clearly that the chironomid richness in low order streams in the Atlantic Forest is, comparatively, as high as the most speciose streams for chironomids in the world (see COFFMAN, 1989; COFFMAN & DE LA ROSA, 1998). If predictions of COFFMAN (1989), that the highest chironomid richness should be found in 3-4 order streams is correct, and the lower richness found here compared with streams studied by Coffman can be attributed, at least partially, to the lower order, our data (only from streams of 1-2 order) places the Atlantic Forest streams as a potential hotspot of chironomids in the world.

Additional studies obviously are necessary to measure how well the model used here can be taken as a general model for estimating chironomid richness and to choose the most appropriate prior for Atlantic forest streams. Although there is still a long way to go, some biological evidence supports that our estimate is reasonable: (1) when making rapid comparisons of *Stenochironomus*, *Endotribelos*, and *Tanytarsus* species collected in other studies (material kindly loaned by M. T. Suriano from Parque Estadual de Campos de Jordão and H. Mendes from Parque Estadual de Intervales), 4 more taxa have been added in the list, showing that our observed data are underestimated; (2) to date, the maximum richness found in lotic systems (250 spp, COFFMAN & DE LA ROSA, 1998) is close to our estimate; (3) according to COFFMAN & DE LA ROSA (1998), saturation probably occurs in chironomid assemblages in similar streams, in other words, streams with similar aspects of heterogeneity have essentially the same number of species; (4) if the general pattern that in tropical streams there are high number of rare species in aquatic insect communities (STOUT & VANDERMEER, 1975; MELO & FROEHLICH, 2001) is also valid for Chironomidae, the priors C and E, which produce the highest value of chironomid richness estimates, are the most appropriate.

Previous studies of chironomid larvae in Brazilian Atlantic forest streams have reported richness ranging from 7-10 in Tanypodinae, 6-14 in Orthocladiinae and 19-34 in Chironominae (ROQUE et al., 2000; SANSEVERINO & NESSIMIAN, 2001; ROQUE et al., 2003; HENRIQUE-OLIVEIRA et al., 2003; SURIANO & FONSECA-GESSNER, 2004). ANDRADE-MORRAYE

(2003), studying larvae, pupae and adults in streams in Parque Estadual de Intervales, reported 8 Tanypodinae, 10 Chironominae and 7 Orthocladiinae genera. WIEDENBRUG (2000) found 92 Chironominae, 53 Orthocladiinae, 20 Tanypodinae species of chironomid pupal exuviae from the surface drift in streams of Rio Grande do Sul, South Brazil. It is practically impossible to compare the diversity found in these different works, because there is little methodological compatibility, but the higher richness found in our study probable reflects only the level of identification, inclusion of all stages, and sampling effort.

Our results support the low diversity of subfamily, tribe and genera in warm streams in Neotropics when compared with temperate ones, mainly due to the absence of cold-adapted chironomids as was pointed out by FITTKAU (1971) and COFFMAN (1998). However, this number of genera must be regarded with caution, since the number of genera probably will increase when the taxonomy becomes more refined (ex. within Pseudochironomini, *Harnischia* complex, *Corynoneura* group) and more material examined.

The characteristic taxonomic depth of many genera, as represented by a moderately large to large number of similar species in Neotropical mainland streams (COFFMAN & DE LA ROSA, 1998), was supported by our results, specially in the Tanytarsini. *Caladomyia* and *Tanytarsus*, two closely-related genera of Tanytarsini, alone contribute 23 % of the total species. Both genera also represent the richest Chironominae genera in highland streams of Colombia (RISS & OSPINA-TORRES, 2000). Furthermore, these data indicate that the use of generic level is an inappropriate descriptor of chironomid richness in the neotropics.

In comparison with other mainland streams of different ecophysiographic settings in Brazil, our results corroborate the conclusions of FITTKAU (1971) and FITTKAU & REISS (1979) concerning the predominance of Chironominae in lowland areas from South America. However, in contrast with the Amazonian streams collected by Fittkau in the 1960s and 1970s, Atlantic forest streams seem to have comparatively higher number and abundance of species of Orthocladiinae. These results can be, at least partially, attributed to the geomorphology of Atlantic coast with high slopes, streams with high

gradient, well oxygenated waters and predominance of hard rock, typical habitats dominated by species of Orthocladiinae (PINDER, 1986). Geomorphological diversity of the streams in Atlantic forest may be an important landscape attribute maintaining regional chironomid species pool (ROQUE et al., 2003). It is interesting to note that while the chironomid assemblages in lowland Amazonian streams are probably strongly influenced by geological structure and weakly by topography and stable climate (FITTKAU, 1971), the Atlantic forest topography heterogeneity and climate may play a more important role in structuring chironomid assemblages. Unfortunately few data are available from streams of other Brazilian biomes. OSPINA-TORRES (1992) studying surface drift samples from streams (igarapés) in Manaus, Amazonas, distinguished 199 kinds of pupal exuviae. Some preliminary data from intermittent streams in Pantanal, called "corixos", shows poor generic chironomid richness (P. Medina Junior, personal communication). SILVA-FILHO (2004) studying streams in the semiarid region of Northeastern of Brazil verified low generic diversity and absence of Orthocladiinae taxa. STUR et al. (2000) found 42 chironomid genera in floating litter along a tropical lowland river, which discharges into the Pantanal. At the present, it is not possible to compare chironomid richnesses in low order streams from different regions in Brazil, but we would like to stress that the richness of chironomid in Atlantic forest low order streams do not seem to reflect species richnesses in other mainland Brazilian regions.

In a broad-scale geographical perspective, our data together with the Coffman's studies in mainland streams in broadleaf forest biomes in Central America and Africa, add more evidence to the VINSON & HAWKINS (2003) proposition that streams within similar biomes support similar numbers of aquatic insects without regarding to biogeographic realm. On the other hand CRANSTON (2000) and MCKIE et al. (2004), examining broad scale patterns of diversity of lotic chironomid in Australia, provide evidence for a homogeneous distribution of richness across this continent and lower richness compared with others continents. According to them this pattern might arise from the particular history and biogeographical circumstances of Australia. Other studies have also provided convincing evidence that broad patterns of species richness can be understood only by placing the local

community in its historical and biogeographical perspective (see studies in RICKLEFS & SCHLUTER (1993) for a comprehensive view)

As we began outlining this paper, we consider that "a first approximation" is the most appropriate word to express our knowledge about the richness of chironomid species in Brazil.

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3. SPATIAL DISTRIBUTION OF CHIRONOMID LARVAE IN LOW-ORDER STREAMS IN SOUTHEASTERN BRAZILIAN ATLANTIC FOREST AT MULTIPLE SCALES

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Introduction

The spatial and temporal distribution of organisms has been widely studied in ecology, with theoretical and practical relevance covering evolution and ecological perspectives. Studies on biodiversity distributional patterns at multiple scales have been recognized as an important way to improve our understanding of variability in nature, particularly in stream ecology (WIENS, 1989; VINSON & HAWKINS, 1998; PARSONS et al., 2004). This approach has brought important practical contributions to conservation (LEWIS et al., 1996; ROQUE et al., 2003) and environmental evaluations (WOHL et al., 1995; CARTER et al., 1996; LEWIS et al., 1996; RICHARDS et al., 1997; TOWNSEND et al., 1997), and has also contributed to the use and improvement of analytical tools (JONHSON & GAGE, 1997).

Considering that: 1) the selection of appropriate scales of measurement is fundamental to the interpretation and understanding of biodiversity patterns and the process and mechanisms that underling them (PARSONS et al., 2004), 2) the scarcity of knowledge regarding the aquatic insects of neotropical lotic environments at multiple scales (BOYERO & BAILEY, 2001), 3) Chironomidae represents one of the most species-rich and abundant group in tropical streams, we address here to assess the Chironomidae larvae distribution in Atlantic Forest streams, looking for patterns from different scales: riffle-pool habitats, streams and sites. We also make an attempt to explore some aspects that could be most influential in determining the chironomid spatial distribution.

Methods

The study area

According to MORELLATO & HADDAD (2000) the Atlantic Forest is composed of two major vegetation types: the coastal forest or Atlantic Rain Forest and the tropical seasonal forest or Atlantic semi-deciduos forest. The Atlantic Rain Forest is mostly at low to medium elevations (< 1000 m a.s.l.) of the eastern slopes of mountain chain that runs along the coastline from southern to northeastern Brazil; the Atlantic-deciduous Forest extends across the plateau (usually > 600 m a.s.l.) in the center and southeastern interior of the country. The Atlantic Rain Forest experiences warm and wet climate without dry season; a seasonal climate with a relatively severe dry season (generally from April to September) predominates over the distribution of the Atlantic Semi-deciduos Forest. Atlantic forests are among the most threatened tropical forest in the world, although are now reduced to only 5 percent of their original cover and most remnants areas are on sheltered steep mountain slopes. Here we used a comprehensive definition of Atlantic forest (OLIVEIRA-FILHO & FONTES, 2000) that includes coastal rain forest, semi-deciduous forests, subtropical Araucaria, and riparian-forested formations.
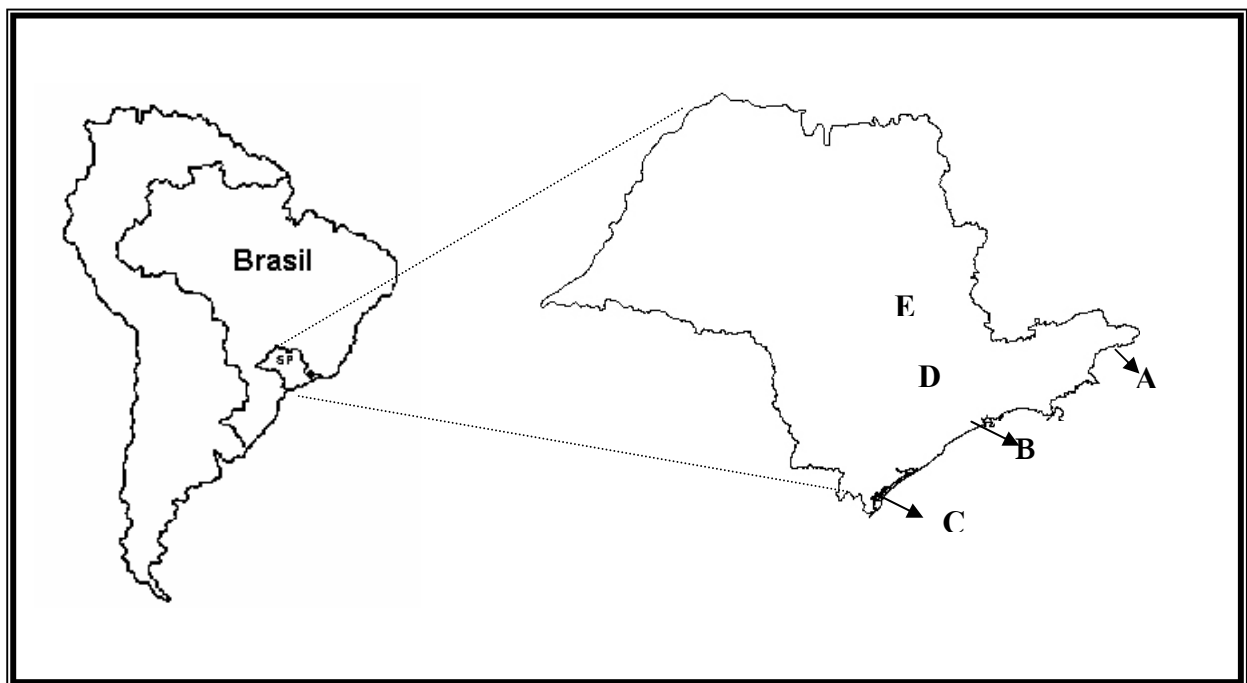
Figure 1. Sampling sites in the State of São Paulo. A – Ubatuba, B – Cubatão, C – Cananéia, D – Jaraguá, E – São Carlos.

We have designed a stratified sampling design regarding a multiple spatial scale approach to assess chironomid larvae distribution. We have incorporated environmental characteristics that may potentially influence on chironomids in the different scales (variation among sites – streams – mesohabitats). A total of 15 low-order (1-2) forested streams located in the State of São Paulo have been analyzed (Fig. 1). We selected 5 sites: A. Parque Estadual da Serra do Mar – Núcleo Picinguaba (Picinguaba, Ubatuba), B. Parque Estadual da Serra do Mar – Núcleo Cubatão (Cubatão), C. Parque Estadual da Serra do Mar – Cananéia (Cananéia), D. Parque Estadual do Jaraguá (Jaraguá), and E. São Carlos City (São Carlos) (Fig. 1). At each site 3 streams with different gradient level (high, medium and low) were chosen.

All the streams studied are located in conservation areas, are shallow deep (< 50 cm), the tree canopy covering more than 70% of their channel, absence of macrophytes, water with high level of oxygen dissolved, low conductivity, and slightly alkaline or acid, temperature ranging from 15-23ºC. The substrates of high gradient streams are characterized by predominance of pebbles while the low ones by great abundance of organic material (wood and leaves). Some general information about the streams are given in table 1.

Table 1. General features of the studied streams in Atlantic forest, São Paulo, Brazil.

Site/stream	Gradient	Oxygen	Cond.	pH	coordinates
Cananéia					
Stream 1	high	8.0	32-34	7.2-7.3	S 24º54'12" W 47º58'36"
Stream 2	medium	6.31	43-46	6.9-7.1	S 24º53'03" W 47º51'22"
Stream 3	low	8.1	50	7.5	
Cubatão					
Stream 1	high	8.6-8.9	28-33	7.1-7.3	S 23º55'45" W 46º30'55"
Stream 2	medium	8.5-8.9	40-47	7.2	S 23º54'15" W 46º28'46"
Stream 3	low	6.6	52	7.5	S 23º54'08" W 46º28'23"
Picinguaba					
Stream 1	high	8.4-8.6	15-26	6.5-7.5	S 23º20'15" W 44º50'14"
Stream 2	medium	8.8-8.9	17-28	6.8-7.3	near S 2320'15" W 44º50'14"
Stream 3	low	6.4	18	6.5	-
Jaraguá					
Stream 1	high	8.8-8.9	79-77	7.4	S 23º27'59" W 46º45'58"
Stream 2	medium	6.5-6.9	30-67	6.9	near S 23º27'59" W 46º45'58"
Stream 3	low	6.81	30	6.81	-
São Carlos					
Stream 1	high	11.7	5	5.6	S 21º56'12" W 47º54'15"
Stream 2	medium	7.9	10	5.4	S 21º57'07" W 47º50'12"
Stream 3	low	7.2-9.0	13-15	6.9-7.2	S 21º58'07" W 47º53'08"

At each stream, we collected 3 samples in riffles and 3 in pools (dry season, 2001). The use of mesohabitat as a minimal scale to collect macroinvertebrates followed PARDO & ARMITAGE (1997). The material was collected with a Surber collector and taken to the laboratory where the chironomids were sorted and identified up to the smallest possible taxonomic level and separated in morphospecies.

We used three-way ANOVA without replication (SOKAL & ROHLF, 1995) to measure the possible effects of different spatial scales on Chironomidae richness and on total abundance. Although for each stream 3 riffles and 3 pools were sampled, we pooled these data in all analyses due to low replication.

Analyses of Chironomidae larvae distribution were undertaken using the Correspondence Analysis (CA) (TER BRAAK, 1985). All taxa were included and chironomid densities were (log10(x+1)) transformed prior to analysis. We also used analyses of indicators (BUFRENE & LEGENDRE, 1997) to assess possible species indicators of the spatial pattern evidenced in the CA.

Results

A total of 66 morphospecies of chironomid larvae were identified, of which 40 Chironominae, 15 Orthocladiinae and 11 Tanypodinae.

The results of the significance tests of three-way ANOVA for the Chironomidae richness and total abundance data indicate that there was a significant effect of the factors site and stream on abundance (Table 2), and stream on richness (Table 3).

Table 2. Analysis of variance of chironomid total abundance.

	Effect (F/R)	Df Effect	MS Effect	df Error	MS Error	F	p
{1}site	Fixed	4	0,670	8	0,063	10,578	0,002
{2}stream	Fixed	2	0,363	8	0,063	5,739	0,028
{3}riffle/pool	Fixed	1	0,011	8	0,063	0,176	0,685
1*2	Fixed	8	0,207	8	0,063	3,280	0,056
1*3	Fixed	4	0,062	8	0,063	0,989	0,465
2*3	Fixed	2	0,012	8	0,063	0,201	0,821

Table 3. Analysis of variance of chironomid richness.

	Effect (F/R)	df Effect	MS Effect	df Error	MS Error	F	p
{1} site	Fixed	4	16,8	8	6,616	2,539	0,122
{2} stream	Fixed	2	38,2	8	6,616	5,778	0,028
{3} pool/riffle	Fixed	1	24,3	8	6,616	3,672	0,091
1*2	Fixed	8	10,6	8	6,616	1,609	0,258
1*3	Fixed	4	2,9	8	6,616	0,448	0,771
2*3	Fixed	2	11,7	8	6,616	1,768	0,231

Ordination of the taxa by 30 riffle-pools/streams/sites data matrix using CA demonstrated a clear trend in separating riffle and pool habitats along the two first factorial axes (Fig. 2). Riffles show an aggregated distribution, while pools show a more dispersed position on the ordination. In general, the first ordinating axis can be interpreted as the influence of the mesoscale.
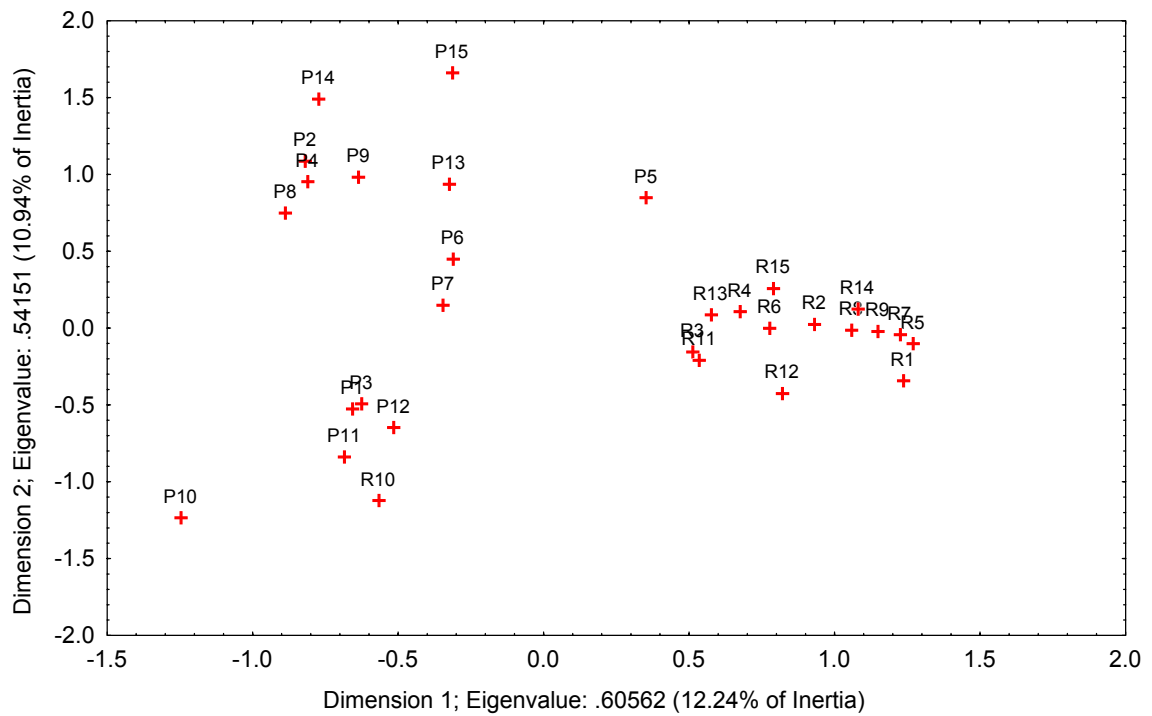
Figure 2. Results of the correspondence analysis (streams and mesohabitats).

R – riffles; P – pools. 1-15 streams: 1 - Jaraguá stream 1; 2 - Jaraguá stream 2; 3 – Jaraguá stream 3; 4 – Picinguaba stream 3; 5 – Picinguaba stream 1; 6 - Picinguaba stream 2; 7 – Cubatão stream 2; 8 – Cubatão stream 3; 9 – Cubatão stream 1; 10 – São Carlos stream 3; 11 – São Carlos stream 2; 12 – São Carlos stream 1; 13 – Cananéia stream 3; 14 – Cananéia stream 2; 15 – Cananéia stream 1
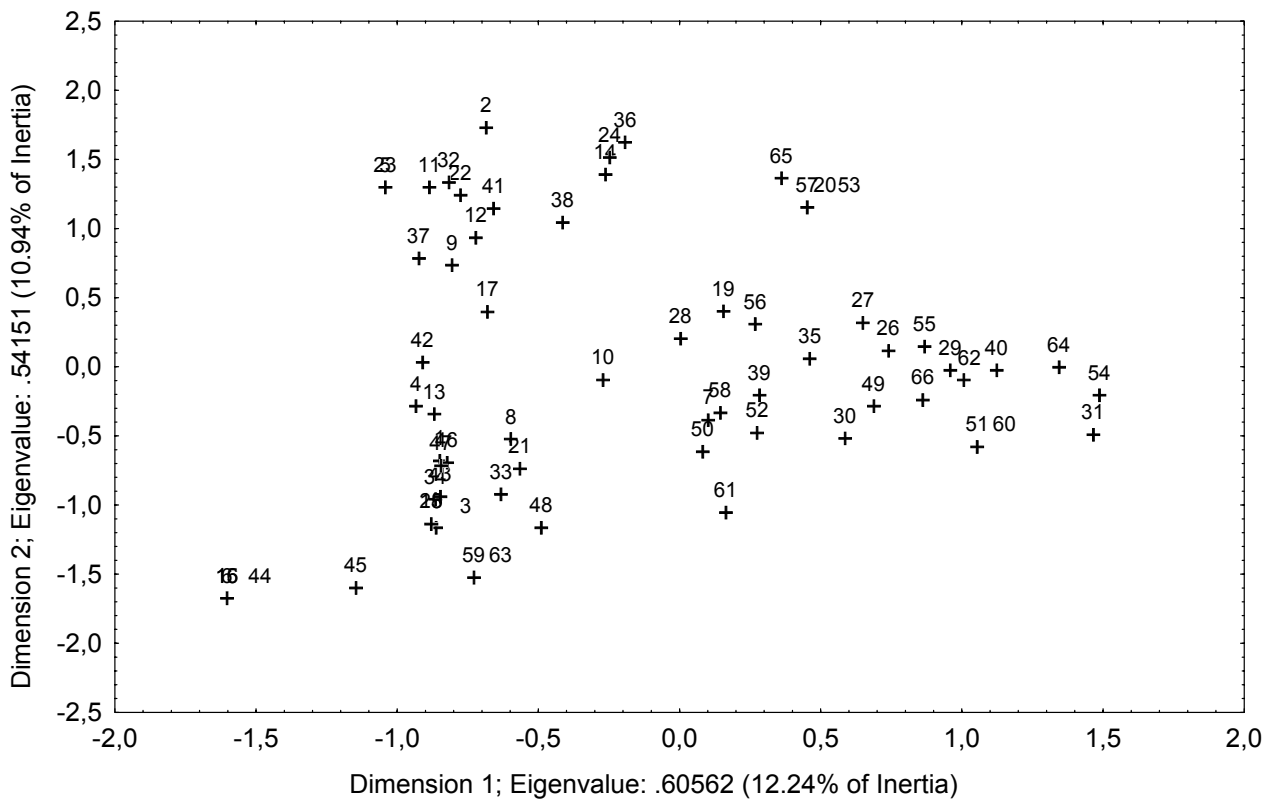
Figure 3. Results of the correspondence analysis (taxa). The taxa codes are given in Table 4.

The results of the species analyses allow us to identify group of morphospecies for pools and riffles. Although a high number of species seems to be related with specific habitat, example most Tanypodinae with pools, only 9 morphospecies showed significative indicator value through Monte Carlo test (p<0,05): *Ablabesmyia* sp. 1, *Djalmabatista* sp. 1, *Endotribelos* spp., Tanytarsini sp. 4, Tanytarsini sp. 7, Tanytarsini sp. 9 were related with pools habitats and *Parametriocnemus*, *Rheotanytarsus*, *Thienemaniella* were associated with riffles (Table 4).

Table 4 . The results of the indicators species analyses. Maxgroup 0 – riffles, Maxgroup 1 – pools.

Code	Taxa	Maxgrp	Observed indicator Value (IV)	IV from randomized groups Mean	S.D	p
1	*Ablabesmyia* sp. 1	1	38.4	23.2	6.88	0.04
2	*Ablabesmyia* sp. 2	1	20.0	11.2	4.64	0.20
3	*Coelotanypus* sp. 1	1	11.6	11.5	5.16	0.50
4	*Djalmabatista* sp. 1	1	47.7	25.2	6.95	0.00
5	*Djalmabatista* sp. 2	1	6.7	6.7	0.21	10.00
6	*Guassutanypus oliverai*	1	6.7	6.7	0.21	10.00
7	*Larsia* spp.	0	27.3	29.2	7.58	0.49
8	*Labrundinia* sp. 1	1	22.5	19.2	6.19	0.32
9	*Fittkauimyia* sp. 1	1	20.0	11.4	4.74	0.22
10	*Pentaneura* sp. 1	1	15.6	13.0	5.76	0.45
11	*Zavrelimyia* sp. 1	1	20.0	11.4	4.91	0.23
12	*Chironomus* spp.	1	23.4	15.5	6.39	0.21
13	*Cryptochironomus* sp. 1	1	13.3	9.2	3.99	0.48
14	C. *Harnischia* sp. 1	1	9.6	11.4	4.81	0.72
15	C. *Harnischia* sp. 2	1	6.7	6.7	0.21	10.00
16	C. *Harnischia* sp. 3	1	6.7	6.7	0.21	10.00
17	*Endotribelos* spp	1	80.6	33.5	6.87	0.00
18	*Lauterborniella* sp. 1	1	6.7	6.7	0.21	10.00
19	*Paratendipes* sp. 1	1	8.1	15.6	6.36	10.00
20	*Paratendipes* sp. 2	1	6.7	6.7	0.21	10.00
21	*Polypedilum* sp. 1	1	22.6	15.7	5.98	0.10
22	*Polypedilum* sp. 2	1	30.4	17.5	6.47	0.09
23	*Polypedilum* sp. 3	1	6.7	6.7	0.21	10.00
24	*Polypedilum* sp. 4	1	15.5	15.8	6.15	0.42
25	*Polypedilum* sp. 5	1	6.7	6.7	0.21	10.00
26	*Polypedilum gr. fallax*	0	6.7	6.7	0.21	10.00
27	Pseudochironomini sp. 1	0	22.5	23.6	7.51	0.45
28	*Stenochironomus* spp.	1	22.3	30.1	6.99	0.96
29	*Rheotanytarsus* sp. 1	0	75.2	33.5	7.00	0.00
30	*Rheotanytarsus* sp. 2	0	10.6	11.1	5.02	0.72
31	*Rheotanytarsus* sp. 3	0	13.3	9.5	4.11	0.53
32	*Stempellina* sp. 1	1	6.7	6.7	0.21	10.00
33	*Stempellinella* sp. 1	1	17.5	14.0	5.71	0.35
34	Tanytarsini sp. 1	1	13.3	8.4	4.77	0.47
35	Tanytarsini sp. 2	0	8.0	13.4	5.73	10.00
36	Tanytarsini sp. 3	1	23.4	15.7	6.30	0.21
37	Tanytarsini sp. 4	1	33.3	15.7	5.82	0.04
38	Tanytarsini sp. 5	1	46.5	34.2	7.91	0.08
39	Tanytarsini sp. 6	0	8.0	11.2	4.58	10.00
40	Tanytarsini sp. 7	0	71.2	28.9	7.49	0.00
41	Tanytarsini sp. 8	1	34.4	23.7	7.47	0.11
42	Tanytarsini sp. 9	1	40.0	18.0	6.33	0.01
43	Tanytarsini sp.10	1	13.3	8.4	4.73	0.47

44	Tanytarsini sp.11	1	6.7	6.7	0.21	10.00
45	Tanytarsini sp.12	0	3.5	8.1	4.92	10.00
46	Tanytarsini sp.13	1	13.3	8.2	5.01	0.49
47	Tanytarsini sp. 14	1	6.7	6.7	0.21	10.00
48	Tanytarsini sp. 15	1	7.0	12.9	5.86	0.88
49	Tanytarsini sp. 16	0	6.7	6.7	0.21	10.00
50	*Zavreliella* sp. 1	0	4.1	8.6	4.63	10.00
51	*Xestochironomus* sp. 1	0	6.7	6.7	0.21	10.00
52	*Corynoneura* sp. 1	0	35.6	27.4	7.53	0.16
53	*Corynoneura* sp. 2	1	6.7	6.7	0.21	10.00
54	*Cricotopus* sp. 1	0	33.3	15.8	6.10	0.05
55	*Gymnometriocnemus* sp. 1	0	6.7	6.7	0.21	10.00
56	*Lopescladius* sp. 1	0	12.1	17.6	6.12	10.00
57	*Metriocnemus* sp. 1	1	6.7	6.7	0.21	10.00
58	*Nanocladius* sp. 1	1	14.5	19.7	6.55	0.81
59	Orthocladiinae sp. 1	0	6.7	6.7	0.21	10.00
60	Orthocladiinae sp. 2	0	6.7	6.7	0.21	10.00
61	Orthocladiinae sp. 3	0	13.3	8.2	5.00	0.48
62	*Parametriocnemus* sp. 1	0	79.4	35.3	7.07	0.00
63	*Paraphaenocladius* sp. 1	0	6.7	6.7	0.21	10.00
64	*Rheocricotopus* sp. 1	0	20.0	11.5	4.73	0.23
65	near *Stackelbergina* sp. 1	1	4.1	8.4	4.62	10.00
66	*Thienemanniella* sp. 1	0	75.0	35.5	7.34	0.00

Discussion

Since DOWNES et al.'s (1993) study on stream macroinvertebrates at multiple scales, an increasing number of studies has showed that the macroinvertebrate community structure in streams is highly variable at multiple spatial scales. Such variability was also evident in our study on Chironomidae.

Sites and streams differed significantly in the total abundance of chironomids. In general, streams from the two inland sites (Jaraguá and São Carlos) show higher total Chironomidae abundance than those from seaward coastal Atlantic region. Factors at large-scale, such as land uses, geology, and climate are known to influence on macroinvertebrate distribution through direct substrate influences such as particle size, as well as to hydrologic influences in stream flow pattern (RICHARDS et al., 1996). In this sense, many factors working synergetically may partly account for the differences among sites found here. For example, the seaward side of the Serra do Mar in the State of São Paulo has

among the highest mean annual rainfall (up to 3600 mm) of the entire Atlantic Forest range, while the inland side has typical seasonal climates with annual rainfall between 1300 and 1600 mm. This pattern can result in higher magnitude and frequency of hydrological disturbances in the coast streams, which can contribute to a low number of chironomids. Hydrological disturbances have been pointed out as one of the most important mechanisms in stream ecology (RESH et al., 1988) and can affect macroinvertebrate communities in different ways, for example, creating and changing habitats, promoting drift, by removing animals from the substrates. Biological aspects can also contribute to explain our results. The high abundance of shrimps, Ephemeroptera, Plecoptera, and Trichoptera in the Atlantic Forest coastal streams (MOULTON et al., 2004) might also be responsible for the lower number of chironomid larvae in these streams in comparison with the inland ones. Experimental studies carried out in Puerto Rico (MARCH et al., 2002), Costa Rica (PRINGLE & HAMAZAKI, 1998) and Brazilian Atlantic forest streams (MOULTON et al., 2004) have shown that shrimps and/or ephemeropterans can influence negatively the abundance of chironomids.

Significant differences in chironomid richness and total abundance among streams were observed. Medium to low gradient streams showed greater richness and abundance than high gradient ones. Stream geomorphology can influence stream ecosystem via changes in nutrient loading, water velocity, proportion of mesohabitats, energy flux, input sediments, time of material retention, decomposition rates, availably of food, and in consequence their biotic communities (FRISSEL et al., 1986; CARTER et al., 1996; RICHARDS et al, 1997). The higher richness and abundance of chironomids in low gradient order streams may be related speculatively to the following non-exclusive aspects that may result in more opportunity for coexistence among chironomids: 1) the chironomid assemblages (mainly non-running water specialist chironomids) in low gradient streams are probably less affected by hydrological disturbances than in high gradient ones; 2) low gradient streams probably have higher hydrological variability than high ones (high mixture of sediments) (see STATZNER & HIGLER, 1986), with clear segregation of habitats in riffle-pool scale; 3) great amount of organic matter accumulated in low gradient streams, 4) refugium availability could be high in low gradient

streams; 5) in general EPT groups are more common in high gradient streams; and 6) low gradient streams probably have higher productivity than high ones.

According to the correspondence analysis, most of the taxa variability was accounted for in the riffle/pool scale. Our results support the results from other studies carried out on chironomids in streams in the Brazilian Atlantic forest (SANSEVERINO & NESSIMIAN, 2001; HENRIQUE-OLIVEIRA et al., 2003; ROQUE et al., 2003) that chironomid larvae distribution is strongly affected by processes working at local scales (eg. riffle-pool habitats). Other authors, attempting to identify scales of variability in stream macroinvertebrate communities have also pointed out the importance of in-stream variability (DOWNES et al., 1993; DOWNES et al., 2000; HEINO et al., 2004). The relationship between chironomid taxa distribution and riffle/pool habitat may be related to biological trade-offs. According to TOWNSEND et al. (1997) and LAMOUROUX et al. (2004) the relationship between biological traits and habitat variables seems to be related to adaptation to physical constraints of the habitat. Adaptation to habitat characteristics in terms of resistance to drag and foraging strategies seems to be one of the most important evolutionary processes influencing the distribution of stream dwelling insects (LAMOUROUX et al., 2004). Small invertebrates with flexible and streamlined body shapes were more common in stressful conditions or relatively coarse substrate. These body forms, morphological adaptations or feeding strategies reduce drag and enable organisms to use small interstices within the bed sediments or keep themselves attached to the substrate. This probably is the case of the species indicative of riffle habitat, such as *Parametriocnemus*, *Rheotanytarsus*, and *Thienemaniella*. In contrast, predators, larger invertebrates, and collectors live in fine sediments deposited in slow-flowing habitats (e.g. indicators of pool habitat: *Ablabesmyia* sp. 1, *Djalmabatista* sp. 1, *Endotribelos* spp., Tanytarsini sp. 4, Tanytarsini sp. 7, Tanytarsini sp. 9).

The influence of different scales in determining the chironomid distribution may be masked by the taxonomic resolution. The accuracy of community descriptions based on the abundance of taxa required identifications to genera and/or families on the local habitat scale, while species identifications were needed on the catchment scale (DOLÉDEC et al., 2000) or biogeographical analysis. Considering

that 1) in genus level, chironomids are widely distributed in the Atlantic forest streams (SANSEVERINO & NESSIMIAN, 2001; HENRIQUE-OLIVEIRA et al., 2003; ROQUE et al., 2003; SURIANO & FONSECA-GESSNER, 2004; ROQUE et al., chapter 1 in this thesis); 2) for some genera, the distinction of morphospecies is difficult using only larval stages; and 3) Chironomidae assemblages in neotropical mainland streams are very speciose, with many genera being represented by a moderately large to very large number of similar species (COFFMAN & DE LA ROSA, 1998; ROQUE et al., chapter 1 in this thesis), it is probable that a broad scale pattern could not be detected due to lack of resolution in identification of the larvae.

As a whole, the variability among scales, the differences on the importance of site, stream or riffle/pool scales on richness, abundance and assemblage structure, and the presence of indicator species in both mesohabitats (riffle and pool) allow us to point out: 1) the identification of the scale importance depends on the chironomid assemblage descriptor and the taxonomic resolution considered; 2) studies focusing on one scale or habitat (e.g. riffles) are not appropriate for studying Chironomidae distribution patterns in low order streams; 3) biological traits of some groups may underlie most evident in-stream chironomid distribution pattern; 4) it is likely that no single physical or biological factor is responsible for the chironomid distribution at different scales.

Finally, although our data clearly cannot provide mechanistic explanations for the patterns observed, we consider that it represents an important step in elaborating well-developed hypothesis about the most influential processes and mechanisms on the variability in chironomid distribution in Brazilian low order streams at multiple-scales.

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4. CHIRONOMIDAE (DIPTERA) LIVING INSIDE FALLEN-FRUITS IN ATLANTIC FOREST STREAMS, SÃO PAULO, BRAZIL

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Introduction

The Chironomidae larvae explore a wide variety of habitats and have a great diversity of feeding behavior and kinds of food. They have been reported using a variety of plant-derived food resources, including parts of higher plants that fall in aquatic systems, such as wood and leaves (PINDER, 1986; BERG, 1995). This subject have been studied in different regions of the world, and in the Neotropical region, particularly in the Brazilian Atlantic Forest, although some studies have been carried out about the distribution of Chironomidae larvae in different stream habitats (SANSEVERINO, 1998; SANSEVERINO & NESSIMIAN, 1998, SANSEVERINO et al, 1998; ROQUE, 2000; HENRIQUE-OLIVEIRA, 2001), none about Chironomidae in specific fallen-parts of plants in streams have been addressed.

The input of material from forest has been suggested as an important ecological driving force to the low order stream dynamics (VANNOTE et al., 1980). In the Atlantic Forest, the forest floor may receive up to 400 kg/ha/yr of fallen-fruits (MORELLATO, 1992) and the streams also receive a great amount (HENRY et al., 1994). Although the fallen-fruits have been recognized as important to ecology of terrestrial and aquatic systems, little information is available about their influence on aquatic invertebrates community in streams.

Given the huge amount of fallen-fruits and the high diversity and density of Chironomidae larvae in streams of Atlantic Forest, we decided to assess the possible use of fallen-fruits by Chironomidae larvae in low order Atlantic Forest streams.

Methods

The study area

According to MORELLATO & HADDAD (2000) the Atlantic Forest is composed of two major vegetation types: the coastal forest or Atlantic Rain Forest and the tropical seasonal forest or Atlantic semi-deciduous forest. The Atlantic Rain forest covers mostly the low to medium elevation (< 1000 m a.s.l.) of the eastern slopes of mountain chain that runs along the coastline from southern to northeastern Brazil; the Atlantic-deciduous Forest extends across the plateau (usually > 600 m a.s.l.) in the center and southeastern interior of the country. The Atlantic Rain Forest experiences warm and wet climate without dry season; a seasonal climate with a relatively severe dry season (generally from April to September) predominates over the distribution of the Atlantic Semi-deciduous Forest.

This study was carried out in streams of 5 areas in Atlantic Forest in the State of São Paulo, three streams situated in Atlantic Rain Forest and two in Atlantic semi-deciduous forest. The general characteristics of the streams, where the fruits were collected, are showed in Table 1.

Table 1. General characteristics of the streams where the fruits were collected.

General Characteristics	Parque Estadual do Jaraguá	Serra do Mar - Cananéia	Serra do Mar – Núcleo Cubatão	Brotas	São Carlos
Vegetation predominant	Atlantic Rain Forest	Atlantic Rain Forest	Atlantic Rain Forest	Riparian-forested formation	Riparian-forested formation
Geographic Coordenates	23°24' S and 45°44' W	24°54'12" S 47°58'36" W	23°54'15" S 46°28'46" W	–	21°57'51" S 47°50'30" W
Stream Order	1 and 2	1 and 2	1 and 2	1	1 and 2
PH	6.68	7.02	7.09	4.67	4.75
OD(mg/l)	6.98	10.9	8.7	5.83	6.95
Conductivity (μS cm-1)	30	30	20	23	10

After collecting the fallen-fruits in the streams, we transported them to the laboratory. When possible, the fruits were kept in an oxygenated aquarium in order to rear the chironomid larvae and obtain the adults. In this study only the specimens collected inside the fruits were considered. Because of the low resolution of taxonomic knowledge for Chironomidae in Brazil (SPIES & REISS, 1996), it was difficult to identify specimens to the species level. Hence, individuals were identified up to the most specific taxonomic level possible, using available literature and they were separated as morphospecies. The material was deposited in the collection of the Laboratório de Entomologia do Departamento da Hidrobiologia da Universidade Federal de São Carlos, São Paulo, Brazil.

Results and Discussion

Fleshy fruits belonging to 12 tree species were collected (Tab. 2). Most of them have been reported as important food recourse for terrestrial insects (PIZO & OLIVEIRA, 2000).

Table 2. Chironomidae (Diptera) collected in different fallen-fruits in low order streams of different sites of Atlantic Forest (São Paulo, Brazil).

Areas/ Fruits	Taxa						
	Endotribelos grodhausi	*E. albatum*	*E.* sp. 1	*E.* sp. 2	*E.* sp. 3	*E.* sp. 4	*E.* sp. 5
P. E. Jaraguá							
Euterpes edullis	X						
Magnoliacea sp.1	X						
Myrtacea sp. 1	X						
Ficus sp. 1	X						
Fruit indet. sp. 1	X						
Cubatão							
Annonacea sp.1					X		
Ficus sp. 2					X		
Myrtacea sp. 2					X		
Rubiacea sp. 1					X		
Cananéia							
Ficus sp. 2		X					
São Carlos							
Callophylum brasiliensis						X	X
Talauma ovata		X					
Fruit indet. sp. 2							
Brotas							
Callophylum brasiliensis			X	X			
Talauma ovata			X	X			

We found Chironomidae larvae mining fruit tissue of all tree species. Seven morphospecies of *Endotribelos* were identified (Tab. 2). The species *E. albatum* Sublette & Sasa and *E. grodhausi* Sublette & Sasa have already been reported to the Neotropical region by SUBLETTE & SASA (1994), but our study amplifies the South limit distribution of these species.

The occurrence of different *Endotribelo*s morphospecies in fruits of different sites suggests a non-homogenous distribution of them in the Atlantic Forest (State of São Paulo), while the presence of the same morphospecies living in different fruits suggests low specific relationship between morphospecies and fruits. However, new studies are required to support this hypothesis.

Food quality is extremely difficult to define, especially for a group of insects like the Chironomidae, which have wide natural diets (PINDER, 1986). The high amount of carbohydrates, proteins and lipids in some fruits suggest that they represent a rich food resource for the Chironomidae larvae (see PIZO & OLIVEIRA, 2000 and GALETTI et. al., 2000 for some fruit nutritional information). Furthermore, microbial colonization probably make the fruits in decomposition more palatable and with a high nutritional value, as some studies about woody debris and macrophytes have demonstrated (PINDER, 1986; BERG, 1995). On the other hand, the anaerobic condition inside fallen-fruits in decomposition and the presence of allelopathic substances in many Neotropical plants (PIZZAMIGLIO, 1991) may difficult their colonization by Chironomidae larvae.

According to OLIVER (1971) few Chironomidae appear to be restricted rigidly to a single type of habitat and food, except some xylophagous groups, such as *Stenochironomus, Xestochironomu*s (BORKENT, 1984) and *Xylotopus* (OLIVER, 1982). In the case of *Endotribelos*, larvae, a strong tendency to penetrate leaves and stems of macrophytes was observed (GRODHAUS, 1987). SANSEVERINO (1998) found plant tissue, fungi and pollen in the stomach contents of *Endotribelos* larvae. Furthermore, *Endotribelos* (identified as *Tribelos*) have been reported in woods (TRIVINHO-STRIXINO & STRIXINO, 1998), in macrophytes (TRIVINHO-STRIXINO & STRIXINO, 1993; TRIVINHO-STRIXINO et al., 2000), and we have found them in the freshwater sponges *Radiospongilla amazonensi*

and *Metania spinata* (unpublished data). These results suggest that although the larvae of *Endotribelos* may be the commonest insect group inside fallen-fruits in aquatic systems, they are not restricted to them.

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5. CONSIDERAÇÕES FINAIS

Nesta seção pretendo compartilhar algumas reflexões pessoais que surgiram ao longo da elaboração desta tese e que julgo serem importantes para discussões sobre o processo de construção de conhecimento científico em relação à diversidade de Chironomidae em córregos brasileiros. Não tenho a pretensão de finalizar esta tese com conclusões gerais, uma vez que cada capítulo apresenta suas discussões e os contingenciamentos de cada aspecto relatado.

Sobre o contexto histórico dos trabalhos envolvendo ecologia de Chironomidae em córregos da Mata Atlântica

Os primeiros trabalhos sobre Chironomidae em córregos da Mata Atlântica, com explícito esforço de identificação de imaturos, foram desenvolvidos pelo Dr. Jorge Nessimian e Ângela Sanseverino no Estado do Rio de Janeiro. Posteriormente outros trabalhos foram realizados no Estado de São Paulo e Rio Grande do Sul (ver referências no capítulo 1). Embora a maioria dos trabalhos, inclusive esta tese, tenha focado aspectos da riqueza de espécies e distribuição das larvas, são poucas as possibilidades de comparações e sínteses, devido principalmente ao uso de diferentes métodos de coleta e à falta de padronização em esforço amostral e identificação dos táxons. No geral, os resultados permitem a elaboração das seguintes proposições: 1) os córregos de baixa ordem da Mata Atlântica estão entre as áreas de maior riqueza de espécies de Chironomidae do mundo; 2) a taxocenose de Chironomidae de córregos de baixa ordem florestados é caracterizada por elevado numero de espécies concentradas em poucos alguns gêneros (*Tanytarsus, Caladomyia, Polypedilum* e *Stenochironomus*); 3) a importância de cada escala espacial depende do descritor de taxocenose de Chironomidae e da resolução taxonômica considerada; 4) estudos focados em apenas um habitat ou escala não são

apropriados para entender a riqueza e distribuição da taxocenose de Chironomidae em córregos; 5) as características morfo-comportamentais de alguns táxons podem representar um dos principais fatores para explicar os padrões encontrados em pequenas escalas; 6) o "input" de matéria orgânica, particularmente frutos, folhas e troncos, proveniente da mata ripária constitui um importante recurso e habitat para larvas de Chironomidae.

De modo geral, fica evidente nos trabalhos que limitações básicas, como por exemplo a falta de conhecimento taxonômico, ainda constituem grandes entraves para a construção de conhecimento sobre ecologia de Chironomidae em córregos. Como exemplo desta deficiência taxonômica basta olhar a lista de espécies descritas identificadas nos capítulos desta tese e o caso das espécies de *Tanytarsus/Caladomyia* cuja identificação em nível de gênero pode mascarar a riqueza de espécies. Para problemas desta natureza não existe solução rápida, pois envolve a descrição das espécies, porém algumas sugestões são apresentadas por FITTKAU (2001) e ROQUE et al. (2004). Vale destacar que um dos desdobramentos posteriores desta tese será disponibilizar ilustrações de todos as morfoespécies identificadas, seguindo estratégia usada pelo Dr. Peter Cranston na Austrália e que parece aplicável à nossa realidade.

Sobre aspectos relacionados à conservação da biodiversidade de Chironomidae no Brasil

Infelizmente, a despeito da reconhecida riqueza de espécies, importância ecológica e sensibilidade a impactos antrópicos, os Chironomidae ainda são amplamente negligenciados em estratégias regionais, nacionais e internacionais visando a conservação da biodiversidade. Como exemplo disso, nota-se que nenhuma espécie de Chironomidae foi incluída nas recentes listas de espécies ameaçadas de extinção produzidas pela IUCN - The World Conservation Union e também, na lista nacional das espécies de invertebrados aquáticos e peixes ameaçados de extinção (Ministério do Meio Ambiente, instrução normativa n°5, 2004). Será que este cenário representa a realidade?

Certamente vários fatores contribuem para esta situação, entre eles: a falta de carisma popular pelo grupo e limitações do conhecimento taxonômico e ecológico. Entretanto o mais preocupante

aspecto é a falta de uma ampla estratégia de cooperação para obtenção de informações que viabilizem a inclusão efetiva destas no processo de tomada de decisão.

Ainda temos um longo caminho para avaliar de forma segura o "status" das espécies de Chironomidae. Entretanto, as informações que já possuímos fornecem indicativos consistentes de que estamos perdendo biodiversidade em algumas áreas. Por exemplo, vários são os trabalhos que demonstram menor riqueza de táxons em áreas sob impactos antrópicos comparadas a áreas naturais florestadas (mesmo quando se considera o nível taxonômico de tribo ou gênero).

Embora não tenhamos dados suficientes que permitam traçar estratégias específicas para a conservação de Chironomidae no Brasil, em linhas gerais as principais necessidades são facilmente identificáveis e basicamente constituem as mesmas válidas para outros grupos: conservação de áreas naturais, recuperação de áreas degradadas e uso sustentável dos recursos naturais.

Reflexões para o avanço do conhecimento científico

Infelizmente me parece que a maioria dos trabalhos desenvolvidos no Brasil, inclusive os meus, investem excessivamente na idéia de explorar o máximo de variáveis explicativas buscando descrever possíveis padrões e levantar processos e mecanismos relacionados. Esta é uma característica da maioria dos trabalhos de limnologia desenvolvidos no mundo (BOURGET & FORTIN, 1995) e me parece que no Brasil este é um legado na formação de muitos pesquisadores. Estas abordagens exploratórias, embora necessárias, levam a uma série de possibilidades e hipóteses, que na maioria das vezes, não são testadas. Não se trata aqui de desvalorizar trabalhos puramente descritivos, nem tão pouco aclamar por uma abordagem Popperiana/Fisheriana clássica. Estou, sobretudo, levantando a necessidade de discussões sobre onde queremos chegar com as nossas pesquisas e se elas estão respondendo apenas perguntas iniciadas por onde, quantos, quem, quando ou, já estamos formulando perguntas com por quês.

Para o amadurecimento teórico do conhecimento sobre ecologia, considero que as discussões de WERNER (1998) e FORD (2000) podem trazer importantes contribuições para o caso particular

dos Chironomidae. De acordo com estes autores os projetos de ecologia devem estar conectados em programas de pesquisa que envolvam, além da pesquisa descritiva, a formulação e teste de hipótese estrategicamente conectadas numa rede de informações com sucessivas sínteses. Neste contexto, o uso de abordagem Bayesiana (capítulo 1) pode ser bastante promissora, pois possibilita incorporar o conhecimento "a priori" e a incerteza associada a diferentes momentos do processo de construção de conhecimento científico.

Finalmente, a elaboração de progressivas sínteses, com todas as incertezas envolvidas no momento, é essencial para o embasamento de processos decisórios relacionados à diversidade de Chironomidae, como por exemplo, nas tomadas de decisão em conservação, avaliações e monitoramento ambiental.

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Aquatic macroinvertebrates (macroinvertebrados aquáticos) – conjunto de invertebrados aquáticos de água doce (ex. insetos, moluscos, oligoquetas, crustáceos decápodes) arbitrariamente selecionados em peneiras com malha de 2-5 mm de abertura.

Assemblage (taxocenose) - conjuntos taxonomicamente determinados de espécies coocorrentes.

Chironomidae – família de insetos pertencente à ordem Diptera (mosquitos, moscas, borrachudos, etc). Como todos representantes desta ordem, os Chironomidae apresentam metamorfose completa (figura abaixo).
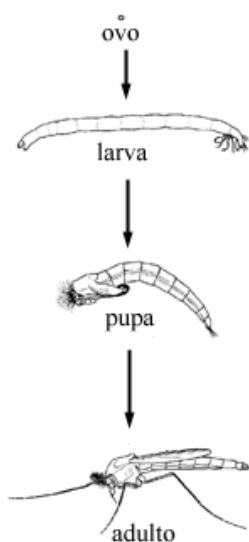
Os Chironomidae se diferenciam dos demais Diptera por apresentarem as seguintes características: Adulto macho com antena plumosa, pernas anteriores usualmente mais longas que as

demais, genitália não invertida, padrão de nervura das asas característico. Larvas apneusticas, longas, cilíndricas, com cápsula cefálica esclerotizada e par de pernas anteriores e posteriores com garras. As larvas de Chironomidae vivem nos mais variados ambientes (ex. terrestres, aquáticos de água doce e salinos). Geralmente os adultos de Chironomidae são confundidos com adultos de Culicidae (mosquitos picadores e pernilongos), mas podem ser geralmente diferenciados pelo maior comprimento e posição estendida das pernas anteriores e ausência de aparelho bucal sugador.

Bayesian statistics (estatística Bayesiana) – O nome Bayseana foi uma homenagem ao reverendo Bayes que formulou os princípios da estatística Bayseana. No paradigma Bayesiano, a probabilidade é uma medida direta da incerteza e pode não representar a freqüência do evento como na estatística Fisheriana.

A inferência é baseada numa distribuição a posterior $p(\theta \backslash X)$ que é a distribuição condicional do parâmetro considerando os dados.

$$p(\theta \backslash X) = p(\theta)\, p(X \backslash \theta)/\, p(X)$$

Onde $p(\theta)$ representa a distribuição a priori do parâmetro. A distribuição a priori pode ser construída com base em informações previas em geral. X representa um fator normalizador (ex. os dados observados).

Community (comunidade) – conjunto de espécies coocorrentes localmente.

Ecological pattern, process and mechanisms (padrões, processos e mecanismos ecológicos) – O reconhecimento de um padrão ecológico (ex. maior número de espécies em baixas latitudes) é o primeiro passo em qualquer trabalho cientifico visando estudo de comunidade, embora isto não signifique que seja uma fácil tarefa. Para o reconhecimento de um padrão é necessário avaliá-lo sob o

critério de um padrão não randômico. Padrões não randômicos em ecologia de comunidades são geralmente associados com certos fatores ambientais e processos biológicos (ex. competição, distúrbios) que tendem a operar em um caminho determinístico, sendo desta forma mais fácil avaliar os mecanismos que os geram. Entretanto padrões randômicos também podem ser resultado de processos físicos e biológicos, mas operando de forma estocástica.

Lotic systems (ambientes lóticos) – termo que compreende ambientes aquáticos em geral com fluxo unidirectional da água da nascente para foz (exemplo: córregos, rios, igarapés, riachos).

Low order streams (córregos de baixa ordem) – A ordem de um córrego se refere a um sistema de classificação de ambientes lóticos baseado na contribuição dos seus tributários. Córregos de baixa ordem (1- 3) representam em geral nascentes ou córregos de pequenas proporções conforme figura.
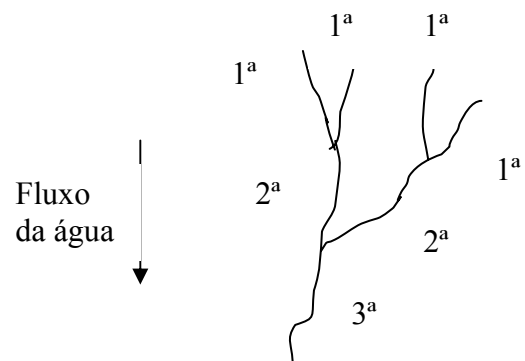
Mesohabitats (mesohabiats) – unidades estruturais de habitats em ambientes lóticos visualmente distintas com aparente uniformidade física.

Mophological species concept (Conceito de espécie morfológica)– identificação de táxons baseada em critérios morfológicos, principalmente discontinuidades em séries de biótipos. Embora seja um conceito bastante criticável (ver discussão em Heywood & Watson, 1995), atualmente ele é o único operacional para trabalhar com ecologia de Chironomidae na região Neotropical.

Perturbation, Disturbance, and Response (perturbação, distúrbio e resposta) – Um distúrbio ocorre quando forças potencialmente modificadoras são aplicadas em populações, comunidades ou ecossistemas. Perturbação descreve a combinação de causas e efeitos. Distúrbio se refere à causa de uma perturbação e a resposta ao efeito do distúrbio.

Species richness (riqueza de espécies) – número de espécies numa região ou área. Este termo é muitas vezes utilizado como medida de diversidade, mas tecnicamente representa apenas um aspecto da diversidade.

Tabela 1. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

Tabela 2. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

Tabela 3. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

Tabela 1. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

| | P. E. Jaraguá | | | | | | Picinguaba | | | | | |
| | Córrego 1 | | Córrego 2 | | Córrego 3 | | Córrego 1 | | Córrego 2 | | Córrego 3 | |
	C1	R1	C2	R2	C3	R3	C6	R6	C5	R5	C4	R4
Ablabesmyia sp. 1					2	8						5
Ablabesmyia sp. 2												1
Coelotanypus sp. 1												
Djalmabatista sp. 1		1	1	10								
Djalmabatista sp. 2												1
Guassutanypus oliverai												
Larsia spp.					3			3	2			
Labrundinia sp. 1		4										2
Fittkauimyia sp. 1												1
Pentaneura spp.		1										
Zavrelimyia sp. 1				3								
Chironomus spp.					1	1		1				12
Cryptochironomus sp. 1						17						
C. *Harnischia* sp. 1												1
C. *Harhischia* sp. 2												
C. *Harhischia* sp. 3												
Endotribelos spp		4		12	1	2		1		3		2
Lauterborniella sp. 1												
Paratendipes sp. 1				1	6			1				
Paratendipes sp. 2										1		
Polypedilum sp. 1		7			5	21						
Polypedilum sp. 2				5								
Polypedilum sp. 3												9
Polypedilum sp. 4												
Polypedilum gr. fallax												
Polypedilum sp. 5												
Pseudochironomini sp. 1							2		2	11	1	
Stenochironomus spp.			1					1		1	2	2
Rheotanytarsus sp. 1	5		165		40	2			1		36	
Rheotanytarsus sp. 2					1	1						
Rheotanytarsus sp. 3	9											
Stempellina sp. 1												
Stempellinella sp. 1						1						

Cont. anexo 1

| | P. E. Jaraguá | | | | | | Picinguaba | | | | | |
| | Córrego 1 | | Córrego 2 | | Córrego 3 | | Córrego 1 | | Córrego 2 | | Córrego 3 | |
	C1	R1	C2	R2	C3	R3	C6	R6	C5	R5	C4	R4
Tanytarsini sp. 1		22										
Tanytarsini sp. 2							1			1	3	
Tanytarsini sp. 3			1							2		1
Tanytarsini sp. 4												3
Tanytarsini sp. 5		1		69							1	53
Tanytarsini sp. 6			2			5					4	
Tanytarsini sp. 7			4		167				7	1	5	
Tanytarsini sp. 8				57	1	1		1			1	
Tanytarsini sp. 9						2						2
Tanytarsini sp.10						8						
Tanytarsini sp.11												
Tanytarsini sp.12												
Tanytarsini sp.13		1				1						
Tanytarsini sp. 14		1										
Tanytarsini sp. 15												
Tanytarsini sp. 16												
Zavreliella sp. 1												
Xestochironomus sp. 1												
Corynoneura sp. 1	2	1			31	1	1		1		1	
Corynoneura sp. 2										1		
Cricotopus sp. 1	1								3			
Gymnometriocnemus sp. 1											1	
Lopescladius sp. 1		1									5	1
Metriocnemus sp. 1										1		
Nanocladius sp. 1	1											
Parametriocnemus sp. 1	10	1	2		1		1				3	
near *Stackelbergina* sp. 1												
Thienemanniella sp. 1	20		3		1				1			
Rheocricotopus sp. 1			1									
Orthocladiinae sp. 1												
Orthocladiinae sp. 2												
Orthocladiinae sp. 3												
Paraphaenocladius sp. 1												

Tabela 2. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

	Cubatão						São Carlos					
	Córrego 1		Córrego 2		Córrego 3		Córrego 1		Córrego 2		Córrego 3	
	C9	R9	C7	R7	C8	R8	C12	R12	C11	R11	C10	R10
Ablabesmyia sp. 1				2		2		15		31	8	18
Ablabesmyia sp. 2		2										
Coelotanypus sp. 1									1	24		3
Djalmabatista sp. 1		2		2		1		4		1	1	34
Djalmabatista sp. 2												
Guassutanypus oliverai												1
Larsia spp.			2	1	3			1	30	201	4	
Labrundinia sp. 1				2				5			4	2
Fittkauimyia sp. 1				2		1						
Pentaneura spp.							1	2				
Zavrelimyia sp. 1				1								
Chironomus spp.												
Cryptochironomus sp. 1						1						
C. *Harnischia* sp. 1												
C. *Harhischia* sp. 2												1
C. *Harhischia* sp. 3												10
Endotribelos spp		2		3		3		3				6
Lauterborniella sp. 1										4		
Paratendipes sp. 1												
Paratendipes sp. 2												
Polypedilum sp. 1								16		6		
Polypedilum sp. 2				1		9						
Polypedilum sp. 3												
Polypedilum sp. 4												
Polypedilum gr. fallax												
Polypedilum sp. 5										1		
Pseudochironomini sp. 1					1	1	1		1			
Stenochironomus spp.				1			3		2	1	6	
Rheotanytarsus sp. 1	5	1			65		28		36			
Rheotanytarsus sp. 2							6					
Rheotanytarsus sp. 3							1					
Stempellina sp. 1		1										
Stempellinella sp. 1									2	1	21	

| | Cubatão | | | | | | São Carlos | | | | | |
| | Córrego 1 | | Córrego 2 | | Córrego 3 | | Córrego 1 | | Córrego 2 | | Córrego 3 | |
	C9	R9	C7	R7	C8	R8	C12	R12	C11	R11	C10	R10
Tanytarsini sp. 1										64		
Tanytarsini sp. 2										1		
Tanytarsini sp. 3												
Tanytarsini sp. 4				1		1				1		
Tanytarsini sp. 5	1	3		3	1	1			4			
Tanytarsini sp. 6												
Tanytarsini sp. 7	3		33		10		4					
Tanytarsini sp. 8						10						
Tanytarsini sp. 9				1		3				39		
Tanytarsini sp.10										20		
Tanytarsini sp.11												2
Tanytarsini sp.12											10	8
Tanytarsini sp.13												
Tanytarsini sp. 14												
Tanytarsini sp. 15							6	5			4	7
Tanytarsini sp. 16									1			
Zavreliella sp. 1									2	1		
Xestochironomus sp. 1							1					
Corynoneura sp. 1				1							4	1
Corynoneura sp. 2												
Cricotopus sp. 1			3		1		1					
Gymnometriocnemus sp. 1												
Lopescladius sp. 1					1							
Metriocnemus sp. 1												
Nanocladius sp. 1			7				9	3	3	2		
Parametriocnemus sp. 1	7		6	1	2		5		5	1		
near *Stackelbergina* sp. 1			1									
Thienemanniella sp. 1	10		2	6	3		101	3	65	1	1	
Rheocricotopus sp. 1	1				1							
Orthocladiinae sp. 1											6	
Orthocladiinae sp. 2							1					
Orthocladiinae sp. 3							1				1	
Paraphaenocladius sp. 1											3	

Tabela 3. Larvas de Chironomidae coletadas nos córregos estudados do Estado de São Paulo, Brasil (dados usados nas análises do capítulo 2).

| | Cananéia | | | | | |
| | Córrego 3 | | Córrego 2 | | Córrego 1 | |
	C13	R13	C14	R14	C15	R15
Ablabesmyia sp. 1						
Ablabesmyia sp. 2						3
Coelotanypus sp. 1						
Djalmabatista sp. 1						
Djalmabatista sp. 2						
Guassutanypus oliverai						
Larsia spp.	10	1				
Labrundinia sp. 1	4					
Fittkauimyia sp. 1						
Pentaneura spp.						1
Zavrelimyia sp. 1				1		
Chironomus spp.				2		
Cryptochironomus sp. 1						
C. *Harnischia* sp. 1	1					2
C. *Harhischia* sp. 2						
C. *Harhischia* sp. 3						
Endotribelos spp	1	6		1		
Lauterborniella sp. 1						
Paratendipes sp. 1	2	1				
Paratendipes sp. 2						
Polypedilum sp. 1						
Polypedilum sp. 2		1		5	1	
Polypedilum sp. 3						
Polypedilum sp. 4	2	6	2	16	0	14
Polypedilum gr. fallax	1					
Polypedilum sp. 5						
Pseudochironomini sp. 1			1			
Stenochironomus spp.	1	2				3
Rheotanytarsus sp. 1	89	1	51		8	
Rheotanytarsus sp. 2						
Rheotanytarsus sp. 3						
Stempellina sp. 1						
Stempellinella sp. 1						

| | Cananéia | | | | | |
| | Córrego 3 | | Córrego 2 | | Córrego 1 | |
	C13	R13	C14	R14	C15	R15
Tanytarsini sp. 1						
Tanytarsini sp. 2						
Tanytarsini sp. 3				1		11
Tanytarsini sp. 4				1		
Tanytarsini sp. 5	1	4		1	1	16
Tanytarsini sp. 6						
Tanytarsini sp. 7	3		2		3	
Tanytarsini sp. 8		7		16	1	
Tanytarsini sp. 9				2		
Tanytarsini sp.10						
Tanytarsini sp.11						
Tanytarsini sp.12						
Tanytarsini sp.13						
Tanytarsini sp. 14						
Tanytarsini sp. 15						
Tanytarsini sp. 16						
Zavreliella sp. 1						
Xestochironomus sp. 1						
Corynoneura sp. 1	1					
Corynoneura sp. 2						
Cricotopus sp. 1						
Gymnometriocnemus sp. 1						
Lopescladius sp. 1	1	1				
Metriocnemus sp. 1						
Nanocladius sp. 1		1				
Parametriocnemus sp. 1	15		21		5	
near *Stackelbergina* sp. 1						2
Thienemanniella sp. 1	11		4		4	
Rheocricotopus sp. 1						
Orthocladiinae sp. 1						
Orthocladiinae sp. 2						
Orthocladiinae sp. 3						
Paraphaenocladius sp. 1						

Manuscrito intitulado "Bayesian estimation of biodiversity through multinominal incomplete distribution" com detalhamento do método estatístico utilizado nas análises do capítulo sobre riqueza de espécies de Chironomidae em córregos de baixa ordem na Mata Atlântica do sudeste brasileiro.

Bayesian estimation of biodiversity through multinomial incomplete distribution

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Abstract

We propose a Bayesian model for estimating the number of species in a habitat where species are supposed having different probability of being ob-

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served. The model proposed is an adaptation of Derenzo- Hildebrand model for estimating the number of particles detected by scanners. We apply the methodology to a real data set estimating the number of nanoinvertebrate species in Brazilian Atlantic forest streams.

1. Introduction

We propose a Bayesian model for estimating the number of species in a habitat where species are supposed having different probability of being observed. The model proposed here is an adaptation of the Derenzo-Hildebrand model.

The Derenzo-Hildebrand model is used for detecting particles in photographic films using a number of scanners. This model consider each particle with different visibility, here represented by the probability that a scanner detect the particle. The same model is considered later by Sanathanan (1972a 1972b and 1973).

The method is based on a fixed number of samples. At each sample the presence of a species is registered has a binary variable. At the end of each sample the number of distinct species is registered.

We use Bayesian inference to obtain the posterior distribution for the total number of species and then producing a summary with mean, mode and credibility intervals for the the number species in the considered habitat. We also

consider three different *a priori* distributions for the number of species and a beta distribution for the probability of seeing a species in a sample. The sensibility of the estimators to the choice of the *a priori* distribution is verified through a simulation study.

We apply the proposed method to estimate the number of macroinvertebrate species in three streams located in the Jaraguá Park, state of São Paulo, Brazil. The data was previously analysed in Roque *et al.* (2003), with other purposes, not estimating the number of species, where a more detailed description, including a map of the region, can be found.

2. The Derenzo-Hildebrand model

A habitat with N species, N unknown, is observed in k independent samples. It is assigned to each species i a k-dimenssional vector of random variables, also named history, $X_i = (X_{i1}, X_{i2}, ..., X_{ik})$, definided as $X_{ij} = 1$ if species i is observed at sample j and $X_{ij} = 0$ otherwise. Consider also $\theta_{ij}, 0 < \theta_{ij} < 1$, the probability of species i being observed in sample j and let $\boldsymbol{\theta} = \{\theta_{ij}; 1 \leq i \leq N, 1 \leq j \leq k\}$.

The probability functions of X_{ij} are

$$P\left(X_{ij} = x \mid N, \boldsymbol{\theta}\right) = \theta_{ij}^x \left(1 - \theta_{ij}\right)^{1-x} I_{\{0,1\}}\left(x\right),$$

where $1 \leq i \leq N$, $1 \leq j \leq k$. We suppose that the random variables X_{ij} are independent.

Then, the random vectors $X_i = (X_{i1}, X_{i2}, ..., X_{ik})$ are independent and assume values in

$$\Omega = \{\boldsymbol{\omega} = (\omega_1, \omega_2, ..., \omega_k) \; : \; \omega_j = 0, 1; \; j = 1, 2, ..., k\}.$$

Consider l the number of elements in Ω and let $\boldsymbol{\omega}_1, \boldsymbol{\omega}_2, ..., \boldsymbol{\omega}_l$ the elements in Ω, where

$\boldsymbol{\omega}_r = (\omega_{r1}, \omega_{r2}, ..., \omega_{rk})$, $r = 1, 2, ..., l - 1$ and $\boldsymbol{\omega}_l = (0, 0, ..., 0)$. Then $l = 2^k$ and, for each $i = 1, 2, ..., N$, we have

$$
\begin{aligned}
p_{ir}(\boldsymbol{\theta}) &= P(X_i = \boldsymbol{\omega}_r \mid N, \boldsymbol{\theta}) \\
&= P((X_{i1}, X_{i2}, ..., X_{ik}) = (\omega_{r1}, \omega_{r2}, ..., \omega_{rk}) \mid N, \boldsymbol{\theta}) \\
&= \prod_{j=1}^{k} P(X_{ij} = \omega_{rj} \mid N, \boldsymbol{\theta}) = \prod_{j=1}^{k} \theta_{ij}^{\omega_{rj}} (1 - \theta_{ij})^{1 - \omega_{rj}},
\end{aligned}
$$

for $r = 1, 2, ..., l$.

Let $n_r = \sum_{i=1}^{N} I_{\{\boldsymbol{\omega}_r\}}(X_i)$ be the number of species that have the history $\boldsymbol{\omega}_r$, for $r = 1, 2, ..., l$, and $n = \sum_{r=1}^{l-1} n_r$ the number of distinct species observed in the k

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samples. Let $n_l = N - \sum_{r=1}^{l-1} n_r = N - n$ be the number of species whose history is $\boldsymbol{\omega}_l$, the number of unobserved species.

The probability distribution for $(n_1, n_2, ..., n_{l-1}, N - n)$, given N and $\boldsymbol{\theta}$, is given by

$$P(n_1, n_2, ..., n_{l-1}, N - n \mid N, \boldsymbol{\theta}) = \sum \prod_{i_1 \in A_1} p_{i_1 1}(\boldsymbol{\theta}) \prod_{i_2 \in A_2} p_{i_2 2}(\boldsymbol{\theta}) ...$$
$$\prod_{i_{l-1} \in A_{l-1}} p_{i_{l-1}(l-1)}(\boldsymbol{\theta}) \prod_{i_l \in A_l} p_{i_l l}(\boldsymbol{\theta}), \quad (2.1)$$

where $\sum$ covers all disjoint subsets $A_1, A_2, ..., A_l$ of $\{1, 2, ..., N\}$ such that the number of elements in A_r is n_r. The set A_r represents the set of species that have history $\boldsymbol{\omega}_r$ and the number of elements in the sum $\sum$ is

$$\binom{N}{n_1} \binom{N - n_1}{n_2} \binom{N - (n_1 + n_2)}{n_3} ... \binom{N - (n_1 + n_2 + ... + n_{l-1})}{N - n} =$$
$$= \frac{N!}{n_1! n_2! ... (N - n)!},$$

where $n = n_1 + n_2 + ... + n_{l-1}$.

The Derenzo-Hildebrand model considers each species having the same probability of being observed in a sample, that is $\theta_{ij} = \theta_i$, for $1 \leq i \leq N$; $1 \leq j \leq k$.

The parameter $\boldsymbol{\theta} = (\theta_1, \theta_2, ..., \theta_N)$ is the vector with the probability of all species in the habitat.

Considering $\mathcal{D}$ the observed data, $\mathcal{D} = (n_1, n_2, ..., n_{l-1})$, follows from (1) the likelihooh function

$$L(N, \boldsymbol{\theta} \mid \mathcal{D}) = \sum \prod_{r=1}^{l} \prod_{i_r \in A_r} \theta_{i_r}^{\sum_{j=1}^{k} \boldsymbol{\omega}_{rj}} (1 - \theta_{i_r})^{k - \sum_{j=1}^{k} \boldsymbol{\omega}_{rj}},$$

for $N \geq n = \sum_{j=1}^{l-1} n_j$, $0 < \theta_i < 1$, $i = 1, 2, ..., N$.

3. Bayesian model

Suppose $\pi(N)$ a prior distribution for N, $N = 1, 2, ...$, and, for a given N, consider $\theta_1, \theta_2, ..., \theta_N$ independent random varibles with Beta distribution with known parameters α e β, $\alpha > 0$ e $\beta > 0$. The joint prior distribution for $(N, \boldsymbol{\theta})$ is

$$\pi(N, \boldsymbol{\theta}) = \pi(\boldsymbol{\theta} \mid N) \pi(N) = \prod_{i=1}^{N} \frac{1}{B(\alpha, \beta)} \theta_i^{\alpha-1} (1 - \theta_i)^{\beta-1} \pi(N),$$

for $0 < \theta_i < 1$, $i = 1, 2, ..., N$; $N = 1, 2, ...$.

The posterior distribution for $(N, \boldsymbol{\theta})$ is then

$$
\begin{aligned}
\pi\left(N, \boldsymbol{\theta} \mid \mathcal{D}\right) \quad &\propto \quad L\left(N, \boldsymbol{\theta} \mid \mathcal{D}\right) \pi\left(N, \boldsymbol{\theta}\right) \\
&= \quad \sum \prod_{r=1}^{l} \prod_{i_r \in A_r} \frac{\theta_{i_r}^{\alpha + \sum_{j=1}^{k} \omega_{rj} - 1} \left(1 - \theta_{i_r}\right)^{\beta - \sum_{j=1}^{k} \omega_{rj} + k - 1}}{B\left(\alpha, \beta\right)} \pi\left(N\right), \quad (3.1)
\end{aligned}
$$

where $N \geq n$, $0 < \theta_i < 1$, $i = 1, 2, ..., N$.

Let x_j be the number of species observed in j samples, $1 \leq j \leq k$. The posterior marginal distribution for N can be obtained by integrating out the θ_i's,

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$$\pi\left(N|\mathcal{D}\right) = \int_0^1 ... \int_0^1 \pi\left(N, \boldsymbol{\theta} \,|\mathcal{D}\right) d\theta_1 ... d\theta_N$$

$$\propto \sum \prod_{r=1}^l \prod_{i_r \in A_r} \frac{B\left(\alpha + \sum_{j=1}^k \omega_{rj}, \beta - \sum_{j=1}^k \omega_{rj} + k\right)}{B\left(\alpha, \beta\right)} \pi\left(N\right)$$

$$= \sum \prod_{r=1}^l \left(\frac{B\left(\alpha + \sum_{j=1}^k \omega_{rj}, \beta - \sum_{j=1}^k \omega_{rj} + k\right)}{B\left(\alpha, \beta\right)}\right)^{n_r} \pi\left(N\right)$$

$$= \frac{N!}{n_1! n_2! ... n_{l-1}! \left(N - n\right)!} \left(\frac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}\right)^{N-n}$$

$$\prod_{j=1}^k \left(\frac{B\left(\alpha + j, \beta - j + k\right)}{B\left(\alpha, \beta\right)}\right)^{x_j} \pi\left(N\right)$$

$$\propto \binom{N}{n} \left(\frac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}\right)^N \pi\left(N\right),$$

for $N \geq n$, and B(.,.) is Beta function.

Therefore the posterior marginal for N is

$$\pi\left(N|n\right) = C\left(\alpha, \beta, k, n\right)^{-1} \binom{N}{n} \left(\frac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}\right)^N \pi\left(N\right), \qquad (3.2)$$

$N \geq n$, where $C\left(\alpha, \beta, k, n\right)$ is the normalizing constant, given by

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$$C(\alpha, \beta, k, n) = \sum_{N \geq n} \binom{N}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^N \pi(N).$$

4. The *a priori* distribution

Following we present three choices of the *a priori* distribution for the number of species N. We consider the uniform distribution on the positive integers, the Jeffreys' and the Poisson distributions. Following we discuss how to choose α and β.

4.1. The uniform *a priori* distribution for N

For N with uniform *a priori* distribution consider $\pi(N) = 1$, for $N = 1, 2, ...$, an improper distribution.

From (3.2) it follows that

$$
\begin{aligned}
C\left(\alpha, \beta, k, n\right) &= \sum_{N \geq n} \binom{N}{n} \left(\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{N} \\
&= \sum_{j=0}^{\infty} \binom{j+n}{n} \left(\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{j+n} \\
&= \left(\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{n} \sum_{j=0}^{\infty} \binom{-n-1}{j} \left(-\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{j} \\
&= \left(\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{n} \left(1 - \frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{-n-1},
\end{aligned}
$$

and the *a posteriori* distribution for N is

$$
\pi\left(N|n\right) = \binom{N}{n} \left(1 - \frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{n+1} \left(\frac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}\right)^{N-n}, \qquad (4.1)
$$

for $N \geq n$.

The *a posteriori* distribution for $N-n$ is a negative binomial distribution with parameters $n+1$ and $1 - \dfrac{B\left(\alpha, \beta+k\right)}{B\left(\alpha, \beta\right)}$.

From the standard results for the negative binomial distribution follows that:

(i) the *a posteriori* mean for N is

$$E\left(N \mid n\right) = n + \frac{n+1}{\dfrac{B\left(\alpha, \beta\right)}{B\left(\alpha, \beta + k\right)} - 1};$$

(ii) the *a posteriori* variance for N is

$$Var\left(N|n\right) = \left(n+1\right) \frac{\dfrac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}}{\left(1 - \dfrac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}\right)^{2}};$$

(iii) and if $\dfrac{n}{1 - \dfrac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}}$ is not an integer, where $[y]$ is the greatest integer

less than or equal to y, the *a posteriori* mode is $\left[\dfrac{n}{1 - \dfrac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}}\right]$. Otherwise,

if $M = \dfrac{n}{1 - \dfrac{B\left(\alpha, \beta + k\right)}{B\left(\alpha, \beta\right)}}$ is an integer, we have two modes, $M - 1$ and M .

4.2. The Jeffreys *a priori* distribution for N

The Jeffreys *a priori* distribution is defined as, $\pi(N) = \dfrac{1}{N}$, for $N = 1, 2, ...$

From (3.2) it follows that the normalizing constant is

$$
\begin{aligned}
C(\alpha, \beta, k, n) &= \sum_{N \geq n} \binom{N}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^N \frac{1}{N} \\
&= \frac{1}{n} \sum_{N \geq n} \binom{N-1}{n-1} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^N \\
&= \frac{1}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \sum_{j=0}^{\infty} \binom{j+n-1}{n-1} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^j \\
&= \frac{1}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \sum_{j=0}^{\infty} \binom{-n}{j} \left(-\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^j \\
&= \frac{1}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \left(1 - \frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^{-n},
\end{aligned}
$$

and the *a posteriori* distribution for N is then given by

$$
\pi(N \mid n) = \binom{N-1}{n-1} \left(1 - \frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^{N-n}, \qquad (4.2)
$$

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$N \geq n$. The *a posteriori* distribution for $N - n$, given $n \geq 2$, is the negative

binomial distribution with parameters n and $1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}$.

From the standard results of the negative binomial distribution it follows that:

(i) the *a posteriori* mean for N is

$$E(N \mid n) = \frac{n}{1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}};$$

(ii) the *a posteriori* variance for N is

$$Var(N \mid n) = \frac{n \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}{\left(1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}\right)^2};$$

(iii) if $\dfrac{n - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}{1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}$ is not an integer, the *a posteriori* mode is

$\left[\dfrac{n - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}{1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}\right]$; otherwise, if $M' = \dfrac{n - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}{1 - \dfrac{B(\alpha, \beta + k)}{B(\alpha, \beta)}}$ is integer, then

there are two modes, $M' - 1$ and M'.

4.3. The Poisson *a priori* distribution for N

The Poisson *a priori* distribution is defined as $\pi(N) = \dfrac{e^{-\lambda}\lambda^N}{N!}$, for $N = 0, 1, 2, ...$ and

known λ. From (3.2) it follows that the normalizing constant is

$$
\begin{aligned}
C(\alpha, \beta, k, n) &= \sum_{N \geq n} \binom{N}{n} \left(\frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^N \frac{e^{-\lambda}\lambda^N}{N!} \\
&= e^{-\lambda} \sum_{j=0}^{\infty} \binom{j+n}{n} \left(\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^{j+n} \frac{1}{(j+x)!} \\
&= \frac{e^{-\lambda}}{n!} \left(\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \sum_{j=0}^{\infty} \frac{1}{j!} \left(\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^j \\
&= \frac{e^{-\lambda}}{n!} \left(\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^n \exp \left\{ \frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right\},
\end{aligned}
$$

and the *a posteriori* distribution for N is then given by

$$
\pi(N|n) = \frac{1}{(N-n)!} \exp \left(-\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right) \left(\frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)} \right)^{N-n}, \qquad (4.3)
$$

for $N \geq n$.

The *a posteriori* distribution for $N - n$, given $n \geq 1$ and λ, is Poisson with mean and variance $\dfrac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)}$. It follows that:

(i) the *a posteriori* mean for N is

$$E(N \mid n) = n + \frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)};$$

(ii) the *a posteriori* mean for N is

$$Var(N \mid n) = \frac{\lambda B(\alpha, \beta + k)}{B(\alpha, \beta)};$$

(iii) the *a posteriori* mode for N is $\left[n + \lambda \frac{B(\alpha, \beta + k)}{B(\alpha, \beta)} \right]$ if $n + \lambda \frac{B(\alpha, \beta + k)}{B(\alpha, \beta)}$ is not an integer. Otherwise, if $M'' = n + \lambda \frac{B(\alpha, \beta + k)}{B(\alpha, \beta)}$ is an integer, there are two modes, $M'' - 1$ and M'' .

4.4. Choosing α and β

Parameters α and β specify the beta *a priori* distribution for the θ_i's, $i = 1, 2, ..., N$. Thus information like "since they are there, species are easy to observe" or "even if they are there, species are hard to observe" can be translated into *a priori* distribution. To help in this task we provide in Figure 1 a sample of densities of beta distributions. The pair over each graphic correponds to the (α, β) parameters. The density corresponding to $(\alpha, \beta) = (1, 1)$ distribute evenly the probability observing the species over the interval $(0,1)$, this is a good choice

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when there is no information about the probability of observing the species. The density where $(\alpha, \beta) = (2, 2)$ concentrate the probability of observing the species near 0.5. The density where (α, β) are (2,3) or (1.5,2) bring the probabilities near zero and (α, β) equal (3,2) or (2,1.5) bring the probabilities near 1, in both cases with different degrees of nearness. These are just a few examples, different choices of (α, β) will lead to different shapes of density covering a wide range of possibilities.

Figure 1 about here

5. Simulation

Before applying the method described above to a real data set we develop a simulation study in order to know how the model would answer to different situations.

In this context, it is interesting to know how the model answer to different choices of *a priori* distributions for the θ_i's. Thus, we generate data sets of observations with different values of the pair of parameters (α, β), the values used for simulations are $(1, 1)$, $(2, 4)$ and $(4, 2)$.

We develop simulations with known number of species $N = 100$, and number of samples $k = 4$. For each pair (α, β) we generate N values of θ_i, for $i = 1, 2, ..., N$,

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with distribution $Beta(\alpha, \beta)$. Following we generate k samples with probability θ_i and consider species i observed if at least one of the k samples is equal to one. The number of observed species is then calculated.

Having generated the samples we apply the method described above for the uniform *a priori* distribution for k. The results of this one case simulation is in Table 1. In the first column are values of each pair (α, β) used for the generations of the θ_i's, in the second column are the values of each pair (α, β) used for the *a priori* distribution and in the third column is the number of different species generated in each case. In the following columns are the results of the application of the method, ie, the mean, the mode, the credibility interval and the probability of the credibility interval repectively. Althought our targeting probability interval were 0.95, as the posterior marginal distribution is discrete the resulting probability presents small variations around this value.

Table 1 about here

As we can observe on Table 1, the choice of the parameters of the *a priori* distribution does have influence on the estimation of the number of species. When the *a priori* distribution has suitable parameters (the parameters (α, β) used for generation and those used for the *a priori* distribution are the same) the method provides good estimates and the credibility intervals contains the true values of

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the parameters, $N = 100$. The same does not occur when the parameters of the *a priori* distribution are baddly chosen. This result emphasizes the importance of the choice of the paramenters of the *a priori* distribution.

The same simulations were done for Jeffreys and Poisson *a priori* distributions for N. As the results are similar to those showed on Table 1, they are not presented here.

Another kind of simulation is done to show the estimation of the number of species as the number of samples increases. The values used for this simulation are $N = 100$, $(\alpha, \beta) = (1.2, 2)$ for generating the data and $(\alpha, \beta) = (1, 1)$ for specifying the *a priori* distribution. Figure 2 shows the cumulative number of new species (solid line); the mode is the point estimate for the number of species (dashed line) and estimates of the 0.95 credibility interval (dotted lines). The dot and dash line shows the target value, $N = 100$. As we can see, the estimates produces good estimates, even for small values of k, and the size of the credibility interval gets narrower as k gets bigger.

The cumulative number of new species is sometimes used as an estimate for the number of species. The solid line indicates that it gets closer to the target value, $N = 100$, as k increases, however it needs more samples to get similar performance for small values of k.

Figure 2 about here

6. Application

Now we apply the proposed method to estimate the number of macroinvertebrate species in three streams (Pison, Pedras, and Canabineiros) in Jaraguá State Park, State of São Paulo, Brazil. The macroinvertebrates were collected in three meso-habitat (riffle, run and pool) at each stream using a Suber collector in a stratified sampling design, totalizing 36 samples (Roque et al., 2002). For each combination of stream and habitat four samples were collected, $k = 4$. Given the difference between these habitats they are treated separately.

In our study, the values of the parameters of the *a priori* distribution for the θ_{ij}'s are chosen $(\alpha, \beta) = (1, 1)$, which corresponds to the uniform distribution. The reason to choose these values is the lack of *a priori* information about the region being studied.

The observed data and results of the application of the method are presented in Table 2. Among the results, we can point out the differences in the expected number of species in the mesohabitats, particularly the high species richness in the riffles of the canabineiro stream, which could be very usefull information, for example, to plan next biodiversity surveys in the area, saving money and time.

Table 2 about here

7. Discussion

The method described here is based on the assumption of total independence among samples and among species. Among its advantages, we can include its simplicity and facility of implementation. Among its pitfalls is the sensitivity to the choice of parameters (α, β). An interesting aspect of the proposed method is that it allows to include *a priori* information when it is available. As seeing above, this is specially relevant for the *a priori* distribution of the θ_i's. The choice of parameters (α, β) are discussed in Section 4.4.

The use of Bayesian approach in quantifying species richness has yet a great potential to be developed. Further studies are needed to incorporate quantitative information (e.g. Solow, 1994). Furthermore the computational difficulties (no statistical package is available for biologists) are also challenges to be overcome.

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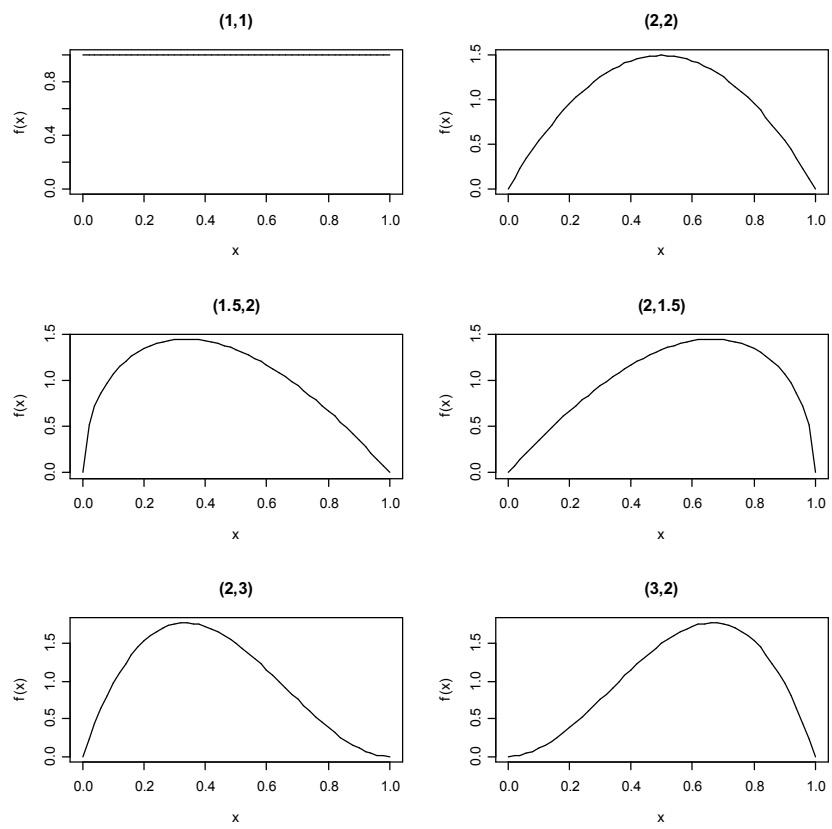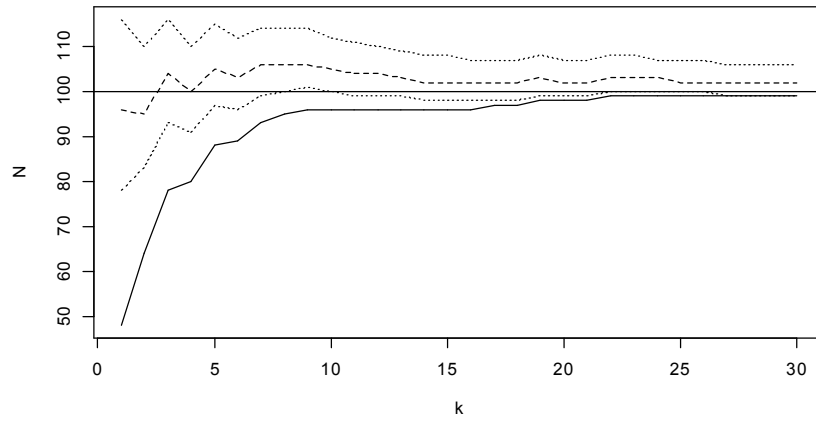Figure 7.1: Possible choices of the *a priori* distribution.

Figure 7.2: Simulations for k=1,2,...,30.

Table 7.1: Results of simulation study.

(α, β) used for simulation	(α, β) for *a priori* distribution	Number of observed species	Mean	Mode	Credibility interval	Probability of credibility. interval.
1,1	1,1	82	102.75	102	(93,112)	0.951
1,1	2,2	82	95.83	95	(89,104)	0.955
1,1	2,1.5	82	91.73	91	(86,98)	0.955
1,1	1.5,2	82	104.48	104	(95,115)	0.952
1,1	3,2	82	88.38	88	(84,94)	0.968
1,1	2,3	82	104.64	104	(95,115)	0.951

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Table 7.2: Results of the analysis for uniform *a priori* distribution for N.

Stream	habitat	Number of observed species	Mean	Mode	Credibility interval	Probability of credibility. interval.
Pison	riffle	29	36.50	36	(31,42)	0.955
Pison	run	36	45.25	45	(39,52)	0.965
Pison	pool	34	42.75	42	(37,49)	0.956
Pedras	riffle	35	44.00	43	(38,50)	0.952
Pedras	run	30	37.75	37	(32,44)	0.968
Pedras	pool	34	42.75	42	(37,49)	0.956
Canabineiros	riffle	51	64.00	63	(57,72)	0.956
Canabineiros	run	42	52.75	52	(46,60)	0.963
Canabineiros	pool	43	54.00	53	(47,61)	0.960