Universidade Federal de São Carlos
Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Integrando processos ambientais e espaciais na ecologia de comunidades aquáticas em escala regional

Candidato: Tadeu de Siqueira Barros

Orientadora: Profa. Dra. Susana Trivinho Strixino
Universidade Federal de São Carlos

Co-orientador: Prof. Dr. Luis Mauricio Bini
Universidade Federal de Goiás

Universidade Federal de São Carlos
Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Integrando processos ambientais e espaciais na ecologia de comunidades aquáticas em escala regional

Tadeu de Siqueira Barros

Tese apresentada ao programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de doutor em Ciências, área de concentração em Ecologia e Recursos Naturais.

São Carlos, 2010.

Ficha catalográfica elaborada pelo DePT da
Biblioteca Comunitária/UFSCar

B277ip

Barros, Tadeu de Siqueira.
Integrando processos ambientais e espaciais na ecologia de comunidades aquáticas em escala regional / Tadeu de Siqueira Barros. -- São Carlos : UFSCar, 2010.
123 f.

Tese (Doutorado) -- Universidade Federal de São Carlos, 2010.

1. Ecologia. 2. Metacomunidades. 3. Nicho (Ecologia). 4.Teoria neutra. 5. Dispersão. 6. Insetos aquáticos. I. Título.

CDD: 574.5 (20ª)

Tadeu de Siqueira Barros

Integrando processos ambientais e espaciais na ecologia de comunidades aquáticas em escala regional

Tese apresentada à Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Doutor em Ciências.

Aprovada em 25 de junho de 2010

BANCA EXAMINADORA

Presidente ______________________________
Profa. Dra. Susana Trivinho Strixino
(Orientadora)

1º Examinador Odete Rocha ______________________________
Profa. Dra. Odete Rocha
PPGERN/UFSCar

2º Examinador Alaide Ap. F. Gessner ______________________________
Profa. Dra. Alaíde Ap. Fonseca Gessner
PPGERN/UFSCar

3º Examinador ______________________________
Prof. Dr. Luís Maurício Bini
UFGO/Goiânia-GO

4º Examinador Pitágoras C. Bispo ______________________________
Prof. Dr. Pitágoras da Conceição Bispo
UNESP/Assis-SP

AGRADECIMENTOS

Aos meus dois mestres, Susana Trivinho Strixino e Luis Mauricio Bini por terem me dado a oportunidade de enxergar tudo “sobre ombros de gigantes”. Vocês são grandes exemplos de vida profissional e pessoal para mim. Espero poder oferecer aos meus alunos a mesma dignidade e respeito que vocês me ofereceram. Essa tese é em parte também dedicada à ambos;

aos meus outros professores, em especial à José Alexandre Diniz Filho e Karl Cottenie, pelos importantíssimos ensinamentos e oportunidades;

aos amigos e parceiros de trabalho – perdoem-me caso esqueça alguns nomes – Mateus, Francisco, Kpilé, Marcão, André, João, Lud, Fernanda(s), Carina, Neander, Delano, Fred, Leandro, Diler, Fabião, Bruno, Guilherme, Natália, Xubaca, Nacho...;

ao pessoal de Guelph por terem tornado a estadia no Canadá tão prazerosa;

ao PPG-ERN, CNPq, UFSCar e Universidade de Guelph pela logística e apoio financeiro;

a Cris e toda minha família pelo apoio irrestrito durante toda essa caminhada.

SUMÁRIO

1. Apresentação

Conforme descrito no item 2 das **normas para defesa pública de tese** (Regimento Interno PPGERN – Normas Complementares – 2008) que prevê que:

"A elaboração do documento final de Dissertação/Tese para defesa pública, poderá ser apresentado: no formato descritivo tradicional ou na forma de um conjunto de trabalhos científicos, redigidos para publicação em revista nacional ou estrangeira. Os trabalhos redigidos, em língua portuguesa ou inglesa, **deverão estar em seu formato final de encaminhamento à publicação, dentro dos aspectos, itens e normas definidas pela revista, nacional ou estrangeira, a que se pretende a futura publicação**",

esta tese será apresentada na forma de um conjunto de trabalhos científicos, redigidos para publicação em revista estrangeira.

O texto está dividido em uma introdução geral em que eu apresento as bases teóricas que motivaram e fundamentaram o desenvolvimento do trabalho, três capítulos em formato de artigo – dois dos quais já publicados e o último submetido, e uma conclusão geral em que faço uma síntese e tento dar coesão entre os capítulos.

Os capítulos são independentes no que diz respeito a objetivos e métodos, portanto, não há uma secção única sobre esses temas. Apesar de estarem em formato de artigos, considero que estão presentes os detalhes necessários para que o leitor tenha um entendimento efetivo dos mesmos. Seguindo as normas do PPG-ERN, cada capítulo está no formato final definido pela revista, portanto, não há um padrão único para citação e referências bibliográficas. A única exceção, que, pensando no conforto do leitor, eu me dei o direito de fazer, diz respeito a formatação e localização de figuras e tabelas. As revistas que submeti os manuscritos pedem figuras em tabelas em folhas separadas no final do texto. Julguei que a tese ficaria mais difícil de ser lida nesse formato, portanto optei por colocá-las no meio do texto, próximas dos locais onde são citadas.

Antes de prosseguir para a tese propriamente dita, quero compartilhar com o leitor um pouco do histórico do desenvolvimento da mesma e também de outros aspectos relacionados ao processo de doutoramento que julgo importante na formação de um pesquisador/professor/orientador, e que talvez possam servir de alguma maneira para um eventual aluno que leia esta parte.

Poucos meses antes de terminar o mestrado, pedi conselhos a minha orientadora, professora Susana, sobre o rumo que ela achava que eu deveria seguir no doutorado. Ela sugeriu que eu procurasse outra universidade, outro orientador, respirar novos ares, pois eu já estava no mesmo laboratório, com as mesmas pessoas, desde o segundo ano da graduação. Além disso, meus interesses já eram um tanto diferentes dos dela, por isso também ela me sugeriu um orientador que atuasse na área que eu começava a enveredar.

Logo após minha defesa de mestrado, consultei o professor Luis Mauricio Bini (UFG) sobre uma possível orientação de doutorado. Naquele momento, eu queria direcionar meu projeto de pesquisa para uma pergunta de interesse geral para a ecologia, independente do grupo de organismos que seria usado, e com algo em uma escala espacial regional. O prof. Bini convidou-me a prestar o exame de seleção para doutorado na UFG e caso fosse aprovado, ele iria me orientar. Concomitantemente, a profa. Susana fez-me uma proposta interessante. Caso eu fosse aprovado na UFG e tivesse bolsa, ela seria minha co-orientadora e eu poderia usar todos os dados do Biota-Fapesp "*Levantamento e Biologia de Insecta e Oligochaeta Aquáticos de Sistemas Lóticos do Estado de São Paulo*", se não passasse na UFG ou não conseguisse uma bolsa, eu continuaria na UFSCar com ela como orientadora e o prof. Bini como co-orientador – foi o que aconteceu. Passei em terceiro lugar no exame de seleção da UFG e apenas duas bolsas foram concedidas ao programa. Em São Carlos havia um número maior de bolsas disponíveis e logo consegui uma bolsa do CNPq. Apesar disso, resolvi que iria morar em Goiânia. A profa. Susana foi uma das pessoas que mais me incentivou a tomar essa decisão!

Mudar de laboratório só me trouxe boas experiências. Tive contato com jeitos diferentes de trabalhar, aprendi novos métodos e conheci gente nova com outras ideias. Logo percebi que os conselhos da profa. Susana faziam total sentido. Rapidamente estabeleci novas parcerias que me proporcionaram a participação em projetos paralelos à minha tese. Algumas delas resultaram em artigos já publicados ou em fase de publicação. Não estou dizendo que um lugar era melhor que o outro – não se trata disso. Os laboratórios eram simplesmente diferentes. E isso acrescentou na minha formação e fez com que eu percebesse a importância de não ficar focado somente em minha própria tese. No anexo I desta tese, eu listo os trabalhos resultantes de projetos que participei paralelamente ao doutorado. Além disso, por estar em uma nova universidade, tive a oportunidade de cursar disciplinas diferentes daquelas oferecidas no meu programa de pós-graduação – algumas como ouvinte e outras como aluno visitante.

Ainda em Goiânia – permaneci lá os dois primeiros anos do doutorado – tive outra nova experiência que considero fundamental para a minha formação como pesquisador, atuei pela primeira vez como revisor de um manuscrito submetido a um periódico científico. Naquele momento – apenas meu primeiro ano como aluno de doutorado – essa tarefa me pareceu assustadora e carregada de responsabilidade. A partir daí, outros periódicos solicitaram minha análise sobre manuscritos submetidos, em alguns casos, mais de uma vez. Considero minha atuação como revisor como uma oportunidade única e rara. Nos últimos três anos e meio atuei como revisor de sete periódicos. Essa experiência tem me ajudado muito, inclusive a melhorar a maneira como redijo meus manuscritos. Além disso, isso fez com que eu compreendesse que para publicar um artigo, outras pessoas têm de trabalhar (gratuitamente) como revisor, ou seja, todos nós temos o dever de fazer o circuito submissão-revisãopublicação funcionar. Mesmo que para isso tenhamos de deixar de fazer o trabalho relacionado aos nossos projetos. O avanço da ciência depende disso! Esse é o tipo de experiência que, em minha opinião, todo aluno de doutorado comprometido com ciência deveria ter.

Após os dois anos em Goiânia e as idas e vindas a São Carlos, decidi, também estimulado por meus orientadores e colegas, tentar uma bolsa para estágio no exterior. Com o auxílio financeiro do CNPq, passei nove meses no Canadá na Universidade de Guelph sob a orientação do prof. Karl Cottenie. Com a sua ajuda, analisei, discuti e escrevi parte dos resultados desta tese. Esse período foi muito frutífero, pois pude discutir e refinar minhas ideias e análises originais e acabamos escrevendo mais um artigo (não previsto no plano original) que surgiu de algumas conversas que tivemos em Guelph. Tive a oportunidade de aprender muito sobre ecologia teórica e numérica em diversas conversas formais e informais com pesquisadores de diversos países, aperfeiçoar minha escrita científica e a trabalhar com mais eficiência. Além disso, essa foi a primeira vez que morei no exterior e com isso pude crescer muito em termos culturais, aperfeiçoar meu inglês e aumentar incrivelmente minha independência.

Deixei para a última parte deste tópico aquele que considero o aspecto que menos consegui desenvolver e que considero também muito importante – o ensino. Nesses anos de mestrado e doutorado não atuei como professor em nenhuma instância do ensino. Essa talvez seja minha grande falha de formação – e também de muitos outros doutorandos brasileiros. Muito disso se deve as regras rigorosas das agências de fomento quanto a atuação legal de bolsistas como professor. Ministrei algumas poucas palestras e um mini-curso, mas acho pouco. A exceção foi ter participado, não oficialmente, como co-orientador de uma aluna de mestrado e, oficialmente, de sua defesa como membro da banca. Porém, após três anos e meio de doutorado, as vésperas de defender minha tese, ao analisar minhas atitudes, tenho a convicção de que tenho seguido passos coerentes com a carreira que almejo.

2. Resumo

Durante décadas a procura pelos processos que estruturam as comunidades e os determinantes da biodiversidade esteve voltada para o papel de fatores ambientais locais e diferenças no nicho das espécies. A teoria neutra de biodiversidade desafiou esta visão assumindo equivalência funcional entre espécies e maior importância de processos espaciais estocásticos. Nesta tese, eu procurei analisar como processos ecológicos locais – relacionados aos nichos das espécies – e regionais – relacionados a dispersão de espécimes – interagem para influenciar a estrutura de metacomunidades. A tese está dividida em três capítulos. No primeiro, eu investiguei um dos padrões mais recorrentes em ecologia, a relação entre abundância local e distribuição regional de espécies. Eu usei características do nicho dos táxons (Chironomidae: Diptera), utilizando métricas locais e de paisagem independentemente, para explicar a relação. No capítulo dois, eu testei se espécies comuns e raras são influenciadas por processos ambientais e espaciais de diferentes maneiras. No último capítulo, eu busquei identificar associações de táxons concordantes entre os Chironomidae que ocorrem no Estado de São Paulo. Além disso, construí modelos contendo informação sobre processos ambientais e espaciais em diferentes escalas para predizer essas associações. Considerando os três estudos, é possível concluir que o entendimento da dinâmica de metacomunidades passa pela inclusão de variáveis locais, de paisagem e espaciais nas análises e que muitas espécies podem não diferir marcadamente em seus nichos realizados. Ou seja, elas ocupam partes do gradiente ambiental de maneira similar, e portanto respondem de maneira similar aos mesmos tipos de processos ecológicos. Isso abre um caminho promissor para programas de monitoramento e conservação da biodiversidade. Podemos, por exemplo, usar um número reduzido de espécies – táxons associados – para monitorar grande parte das comunidades. Em minha opinião, agora devemos nos aprofundar em conseguir medir melhor processos espaciais como dispersão e colonização.

3. Abstract

For decades the search for determinants of biodiversity and structuring processes of natural communities has been concentrated on the role of environmental factors and differences in species niche. The neutral theory of biodiversity challenged this view by assuming functional equivalence between species and a major role of stochastic spatial processes. In this thesis, I aimed at analyzing how local and regional ecological processes interact to influence the structure of aquatic metacommunities. The thesis has three chapters. In the first one, I investigated one of the most widespread patterns in ecology, the relationship between species local abundance and regional distribution. I used niche characteristics, estimated independently from local and landscape metrics, to explain the relationship. In the second chapter, I tested whether common and rare species are influenced by environmental and spatial processes in a different manner. In the last chapter, I tried to identify taxon association within the Chironomidae that occur in São Paulo State. Besides, I built ecological models considering information from environmental and spatial processes at different scales aiming at predicting theses associations. In general, I conclude that to understand the dynamics of aquatic metacommunities one must include local, landscape and spatial variables in the analyses. Furthermore, it seems that some species do not differ in their realized niches. In other words, they occupy parts of the environmental gradient in a similar way, thus they respond in a similar way to the same type of ecological processes. This opens an avenue for monitoring and conservation programs. For example, we can use a reduced number of species to monitor entire communities. In my opinion, now we need to advance the way we measure and include spatial processes like dispersal in our models.

4. Introdução geral

As comunidades biológicas são bons exemplos de sistemas complexos (Nekola & Brown, 2007). Elas compreendem um grande número de entidades que interagem em muitas escalas de observação, e sua dinâmica geralmente não é linear. Isto poderia nos levar a pensar que a maioria das comunidades é imprevisível ou até mesmo aleatória. Alguns autores, inclusive, acreditam que a ecologia de comunidades nunca terá regras gerais que se apliquem a situações naturais (e.g., Lawton, 1999). Geralmente, não é possível predizer com exatidão a trajetória do desenvolvimento de uma comunidade biológica ou a dinâmica de suas populações (Maurer, 1999). Entretanto, apesar de não ser possível predizer o destino de todos os indivíduos em uma comunidade, o tamanho exato de cada uma de suas populações, ou nem mesmo sua composição específica exata, ainda é possível predizer algumas de suas propriedades. Por exemplo, é provável que muitas espécies desta comunidade sejam raras e poucas sejam comuns (Preston, 1948; Gaston, 1994). É provável também que as espécies que são mais amplamente distribuídas na escala regional sejam as mais abundantes na escala local (Hanski, 1982; Brown, 1984). Isso indica a existência de processos ecológicos gerais que afetam, pelo menos em algum grau, a estrutura e dinâmica das comunidades. Parafraseando McGill et al. (2006), ainda há esperança para a busca de regras gerais em ecologia de comunidades.

Durante décadas, a procura pelo entendimento desses processos esteve fortemente voltada para o papel de fatores ambientais e diferenças relacionadas ao nicho dos táxons (Tokeshi, 1999). Apesar de muitos trabalhos em ecologia citarem o *Concluding remarks* de G. Evelyn Hutchinson (Hutchinson, 1957) para fazer referência a definição de nicho, foi Joseph Grinnell, há quase um século (Grinnell, 1917), quem formalizou o conceito pela primeira vez. Em seu trabalho, Grinnell definiu o nicho como um conjunto de fatores ambientais que restringia cada espécie, através de relações "fisiológicas e comportamentais", a um limite geográfico onde ela poderia prosperar. Entre esses fatores, ele considerou principalmente microhabitats e fatores abióticos. Ou seja, na visão de Grinnell, o nicho era um atributo do ambiente, um local abstrato no ambiente. Uma década depois de Grinnell, outro cientista propunha o nicho sob uma nova perspectiva. Elton (1927) define o conceito de nicho com ênfase ao efeito que uma dada espécie exerce no ambiente. Isto é, o nicho corresponde à função da espécie no ambiente ou comunidade – em suas palavras, "aquilo que elas estão fazendo". Ali surgia a noção que uma espécie pode modificar o nicho que ela ocupa através do impacto que ela causa no ambiente. Note que essa função também era atributo do ambiente. Uma dada espécie poderia, ou não, ocupá-la. Porém, diferentemente de Grinnell, Elton deu maior importância para os recursos e interações bióticas. A inovação feita por Hutchinson foi ter redefinido o nicho como um atributo das espécies em relação a seu ambiente – biótico e abiótico (Cowell & Rangel, 2009). Sob esta visão, cada espécie tem seu próprio e único nicho. Hutchinson criou uma correspondência entre o nicho da espécie, definido como um hiper-volume multidimensional abstrato, e o espaço físico real em que as mesmas vivem. Segundo Hutchinson, o hiper-volume é definido por eixos que representam todos os fatores que podem influenciar a aptidão da espécie. Portanto, cada ponto desse hiper-volume corresponde a um conjunto de condições e recursos do ambiente que permitem que a espécie persista. Para uma melhor ilustração convém usar as próprias palavras de Hutchinson (1957): "considere duas variáveis ambientais independentes e_1 e e_2 que podem ser medidas ao longo de coordenadas retangulares ordinais..., uma área é definida, cada ponto dessa área corresponde a um estado ambiental que permite que a espécie exista indefinidamente". A espécie ocorre em qualquer área do espaço físico real em que as condições correspondem a uma área do hiper-volume e nunca fora dele. Esse foi, mais tarde, reconhecido como o nicho fundamental da espécie. Hutchinson argumentou que o nicho fundamental de uma espécie nunca seria totalmente preenchido, pois no mundo natural, ela sofreria a influência de outras espécies. Por esse motivo, o nicho *realizado* das espécies – aquela porção do hiper-volume que a espécie consegue preencher de fato – é sempre menor que o seu nicho fundamental. Alguns trabalhos mais atuais, no entanto, tem mostrado que teoricamente o nicho realizado pode ser maior que o fundamental (Pulliam, 2000). Esse tipo de situação aconteceria em sistemas sob a dinâmica fonte-sumidouro ("source-sink"). Ambientes fonte são aqueles em que a espécie se reproduz a uma taxa maior que sua taxa de mortalidade, enquanto em ambientes sumidouro ocorre o inverso. Nesses, não existem condições necessárias para existência da espécie – teoricamente não correspondente ao seu nicho fundamental. Entretanto, a espécie pode ocorrer no local devido à dispersão de indivíduos provenientes de ambientes fonte, fazendo assim com que seu nicho realizado seja maior que o fundamental.

Uma grande parte da ecologia de comunidades foi desenvolvida considerando a existência de diferenças nos nichos das espécies. Na teoria, essas diferenças fazem com que as espécies limitem suas próprias populações (interação intra-específica) mais do que elas limitam as populações de outras espécies (interação inter-específica), promovendo então a coexistência (Chesson, 2000). Por exemplo, Brown (1984) sugeriu que espécies com nichos mais amplos poderiam ocupar, através de suas habilidades em utilizar um maior espectro de recursos ou condições no espaço físico, mais lugares e também atingir abundâncias elevadas nestes locais quando comparadas com espécies com nichos menores (maiores detalhes sobre este aspecto são apresentados no capítulo 1 desta tese). Segundo Hubbell (1997), a ecologia de comunidades esteve, durante muito tempo, focada em processos que acontecem em escala reduzida, superestimando a importância das interações entre espécies e as diferenças entre nichos como forças estruturantes de comunidades locais. A teoria neutra de biodiversidade (Hubbell, 2001) desafiou esta visão assumindo equivalência funcional entre espécies. Nesta teoria, nenhum dos processos relacionados ao nicho das espécies é importante para a organização e manutenção da diversidade biológica. Em seu livro sobre o tema, Hubbell propõe o mecanismo de deriva ecológica como o processo responsável pelos padrões de diversidade observados. Sob o modelo neutro, as comunidades locais têm um número fixo de indivíduos e são estruturadas por processos aleatórios relacionados à morte, nascimento, dispersão e especiação.

Desde então, a ecologia de comunidades experimentou o surgimento e desenvolvimento de uma nova abordagem que define como os processos locais e regionais podem interagir para estruturar espacialmente grupos de comunidades em uma região (Leibold et al., 2004; Holyoak et al., 2005). Processos locais referem-se às interações entre espécies em pequenas escalas como competição e predação, que geralmente, junto com as condições e recursos ambientais controlam o número de espécies coexistentes em um local (Chase & Leibold, 2003). Por outro lado, processos regionais incluem a dispersão de organismos entre comunidades locais, a entrada de novas espécies do conjunto regional, especiação e extinção (Ricklefs, 1987). Este conjunto de comunidades em uma paisagem e que estão conectadas por dispersão de seus espécimes constituintes tem sido atualmente denominado como metacomunidade (Leibold et al., 2004).

A ecologia de metacomunidades é uma das subdisciplinas que tem recebido mais atenção recentemente (Cottenie, 2005; Leibold et al., 2004). Metacomunidades são estruturadas por processos locais e regionais, e diferentes tipos de metacomunidades podem ser teoricamente distinguidos pela influência relativa desses processos como agentes que estruturam as comunidades locais (Cottenie et al., 2003). A teoria de metacomunidades ainda está em pleno desenvolvimento (Scheiner & Willig, 2008), principalmente em relação ao debate nicho versus neutro (Chase, 2005; Hubbell, 2001). Atualmente se aceita que processos neutros e processos relacionados ao nicho não existem independentes um do outro e que estudos sobre a estrutura de comunidades devem considerar ambos (Chase, 2007; Vergnon et al., 2009). Neutralidade e diferenciação de nicho podem ser vistos como dois extremos de um gradiente de processos que determinam os diferentes tipos de metacomunidade, com comunidades reais posicionadas em algum lugar no meio desse contínuo, sob influência de ambos (Leibold & McPeek, 2006). Atualmente, contínuo de possibilidades tem guiado a maneira com que os ecólogos pensam a ecologia de comunidades e é parte de um conjunto de modelos que definem o conceito geral de metacomunidades – proposto formalmente por Leibold et al. (2004).

Segundo esses autores, metacomunidades podem ser categorizadas em quatro tipos de modelos: escolha de espécies (*species sorting*), dinâmica de manchas (*patch dynamics*), efeito em massa (*mass effects*) e modelo neutro. Em um extremo do gradiente, o modelo neutro trata as espécies como entidades similares em relação a suas habilidades competitivas e de dispersão. Além disso, os habitats são homogêneos em termos de benefícios para as espécies que neles ocorrem (Driscoll & Lindenmayer, 2009). Isto significa que todas as espécies que interagem com o habitat têm potencial para colonizar aquele habitat, mas que eventos estocásticos e restrição na dispersão irão determinar quais espécies conseguirão se instalar e permanecer no local (Hubbell, 2001; Leibold et al., 2004). No outro extremo do gradiente, o modelo de escolha de espécies assume que a qualidade ambiental dos habitats varia e que as espécies são adaptadas a condições ambientais particulares do local, assumindo também que existe dispersão suficiente entre os locais. Neste modelo, as espécies são distribuídas entre os habitats através de um filtro ambiental local. Entre esses dois extremos estão o modelo de dinâmica de manchas e o modelo de efeitos em massa. O primeiro assume que a qualidade ambiental entre manchas de habitat é homogênea e que a dominância das espécies é relacionada inversamente à habilidade de dispersão. De acordo com esse modelo, as espécies coexistem em habitats homogêneos através de um balanço entre competição e dispersão. Isto é, uma espécie pode permanecer em um dado local por ser uma boa competidora, ou por receber novos espécimes de outros locais. Já no modelo de efeitos em massa, também há diferença nos nichos das espécies. Nos locais com condições adequadas as populações apresentam taxa de crescimento intrínseco maior que um, porém, devido à dispersão elevada, são capazes de colonizar e permanecer em locais com condições não ideais (sistemas "source-link"). Na síntese proposta por Leibold et al. (2004), os autores desenvolvem a teoria relacionada às metacomunidades definindo os quatro diferentes tipos de metacomunidades correspondentes à esses modelos e com o mesmo nome. No ano seguinte, Cottenie (2005) usou uma técnica estatística – análise de redundância e partição da variância – para decompor a variação em 173 conjuntos de dados em componentes ambientais e espaciais, assumindo que a esse tipo de abordagem estatística poderia caracterizar efetivamente sistemas naturais nos quatro tipos de metacomunidades propostos. Ele encontrou que 73% das metacomunidades analisadas tinham um componente ambiental significativo explicando a variação na composição de espécies. Grande parte dos trabalhos subsequentes também aponta para um papel mais importante dos fatores ambientais, indicando que o modelo de escolha de espécies tem maior probabilidade de ocorrência que os outros tipos. Outros autores, no entanto, mostram que algumas metacomunidades em lagos tropicais não podem ser associadas a nenhum tipo de modelo (Nabout et al. 2009). Uma proposta alternativa interessante foi apresentada por Pandit et al. (2009), na qual uma distinção entre as espécies é considerada (especialistas vs. generalistas) antes do teste dos modelos. Segundo esses autores, uma metacomunidade natural pode exibir dinâmicas complicadas, com alguns grupos de espécies (e.g., especialistas) respondendo aos processos ambientais e outros grupos (e.g., generalistas) à dispersão.

Sistemas aquáticos continentais são áreas discretas contidas em uma paisagem terrestre. Apesar desta aparente falta de conectividade entre diferentes locais, muitos grupos de invertebrados aquáticos atingem distribuições amplas através dos processos dispersivos (Bilton et al., 2001). Vetores potenciais para a dispersão desses grupos incluem o vento, correntes de água, chuvas e a deriva em córregos (Cáceres & Soluk, 2002). Porém, parece que a dispersão ativa é o principal mecanismo envolvido neste processo. A dispersão ativa resulta predominantemente do voo de insetos adultos alados, que pode variar entre diferentes grupos taxonômicos e condições ambientais (Bilton et al., 2001). O estudo da dispersão é difícil, uma vez que medidas diretas impõem diversas restrições metodológicas (Southwood & Henderson, 2000). Uma maneira de superar os problemas relacionados à medição direta da dispersão é através da abordagem de metacomunidades (detalhes sobre o método de geração de variáveis espaciais no capítulo 2 desta tese). Estudos com esta abordagem têm resultado em relativo sucesso em comunidades de zooplâncton (Cottenie et al., 2003), e também como um método mais geral para diversos sistemas (Cottenie, 2005). Insetos aquáticos são similares às já bem estudadas metacomunidades de zooplâncton no sentido de que eles também formam metacomunidades em habitats discretos em uma matriz inóspita. Entretanto, os macroinvertebrados possuem um nível adicional de complexidade, uma vez que, comparados as espécies do zooplâncton, a dispersão ativa dos adultos poderia potencialmente resultar em processos completamente diferentes como seleção de habitat, diferenças na dispersão causadas por diferentes tamanhos de corpo e de asa.

Além disso, há um complicador adicional quando o foco é o ambiente aquático. Esses habitats recebem grande parte da água e matéria da paisagem circundante. Porém, a maneira com que as condições ambientais locais interagem com a paisagem e os processos que operam nessa escala ainda é pouco compreendida (Bengtsson et al., 2002). Recentemente tem havido um esforço para que os ecólogos estudem os riachos dentro de uma perspectiva de paisagem (Wiens, 2002), em substituição à visão de hierarquia linear comumente representada pela ordem do riacho (Vannote et al. 1980). Esses, aliás, são outros dois grandes avanços da ecologia nos últimos 20 anos – que processos ecológicos variam com a escala; e que muitos sistemas ecológicos estão organizados de maneira hierárquica (Cushman & McGaridal, 2002).

Temos evidências de que variáveis ambientais locais, como o tipo de substrato predominante, podem ser afetadas pelas características da paisagem de uma forma hierárquica (Frissell et al., 1986; Poff, 1997; Vinson & Hawkins, 1998). Os estudos que incorporam métricas de paisagem (exemplos de métricas no capítulo III desta tese) diferem, no entanto, em relação à principal escala de variação. Alguns autores sugerem que as características da paisagem são mais importantes na estruturação de comunidades aquáticas, enquanto outros, que as variáveis do corpo d'água agem como filtro determinante (Richards et al., 1997; Death & Joy, 2004).

Nesta tese, eu quantifiquei a importância relativa de processos ecológicos locais (relacionados ao nicho das espécies) e regionais (relacionados a dispersão de espécimes na paisagem) na estruturação de conjuntos de comunidades locais, i.e., metacomunidades. A tese está dividida em três capítulos. Em cada um deles eu, juntamente com meus colaboradores e orientadores, usei diferentes conjuntos de dados contendo informações sobre a distribuição, abundância e composição de espécies de ambientes aquáticos, predominantemente riachos de baixa ordem sob diferentes graus de preservação e/ou impacto. No primeiro capítulo, nós investigamos um dos padrões mais recorrentes em ecologia – a relação inter-específica entre abundância local e distribuição regional de espécies – em riachos da Mata Atlântica. No capítulo dois, nós usamos a abordagem de teoria de metacomunidades para explicar a ocorrência de espécies comuns e raras em escala regional. Neste capítulo nós usamos dez bases de dados sobre comunidades aquáticas em diferentes regiões e tipos de ambientes aquáticos do Brasil, e.g., pequenos riachos, lagos interconectados, ambientes higropétricos em topos de montanhas. Nosso objetivo central foi testar se espécies comuns e raras são influenciadas por processos ambientais e espaciais de diferentes maneiras. No terceiro e último capítulo, nós buscamos identificar associações de táxons, entre os Chironomidae que ocorrem em riachos do estado de São Paulo sob diferentes níveis de preservação, que respondessem de maneira similar a gradientes ambientais e construímos alguns modelos contendo informação sobre processos ambientais e espaciais em diferentes escalas para predizer essas associações.

Referências bibliográficas

Bengtsson J., et al. 2002. *Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations*. In: Biodiversity and Ecosystem Functioning – Synthesis and Perspectives (Eds M. Loreau., S. Naeem & P. Inchausti.), pp. 209–220. Oxford University Press Inc, New York.

Bilton, D.T., Freeland, J.R. & Okamura, B. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, 32, 159-181.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255-279.

Cáceres, C.E. & Soluk, D.A. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia*, 131, 402-408.

Chase, J.M. & Leibold, M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.

Chase, J.M. 2005. Towards a really unified theory for metacommunities. *Functional Ecology*, 19, 182-186.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences*, 104, 17430.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, 31, 343-366.

Colwell, R.K. & Rangel, T.F. 2009. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences*, 19651-19658.

Cottenie, K., Michels, E., Nuytten, N. & De Meester, L. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology*, 84, 991-1000.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, 8, 1175-1182.

Cushman, S.A. & McGarigal, K. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology*, 17, 637-646.

Death, R.G. & Joy, M.K. 2004. Invertebrate community structure in streams of the Manawatu-anganui region, New Zealand: the roles of catchment versus reach scale influences. *Freshwater Biology*, 49, 982-997.

Driscoll, D.A. & Lindenmayer, D.B. 2009. Empirical tests of metacommunity theory using an isolation gradient. *Ecological Monographs*, 79, 485-501.

Elton, C. 1927. *Animal ecology*. Sidgwick and Jackson, London, England.

Frissel C.A., Liss W.J., Warren C.E. & Hurley M.D. 1986. A hierarchical framework for stream habitat classification: viewing streams in the watershed concept. *Environmental Management*, 10, 199-14.

Gaston, K.J. 1994. *Rarity*. London: Chapman & Hall.

Grinnell, J. 1917. The niche relationship of the California thrasher. *Auk,* 34, 427-433.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38, 210-221.

Holyoak, M., Leibold, M.A. & Holt, R. D. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.

Hubbell, S.P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16, 9-21.

Hubbell, S.P. 2001. *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Hutchinson, G.E. 1957. *Concluding remarks*. Cold Spring Harbor Symp Quant Biol, 22, 415-427.

Lawton, J.H. 1999. Are there general laws in ecology? *Oikos*, 84, 177-192.

Leibold, M.A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601-613.

Leibold, M.A. & McPeek, M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399-1410.

Maurer, B.A. 1999. *Untangling ecological complexity? The macroscopic perspective*. Chicago: University of Chicago Press.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178-185.

Nabout, J.C., Siqueira, T., Bini, L.M. & Nogueira, I.D.S. 2009. No evidence for environmental and spatial processes in structuring phytoplankton communities. *Acta Oecologica*, 35, 720-726.

Nekola, J.C & Brown, J.H. 2007. The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology Letters*, 10, 188-196.

Pandit, S.N., Kolasa, J. & Cottenie, K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, 90, 2253-2262.

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16, 391-409.

Preston, F.W. 1948. The commonness, and rarity, of species. *Ecology*, 29, 254-283.

Pulliam, H.R. 2000. On the relationship between niche and distribution. *Ecology Letters*, 3, 349-361.

Richards, C., Haro, R. J., Johnson, L. B. & Host, G. E. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*, 37: 219-230.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science*, 235, 167-171.

Scheiner, S.M. & Willig, M.R. 2008. A general theory of ecology. *Theoretical Ecology*, 1, 21-28.

Southwood, T.R.E. & Henderson P.A. 2000. *Ecological Methods*. Oxford, UK: Blackwell Science.

Tokeshi, M. 1999. *Species coexistence: ecological and evolutionary perspectives*. Oxford: Blackwell Science.

Vannote, R.L., Minshall, W.G., Cummins, K.W., Sedell, J.R. & Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130-37

Vergnon, R., Dulvy, N.K. & Freckleton, R.P. 2009. Niche versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters*, 12, 1079-1090.

Vinson, M. R. & Hawkins, C. P. 1998. Biodiversity of Stream Insects: Variation at Local, Basin, and Regional Scales. *Annual Review of Entomology*, 43, 271-293.

Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, 47, 501-515.

5. Capítulo I

Este capítulo foi publicado na forma de artigo científico no periódico Hydrobiologia.

Siqueira, T., Bini, L.M., Cianciaruso, M., Roque, F., & Trivinho-Strixino, S. (2009). The role of niche measures in explaining the abundance–distribution relationship in tropical lotic chironomids. Hydrobiologia, 636, 163-172.

The role of niche measures in explaining the abundance-distribution relationship in tropical lotic chironomids

Tadeu Siqueira[1,2], Luis Mauricio Bini[2], Marcus Vinicius Cianciaruso[2], Fabio Oliveira Roque[3] & Susana Trivinho-Strixino[4]

[1]*Programa de Pós-graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, SP, Brazil, PO Box 676;* [2]*Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, GO, Brazil;* [3]*Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados, Dourados, MS, Brazil;* [4]*Laboratório de Entomologia Aquática, Departamento de Hidrobiologia, São Carlos, SP, Brazil*

Keywords: abundance-occupancy relationship, aquatic insects, OMI analysis, tropical streams, rarity

Abstract. The positive relationship between species regional distribution and local abundance is one of the most ubiquitous patterns in ecology. Among the hypotheses proposed to explain the relationship, the niche breadth and the niche position (or habitat availability) hypothesis are the most investigated. An unappreciated issue, but that is likely to be important for the understanding of the relationship is the nature of variables used to estimated niche measures. Here we analyzed the form of this relationship in lotic chironomid genera and tested whether niche measures estimated from local and landscape variables explain the observed pattern. Analyses were based in forty-seven forested streams within Southeastern Brazil. From our dataset we randomly partitioned the data in two non-overlapping sets to estimate taxa distribution and abundance (Distribution Data; n = 23 sites) and to generate niche measures (Niche Data; n = 24). We repeated that process 1,000 times, and for each one we generated niche breadth and position measures using in-stream and landscape variables, and estimated abundance and distribution for each taxa. With these, we estimated the relationship between both abundance and distribution and niche measures using ordinary least-squares regressions. We found no relationship between niche position estimated from local variables and local abundance nor regional distribution. There was a negative relationship between niche position estimated from landscape and local abundance, and regional distribution. We found a positive relationship between niche breadth (local and landscape) and both local abundance and regional distribution. When the relationship was significant, both niche position and niche breadth explained less than a half of total variation in abundance and distribution. This suggests that not only niche based processes, but also other mechanisms may be responsible for the abundance-distribution relationship in lotic chironomids. A novel finding of this study was that, although there was much unexplained variability around the relationships, niche breadth was a better predictor of abundance and distribution than niche position. We suggest that future studies should investigate if spatial processes, like dispersal, together with environmental processes affect interspecific abundance-distribution relationships.

Introduction

One of the most extensively investigated large-scale patterns in ecology is the relationship between species local abundance and their regional distribution (Williams, 1960; Brown, 1984; Gaston & Blackburn, 2000). In most cases the relationship is positive, i.e., locally abundant species tend to be widespread (Gaston et al., 1997). This pattern is stronger for marine than for terrestrial systems, whereas the weakest relationships are found in freshwater systems (Blackburn et al., 2006). However, it tends to hold despite variations in the way data is gathered and analyzed (Gaston, 1994) and the taxonomic group considered (e.g., Gaston et al., 1998; Heino, 2005; Soininen & Heino, 2005; Harcourt et al., 2005; Heino & Virtanen, 2006).

Various hypotheses have been proposed to explain this relationship. These are mainly related to niche-based mechanisms, metapopulation dynamics, range position, and sampling artifacts related to phylogenetic and spatial non-independence (see Gaston et al., 1997). The niche breadth hypothesis (Brown, 1984) and the niche position (or habitat availability) hypothesis (Hanski et al., 1993; Venier & Fahrig, 1996) are among the most investigated with the latter receiving good support (Gaston & Blackburn, 2000). In short, the former predicts that species occupying broader range of habitats and exploiting diverse environmental conditions and resources (i.e., wide niche breath) would be able to occupy more places. The latter hypothesis predicts that species utilizing common and widespread resources (or habitats) in a given region would be widespread and abundant. Some studies have demonstrated positive correlations between niche breadth and distribution, although few have demonstrated positive correlation between niche breadth and abundance (Gaston et al., 1997).

The niche of a species can be defined as the environmental conditions that allow this species to satisfy its minimum requirements so that birth rate of a local population is equal to or greater than its death rate (Hutchinson, 1957; Chase & Leibold, 2003). For freshwaters, environmental characteristics of the water body (e.g., water flow and chemistry) are believed to be closely linked to characteristics of the surrounding landscape (Frissell et al., 1986; Wiens, 2002). According to Poff's (1997) landscape filter concept, environmental factors act to determine the occurrence and abundance of species at different spatial scales. That is, to be part of a local community, species in the regional pool must have appropriate characteristics to "pass" through the nested filters (Poff, 1997). So, one could hypothesize that niche properties measured at the local and landscape levels would provide different explanations for the abundance-distribution relationship.

Most studies on the relationship between distribution and abundance were developed in temperate regions and focused on terrestrial ecosystems (see Blackburn et al., 2006). An investigation on tropical freshwater organisms would certainly contribute to reduce system (and, indirectly, taxonomic) biases and to unravel the role of the mechanisms proposed to account for the relationship. Aquatic chironomids (Chironomidae: Diptera) are a useful group for exploring the abundance-distribution relationship due to their ecological importance as well as to applied aspects. Besides representing one of the most species-rich and abundant group in most aquatic environment, chironomids also present a range of life-history that differs markedly, for example, in lifespan, locomotion, feeding habits and physiological tolerance to oxygen deficit (Pinder, 1986).

It has been demonstrated that some assemblage patterns hold for different taxonomic resolutions on stream macroinvertebrates (e.g., species, genus, and family levels: Marchant et al., 1995; Lenat & Resh, 2001; Melo, 2005). Similarly to species distributions, the distribution of higher taxa seems to be related to environmental and spatial variables as well (Murphy & Davy-Bowker, 2005). The reliability of the higher-taxa approach to detect general ecological patterns depends on how species within higher taxa respond to environmental gradients. If their responses are correlated, ecological patterns (e.g., abundance-distribution relationship) can be detected independently of the taxonomic resolution. Having this in mind, one could expect that the abundance-distribution relationship would also occur at higher taxonomic levels other than species, which would be desirable bearing in mind the limited knowledge available for Neotropical fauna. This seems especially suitable for chironomids, in which there are a high number of synonyms and unclear descriptions (Spies & Sæther, 2004) that create problems associated with differing species validity (Ferrington, 2008).

In this study, we investigated the relationship between local abundance and regional distribution of lotic chironomids. First we analyzed the form of the relationship in an attempt to find out if a positive relationship holds at the genus level. Based on a 'higher-taxon approach', we hypothesized that there would be a positive relationship between distribution and local abundance in lotic chironomid genera. If so, we asked if the relationship could be explained by niche characteristics of taxa estimated using local and landscape environmental variables. Following Poff's (1997) landscape filter concept, we hypothesized that niche breadth (Brown, 1984) and niche position (Hanski et al., 1993) estimated using both local in-stream and landscape variables would explain the positive relationship. We expected that both local abundance and regional distribution of chironomid genera would be positively related to their niche breadth and negatively related to their niche position. Moreover, these relationships should be significant when defining the niche with local and landscape features. However, given that the finest grained environmental filter through which a species go by is the local one (Poff, 1997), we predicted that the amount of variation explained in the relationships should be higher when using niche breadth and position estimated from the local scale.

Material and methods

Studied sites and measured variables

We used data on chironomid larvae distribution extracted from the "Macroinvertebrates Database" compiled by the research group of the "Laboratório de Entomologia Aquática - Universidade Federal de São Carlos". This data was collected during the dry seasons of 2001, 2005, and 2006 using Surber sampler (0.1 m^2 area and 250 mm mesh size) in 47 forested streams of southeastern Brazil (20-25°S, 44-53°W; Fig. 1). Our research group has been continually visiting all sampling areas since 2001 and did not notice any drastic change in land use during this period.

Sites were typical of Brazilian Atlantic Forest (sensu Oliveira-Filho & Fontes, 2000) headwater streams with water depths less than 50 cm, tree canopy coverage exceeding 70% of the channel, and absence of macrophytes. The riparian vegetation along all streams was well preserved. Six sampling units (3 samples from pool and 3 from riffle sites) of chironomid larvae were taken randomly from a 100 m reach within each stream using a Surber sampler. For each stream, sampling units were pooled prior to statistical analysis. We mounted specimens on slides and identified them to genus level.

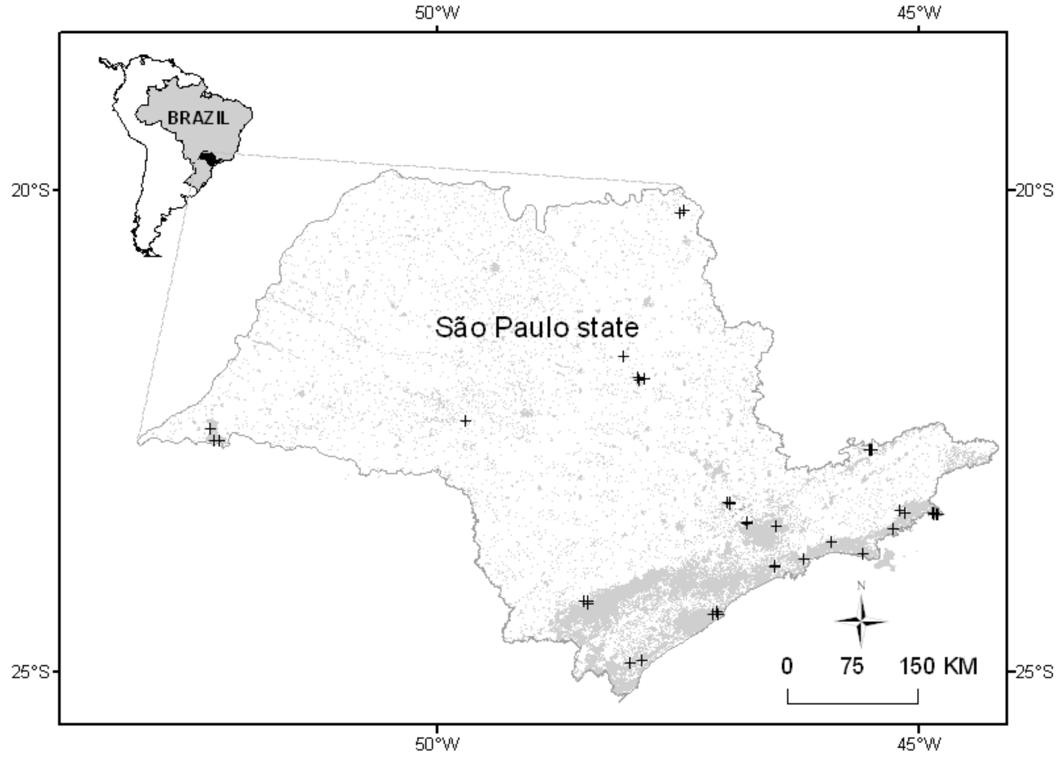

Figure 1. The geographical location of the studied streams in the São Paulo state, Brazil. Areas in grey within the limits of São Paulo state represent forested areas.

Environmental data

Local environmental measurements were taken at each site to characterize habitat conditions. Conductivity, pH and dissolved oxygen were measured in situ using a Horiba U-10 or a Yellow Springs-556 water checker equipped with multiple probes. Percentage of canopy cover and predominant substrates were estimated visually. Substrates were classified as the proportion of the stream bottom covered by boulder and cobble (>256 mm), gravel (2-255 mm), sand (0.125-2 mm), and mud (<0.125 mm).

To compute the landscape metrics, we delineated a circular buffer area (500 m radius, ca 78.5 ha) around a point located in the center of the stream channel of each of the 47 sampling sites (see Umetsu et al., 2008; for application of landscape metrics based on buffers of varying width). Some of our landscape metrics were derived from a land cover map at a scale of 1:50,000 from the Forestry Institute of São Paulo (Metzger et al., 2008). Macro-regional climatic variables, derived from coarse-scale maps were also included in this set of variables. Landscape metrics derived from the land cover map were: cover area of forest; the total edge contrast index (TECI), and the edge density (LED). The macro-regional variables were: the enhanced vegetation index (EVI), the rainfall and the solar radiation, all of which are indicative of primary production and biomass accumulation. We included four variables based on EVI measures: the EVI for the autumn (EVI AR) and for the winter (EVI AM), and both the range (EVI WR) and mean (EVI WM) between the two seasonal variables. We also included a measure of elevation in our set of landscape metrics. This metric was calculated using the mean value of the altitude across a 500 m radius circle around each sampling site provided by the Shuttle Radar Topography Mission (SRTM/NASA; http://www2.jpl.nasa.gov/srtm). Cover area of forest, total edge contrast index, and edge density were calculated using FRAGSTATS 3.3 (McGarigal et al., 2002), whereas the enhanced vegetation index and elevation were calculated using the Zonal statistics tool in ArcGis 9.

Niche measures and data analysis

From our database we randomly selected 23 sites to estimate the taxa distribution and abundance and 24 to generate niche measures. Hereafter these datasets are referred as

“Distribution Data” and “Niche Data”. The reason for using two independent datasets is to overcome the circularity that occurs when one estimates species’ distribution and niche from the same data. This statistical bias is mainly associated with the problem of dissociating sample size effects from real differences between the niche breadth and position of common and rare species (Gaston, 1994). However, only that does not guarantee that our estimations are truly unbiased. For example, let us suppose that, by chance, the “Niche Data” included the most similar streams regarding environmental conditions. This would enhance the chance of reducing niche measures variability among different taxa, and thus, produce a biased model. For this reason, we randomly generated 1,000 Distribution and Niche datasets, and for each one we applied the steps explained below.

For each genus within the Distribution datasets, we calculated the regional distribution by summing the number of sites occupied by that genus, and genus local abundance as the number of larvae of a given genus found in each stream. The ecological niche of a taxon can be represented by using its mean position and breadth along various environmental axes (Schoener, 1989). We applied the Outlying Mean Index analysis (Dolédec et al., 2000; see Thuiller et al., 2005, Broennimann et al., 2006 for other applications of this method) to generate measures of niche position and niche breadth for each taxon using the local and landscape variables measured within the Niche Data. The OMI (niche position hereafter) is a measure of the distance between the mean habitat conditions used by a taxon (centroid), and the mean habitat condition of the entire sampling area (origin of the niche hyperspace). The niche position of the taxon is assessed through their niche deviation from a reference. This reference represents a theoretical ubiquitous taxon that tolerates the most common habitat conditions. Genera that display high values of niche position have marginal niches (its environmental requirements are far from the mean conditions of the study area). Thus, we tested the niche availability hypothesis (Hanski et al., 1993; Venier & Fahrig, 1996) using OMI niche position. The Outlying Mean Index analysis also provides a measure of tolerance or niche breadth. Genera with high values of niche breadth are generalists, occurring across large portions of environmental gradients (wide habitat niche breadth).

Most former studies on the abundance-distribution relationship regarded abundance as the response variable. However, we cannot be sure whether the predominant direction of causality (if present) runs from local abundance to regional distribution or from the opposite (for a discussion see Gaston & Blackburn, 2000). Thus, we estimated the relationships between both local abundance and regional distribution (response variables) with the explanatory variables niche breadth and niche position (both defined using local and landscape variables) using ordinary least-squares regression. All these variables were log-transformed before analysis.

We did each regression mentioned above 1,000 times – using the randomly partitioned datasets (Distribution and Niche datasets) – producing a distribution of coefficients of determination (r^2), *p*-values and regression coefficients, which we used to access the average explanatory power of each model. We only considered significant those models with less than 50 non-significant regressions ($\alpha = 5\%$). All analyses were performed in the R-language environment (R Development Core Team 2007) using the package “ade4” (Dray and Dufour 2007) for generating niche measures.

Results

We identified 41 chironomid genera occurring in all sampled streams. The most widely distributed taxa were *Endotribelos* (41 streams), the *Tanytarsus/Caladomyia* complex (40), *Polypedilum* (38), *Parametriocnemus* (35), *Rheotanytarsus* (33), and *Larsia* (31). Likewise, the most abundant taxa were the *Tanytarsus/Caladomyia* complex, *Polypedilum*, *Parametriocnemus*, *Rheotanytarsus*, *Endotribelos* and *Larsia*. As we expected, there was a positive relationship between genus distribution and local abundance. This relationship was significant ($p \leq 0.05$) in all 1,000 randomizations, with the models accounting for most of the variability in regional distribution (Mean $r^2 = 0.88$, Fig. 2).

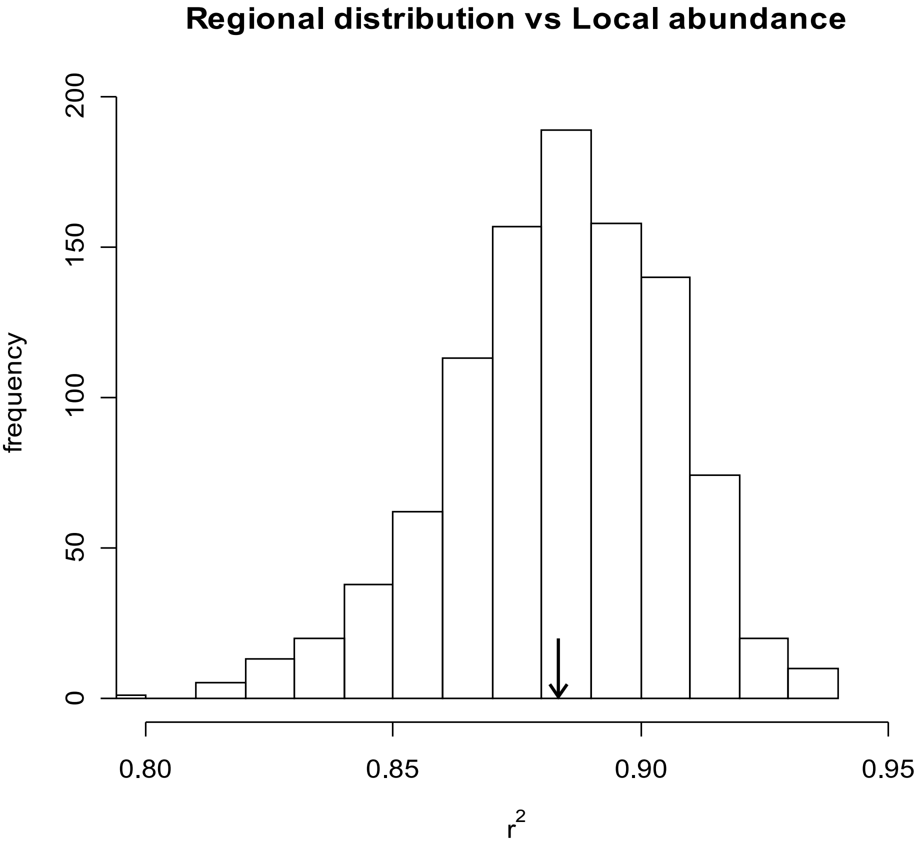

Figure 2. Distribution of coefficients of determination (r^2) of the regressions between regional distribution and local abundance. The arrow indicates the mean value of r^2 (0.88) across all 1,000 data subsets. All regression models between regional distribution and local abundance were significant at $p \leq 0.05$.

Niche position, as defined by local environmental variables, was not significantly related neither with local abundance nor with regional distribution in 52.4% and 62.4% of all datasets, respectively (Fig. 3a and 3c). On the other hand, when estimated from landscape variables, there was a significant negative relationship between niche position and local abundance in 99.8% of all datasets (Fig. 3b), and regional distribution in 99.7% of all datasets (Fig. 3d). We found a significant positive relationship between niche breadth (estimated using local and landscape variables) and both local abundance and regional distribution in more than 95% of all datasets (Fig. 4).

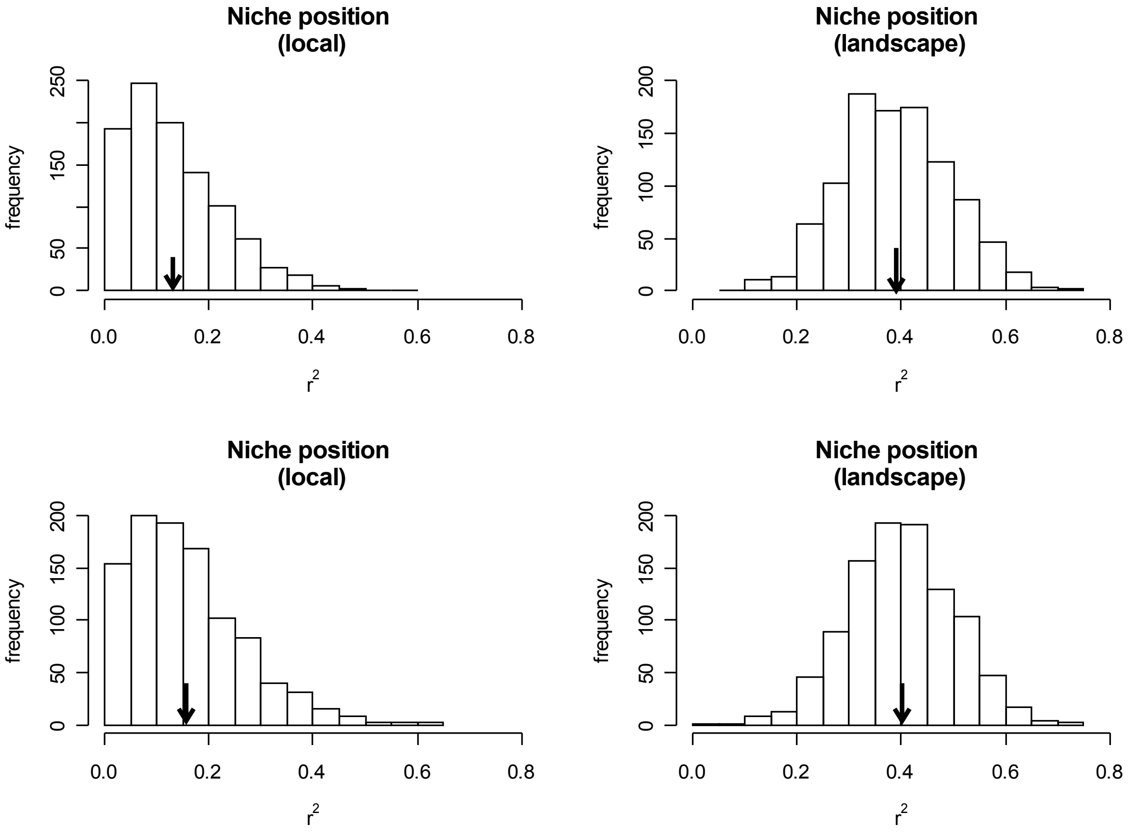

Figure 3. Distribution of r^2 values generated based on 1,000 regressions between niche position and local abundance and regional distribution. Arrows indicate the mean value of r^2 across all 1,000 data subsets (a. $r^2 = 0.13$*, b. $r^2 = 0.39$, c. $r^2 = 0.16$*, d. $r^2 = 0.40$). * = non-significant models (a- 47.6% of regressions with $p > 0.05$, c- 37.6% of regressions with $p > 0.05$).

In general, niche position and niche breadth explained less than a half of total variation in both local abundance and regional distribution (Fig. 3 and Fig. 4). So, in summary, niche breadth models significantly explained variation in abundance and distribution at both scales, whereas niche position models were significant only when we used landscape variables. Furthermore, in cases where they were significant, niche position and niche breadth models explained similar amounts of total variation in the response variables (Fig. 3 and Fig. 4).

Discussion

Results obtained here confirm our expectation that the positive abundance-distribution relationship already observed in many taxa (see Gaston & Blackburn, 2000) also holds true for lotic chironomid genera. This result adds new evidence to the conclusion that higher taxonomic levels can be used to detect local assemblage patterns (e.g., Marchant et al., 1995; Melo, 2005) as well as macroecological relationships (e.g., Harcourt et al., 2005). Unfortunately we do not have data on species level, thus it was not possible to analyze how much information was lost, if any, when using genus level identification. Some authors criticize the use of higher taxa (e.g., genus, family) in ecological studies arguing that the only valid taxonomic level is the species (e.g., de Queiroz & Gauthier, 1992; Mallet, 1995). Furthermore, the use of a higher taxonomic level also aids in minimizing the potential statistical problem of phylogenetic dependency (which is a type of pseudo-replication) making the analyses more conservative. This is especially advantageous here since phylogenetic non-independence is one of the proposed artifactual mechanisms that can generate a positive abundance-distribution relationship (Gaston & Blackburn, 2000).

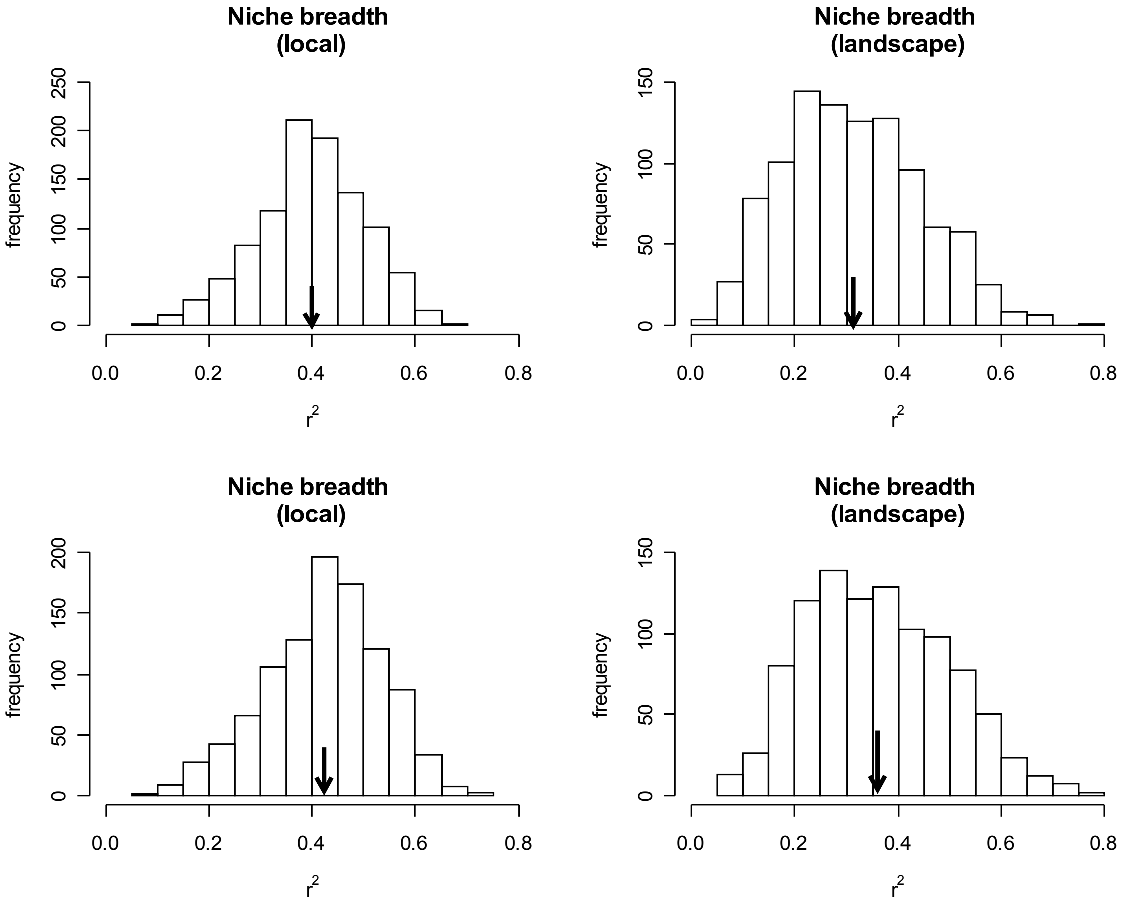

Figure 4. Distribution of r^2 values generated based on 1,000 regressions between niche position and local abundance and regional distribution. Arrows indicate the mean value of r^2 across all 1,000 data subsets (a. $r^2 = 0.40$, b- $r^2 = 0.39$, c. $r^2 = 0.42$, d. $r^2 = 0.36$). More than 95% of regressions were significant at $p \leq 0.05$.

In general, we found that most of the variation in abundance and distribution was not explained by niche measures. These results are partly similar to previous studies on freshwater organisms. Tales et al. (2004) found support for the niche position hypothesis (Hanski et al., 1993; Venier & Fahrig, 1996) as a mechanism to explain the abundance-distribution relationship. However, they found that niche breadth was not a good explanation for variation in abundance and distribution of riverine fish. On the other hand, Heino (2005) found significant relationships between both niche position and niche breadth and abundance-distribution in stream insects. A general characteristic of these studies and ours is that there is much unexplained variability around these relationships. Our results differ from those reported by Heino (2005) in the sense that in his study niche position explained more variation in both abundance and distribution than niche breadth. Here, niche position estimated using local environmental variables did not explain variation in either local abundance or regional distribution. So, the observed positive relationship between abundance and distribution is not a consequence of taxa niche position, regarding local environmental variables. This result is surprising given that most studies on the abundance-distribution relationship have found stronger support for the niche position hypothesis (see review in Gaston et al., 1997). This lack of support for the niche breadth hypothesis reported by several previous studies is due to, in part, difficulties in generating adequate niche breadth measurements (Gaston, 1994). Given the multidimensional nature of the niche (Hutchinson, 1957), important variables describing niche breadth might be missing from analyses. Also, an artifactual relationship is expected to arise because of the estimation of niche position is always unbalanced (Gaston et al., 1997). That is, rare and less widespread species contribute with a great number of zeros to the species matrix, thus it is expected that those species will attain high values of niche position, i.e., marginal niches. The use of an independent data to estimate niche breadth through a resampling procedure like ours does not completely solve this particular problem but minimize it.

Here we adopted a simple analytical procedure never used before – as far as we know – to estimate the average expected relationships between organism's abundance and distribution, and their niche. A resampling procedure like ours is an useful tool to minimize the problem of dependence explained above, and also to avoid the biased choice of two independent data sets. It is important to notice that we found considerable variability in the coefficients of determination (r^2). For example, we showed that it is possible to find, depending on the particular data subset, models with low explanatory power but also models explaining almost

80% of the variance in the data (Fig. 4d). Also, we showed that sometimes almost a half of the possible models can be non-significant (Fig. 3a). In that sense, we think that future studies seeking for such relationships would benefit from an approach similar to the one we used here because it is a step towards leaving particular explanations (related, for example to a single data set) to a more general view of the processes that might being operating in nature.

Besides explaining only less than a half of the total variation in local abundance and regional distribution, these relationships seem to be affected by the type of variable used to generate niche measures. Local environmental features of a stream can be partially determined by factors acting at the scale of the surrounding landscape (Hynes 1970). The OMI analyses we used here provided a description of the variability of habitats used by each taxa in the in-stream and surrounding environmental space. Thus, considering the expected association between in-stream and catchment environmental factors, one would expect that niche measures provided similar responses at both local and landscape levels. This was not the case here. For example, we found that niche position did not explain variation in any response variables when it was estimated from local environmental factors; but was related to both abundance and distribution when estimated from landscape variables. Note however, that this is not a matter of landscape variables being necessarily more suitable to estimating niche measures. Niche breadth estimated from both local and landscape variables explained similar amounts of variation in local abundance and regional distribution. A number of studies have focused on how local and landscape characteristics of a stream can act to influence the distribution and abundance of macroinvertebrates (Corkum, 1992). Some of these studies have suggested that both scales act in structuring local communities, whereas others have found that local stream variables play a major role (see Richards et al., 1997; Death & Joy, 2004). Here we demonstrated that landscape based models were significant independently of the response and predictor variables, whereas local based models were significant only when niche breadth was the predictor variable. Thus, at this moment we can only agree with the view that stream communities are structured by processes operating at different spatial scales (Vinson & Hawkins, 1998), without ruling out which scales and factors are the most influential.

Given the high amount of unexplained variation in our regression models and assuming that we have measured appropriate environmental variables to represent niche, we postulate that niche based processes may not be the main causes for the abundance-distribution relationship in lotic chironomids. In addition to niche position and breadth, some other mechanisms have been proposed as possible determinants of the positive relationship between abundance and distribution of species (Gaston et al., 1997). These other mechanisms are generally classified as statistical, range position, and population dynamic explanations. Since they are not mutually exclusive, it is likely that the abundance-distribution relationship could be a result of multiple processes (Gaston et al., 2000). Statistical explanations are mainly related to sampling artifacts, e.g., non detection of uncommon taxa that are actually present at a given site, and phylogenetic non-independence, i.e., related taxa do not constitute independent data points in analysis. Previous studies have refuted these two statistical explanations by using large data sets of well know groups and by controlling for phylogenetic non-independence (see Murray et al., 1998). Although we have not controlled for phylogeny here (there is no available phylogeny for Chironomidae), the most abundant and distributed genera belong to different tribes and subfamilies, so we believe this was not a major cause for the observed relationship. Range position explanations state that because, in general, species abundance are higher at the centers of its geographical range, species whose range limits are located within the study region would have lower abundances (Gaston & Blackburn, 2000). This mechanism was also rejected by a number of studies (see Gaston et al., 1997). As our study was based on genus, the likelihood of this mechanism is diminished here because the sampled genera have geographical ranges that extrapolate our study area. Finally, population dynamic explanations stem from metapopulation models, mainly the rescue effect hypothesis (Hanski, 1991). In this, dispersal between patches decreases the probability of local population extinction, and increases the proportion of patches occupied by a given species. Experimental evaluations of this hypothesis have been conducted but lead to equivocal conclusions. Gonzalez et al. (1998) experimentally interrupted dispersal between moss fragments resulting in a decline in both abundance and distribution, and the loss of the positive abundance-distribution relationship. When dispersal was reestablished there was an increase in both abundance and distribution, and the positive relationship between them appeared again. On the other hand, Warren & Gaston (1997) found positive relationships in all treatments of an experiment with protists, even in those where patches were isolated by dispersal limitation. Unfortunately we do not have information on metapopulation dynamics for the analyzed data. So, a direct investigation of this mechanism is not possible at present.

Recent advances in community ecology point that niche-assembly and dispersal-assembly models are not mutually exclusive in explaining the same community patterns (Chave et al., 2002, Mouquet & Loreau, 2002). For instance, Cottenie (2005) suggested that when both environment and spatial processes are acting, local communities are structured by a combination of species sorting and mass effects dynamics. Species sorting dynamics emphasizes the importance of species niche and environmental heterogeneity in determining community structure and also assumes moderate dispersal rates (Chave et al. 2002). A mass effect describes a sink-source process of dispersal in heterogeneous environments high enough to change population abundances (Holt 1993). There is a parallel here between these and the proposed mechanisms for the abundance-distribution relationship (niche based hypothesis and rescue effect hypothesis). Thus, we believe that future studies should investigate if spatial processes, like dispersal, together with environmental processes affect the abundance-distribution relationship in the context of community structure. This perspective has recently been combined in a unified framework for explaining how compositions of local communities vary in space. The metacommunity framework (Leibold et al., 2004) offers the theoretical background and the analytical tools to integrate local and regional processes in a more inclusive concept for understanding community dynamics.

In summary, the main picture emerging here is that niche-based processes are not the unique cause for variation in the abundance and distribution of lotic chironomids. A novel finding of this study was that we found more support for the niche breadth hypothesis (Brown, 1984) than for the niche position hypothesis (Hanski et al., 1993). We also demonstrated the pertinence of using higher taxa data to analyze the relationship between distribution and abundance. Finally, we showed how a simple resampling procedure can be useful tool to minimize the lack of independence in estimating niche, abundance and distribution of taxa from the same data set.

Acknowledgements

We thank Joaquín Hortal and Professor José Alexandre Diniz-Filho for valuable comments during the elaboration of this study. Adriano S. Melo, Karl Cottenie and an anonymous referee provided important criticism in an early version of this manuscript and we also thank them. Financial support was provided by the Brazilian Council for Scientific and Technological Development (CNPq) to T. Siqueira and L.M. Bini, and by The State of São Paulo Research Foundation (BIOTA/FAPESP) to F.O. Roque and S. Trivinho-Strixino.

References

Blackburn, T. M., P. Cassey & K. J. Gaston, 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. Journal of Animal Ecology 75: 1426-1439.

Broennimann, O., W. Thuiller, G. Hughes, G. F. Midgley, J. M. R. Alkemade & A. Guisan, 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Global Change Biology 12: 1079-1093.

Brown, J. H., 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255-279.

Chase, J. M. & M. A. Leibold, 2003. Ecological niches – linking classical and contemporary approaches. The University of Chicago Press, Chicago, IL.

Chave, J., H. C. Muller-Landau & S. A. Levin, 2002. Comparing classical community models: theoretical consequences for patterns of diversity. The American Naturalist 159: 1-23.

Corkum, L. D., 1992. Spatial distribution patterns of macroinvertebrates along rivers within and among biomes. Hydrobiologia 239: 101-114.

Cottenie, K, 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175-1182.

Death, R. G. & M. K. Joy, 2004. Invertebrate community structure in streams of the Manawatu-Wanganui region, New Zealand: the roles of catchment versus reach scale influences. Freshwater Biology 49: 982-997.

Dolédec, S., D. Chessel & C. Gimaret-Carpentier, 2000. Niche separation in community analysis: a new method. Ecology 81: 2914-2927.

Dray, S., & A. B. Dufour, 2007. The ade4 package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22: 1-20.

Ferrington Jr., L. C., 2008. Global diversity of non-biting chironomids (Chironomidae; Insecta-Diptera) in freshwater. Hydrobiologia 595: 447-455.

Frissell, C. A., W. J. Wiss, C. E. Warren & M. D. Huxley, 1986. A hierarchical framework for stream classification: viewing streams in watershed context. Environ Manage 10: 199-214.

Gaston, K. J., 1994. Rarity. Chapman & Hall, London.

Gaston, K. J. & T. M. Blackburn, 2000. Pattern and process in macroecology. Blackwell, London.

Gaston, K. J., T. M. Blackburn & J. H. Lawton, 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. Journal of Animal Ecology 66: 579-601.

Gaston, K. J., T. M. Blackburn, R. D. Gregory & J. J. D. Greenwood, 1998. The anatomy of the interspecific abundance-range size relationship for the British avifauna: I. Spatial patterns. Ecology Letters 1: 38-46.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn & J. H. Lawton, 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37: 39-59.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn & I. Evans-Freke, 1998. Metapopulation dynamics maintain the positive species abundance-distribution relationship. Science 281: 2045-2047.

Hanski, I., 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42: 17-38.

Hanski, I., J. Kouki & A. Halkka, 1993. Three explanations of the positive relationship between distribution and abundance of species. In Ricklefs R. E. & D. Schluter (eds), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago: 108-116.

Harcourt, A. H., S. A. Coppeto & S. A. Park, 2005. The distribution–abundance (density) relationship: its form and causes in a tropical mammal order, Primates. Journal of Biogeography 32: 565-579.

Heino J., 2005. Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? Ecography 28: 345-354.

Heino, J. & R. Virtanen, 2006. Relationships between distribution and abundance vary with spatial scale and ecological group in stream bryophytes. Freshwater Biology 51: 1879-1889.

Holt, R. D, 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In Ricklefs R. E. & D. Schluter (eds), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago: 77-88.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 145-159.

Hynes, H. B. N., 1970. The ecology of running waters. University of Toronto Press, Toronto.

Lenat, D. R. & V. H. Resh, 2001. Taxonomy and stream ecology: the benefits of genus and species identifications. Journal of the North American Benthological Society 20: 287-298.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law & D. Tilman, 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613.

Mallet, J., 1995. A species definition for the modern synthesis. Trends in Ecology and Evolution 10: 294-299.

Marchant, R., L. A. Barmuta & B. C. Chessman, 1995. Influence of sample quantification and taxonomic resolution on the ordination of macroinvertebrate communities from running waters in Victoria, Australia. Marine and Freshwater Research 46: 501-506.

McGarigal K., S. A. Cushman, M. C. Neel & E. Ene, 2002. Fragstats: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html

Melo, A., 2005. Effects of taxonomic and numeric resolution on the ability to detect ecological patterns at a local scale using stream macroinvertebrates. Archiv fur Hydrobiologie 164: 309-323.

Metzger, J. P., M. C. Ribeiro, G. Ciocheti & L. R. Tambosi, 2008. Uso de índices de paisagem para a definição de ações de conservação e restauração da biodiversidade do Estado de São Paulo. In: Rodrigues, R. R., C. A., Joly, M. C. W., Brito, A. Paese, J. P. Metzger, L. Casatti, M. A. Nalon, N. Menezes, N. M. Ivanauskas, V. Bolzani, V. L. R. Bononi (eds), Diretrizes para Conservação e Restauração da Biodiversidade no Estado de São Paulo. Secretaria do Meio Ambiente & FAPESP, São Paulo: 120-127.

Mouquet, N. & M. Loreau, 2002. Coexistence in Metacommunities: The Regional Similarity Hypothesis. The American Naturalist 159: 420-426.

Murphy, J. F. & J. Davy-Bowker, 2005. Spatial structure in lotic macroinvertebrate communities in England and Wales: relationships with physicochemical and anthropogenic stress variables. Hydrobiologia 534: 151-164.

Murray, B. R., C. R. Fonseca & M. Westoby, 1998. The macroecology of Australian frogs. Journal of Animal Ecology 67: 567-579.

Oliveira-Filho, A. T. & M. A. L. Fontes, 2000. Patterns of floristic differentiation among Atlantic forests in south-eastern Brazil, and the influence of climat. Biotropica 32: 793-810.

Petersen, R. C., 1992. The RCE: a Riparian, Channel, and Environmental Inventory for small streams in the agricultural landscape. Freshwater Biology 27: 295-306.

Pinder, L. C. V., 1986. Biology of freshwater Chironomidae. Annual Review of Entomology 31: 1-23.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society: 16: 391-409.

de Queiroz, K. & J. Gauthier, 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449-480.

R Development Core Team, 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-roject.org.

Richards C., R. J. Haro, L .B. Johnson & G. E. Host, 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37: 219-230.

Schoener, T. W., 1989. The ecological niche. In Cherret J. (ed), Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific, Oxford: 790-813.

Soininen, J. & J. Heino, 2005. Relationships between local population persistence, local abundance and regional occupancy of species: patterns in diatoms of boreal streams. Journal of Biogeography 32: 1971-1978.

Spies, M. & O. A. Sæther, 2004. Notes and recommendations on taxonomy and nomenclature of Chironomidae (Diptera). Zootaxa 752: 1-90.

Tales, E., P. Keith & T. Oberdorff, 2004. Density-range size relationship in French riverine fishes. Oecologia 138: 360-370.

Thuiller, W., S. Lavorel & M. B. Araujo, 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14: 347-357.

Umetsu F., J. P. Metzger & R. Pardini, 2008. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. Ecography 31: 359-370.

Venier, L. A. & L. Fahrig, 1996. Habitat availability causes the species abundance-distribution relationship. Oikos 76: 564-570.

Vinson, M. R. & C. P. Hawkins, 1998. Biodiversity of stream insects: variation at local, basin, and regional spatial scales. Annual Review of Entomology 43: 271-293.

Warren, P. H. & K. J. Gaston, 1997. Interspecific abundance-occupancy relationships: a test of mechanisms using microcosms. Journal of Animal Ecology 66: 730-742.

Wiens, J. A., 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47: 501-515.

Williams, C. B., 1960. The range and pattern of insect abundance. American Naturalist 94: 137-151.

6. Capítulo II

Este capítulo, após aprovação pela banca de qualificação, foi submetido ao periódico Ecography.

Running head: Common versus rare species in metacommunities

Title: Common and rare species respond similarly to environmental processes in metacommunities

Tadeu Siqueira[1,2], Luis Mauricio Bini[3], Fabio Oliveira Roque[4], Mateus Pepinelli[5], Raphael Campitelli Ramos[6], Sheyla Regina Marques Couceiro[7], Susana Trivinho-Strixino[2] and Karl Cottenie[1]

[1]*Department of Integrative Biology, University of Guelph, Guelph, N1G 2W1, Canada;* [2]*PPG-ERN, Universidade Federal de São Carlos, São Carlos, 13565-905, Brazil;* [3]*Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, 74.001-970, Brazil;* [4]*Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados, Dourados, 79804970, Brazil;* [5]*Universidade de São Paulo, Ribeirão Preto, 14040-901, Brazil;* [6]*PPG-SEA, Universidade de São Paulo, São Carlos, 13.560-970, Brazil;* [7]*Instituto Nacional de Pesquisas da Amazônia, Manaus, 69060-001, Brazil*

E-mail: tsiqueira.bio@gmail.com

Abstract. Classic ecological theory relates rarity with either niche differentiation among species or spatially related processes. There is a clear parallel between these processes and the models proposed to explain the structure of metacommunities. Based on a metacommunity perspective and a variety of tropical invertebrate data we attempt to answer three questions: *i*- Do common and rare species respond differently to environmental and dispersal processes? *ii*- How does the composition of common and of rare species form? *iii*- Why are some species rare and others common? The main hypothesis we test is that common and rare species respond differently to environmental and spatial processes. We refine this into two more specific competing hypotheses with different predictions based on two sets of theories: metacommunity theory, and previous findings regarding the common versus rare species debate. We used redundancy analysis to determine the proportion of variation explained by environmental and spatial processes in common and rare species matrices, and procrustes analysis to compared the responses of common and rare species to these processes. We show strong evidence supporting the idea that common and rare species are mainly affected by environmental gradients and to a lesser extent also by spatial processes. Surprisingly and contrary to our expectation, however, the responses of common and rare species to environmental gradients are very similar. We also show a lack of influence of competitive interactions between common and rare species. Niche differences among species alone, thus, appear an unlikely sole cause for patterns of rarity in nature. We extend the view that species sorting dynamics are the dominant processes structuring metacommunities, and that focusing on these processes can optimize our efforts in conservation. Finally, we consider that commonness and rarity cannot be analyzed at the local scale–communities are not isolated units–nor with pairwise comparisons. Therefore, future studies on this important and complicated issue would benefit from adopting a metacommunity perspective.

Key-words: commonness, community assembly, dispersal, metacommunity models, niche processes, PCNM variables, rarity, spatial processes, species sorting, variation partitioning

Introduction

One of the most consistent phenomena in nature is that communities are composed of a few common species and many rare species (Preston 1948, Gaston 1994). Most previous studies on the common versus rare species debate were based on pairwise comparisons, in which a common species was compared with a closely related rare species (Kunin and Gaston 1993). Although no consensus has emerged, the proposed determinants of commonness and rarity usually fall under one of two broad categories. The first is related to niche differentiation among species regarding environmental preferences (Brown 1984), body size (Duncan and Young 2000), competitive abilities (Rabinowitz et al. 1984), and reproductive strategies (Kunin and Shimida 1997). For instance, Magurran and Henderson (2003) showed that abundant estuarine fish species were associated with muddy substratum whereas rare species with rock, sand, gravel or weed substratum. The second category includes differences in species dispersal abilities (Resh et al. 2005) and colonization dynamics (Rabinowitz and Rapp 1985). For instance, Resh et al. (2005) found that common taxa in long term benthic macroinvertebrate surveys were more likely than rare taxa to disperse by drift and have high female dispersal potential.

There is a striking parallel between these two categories and the models proposed to explain variation in the composition of metacommunities (see Chave 2004, Leibold and McPeek 2006). The metacommunity theory has recently integrated, through its four paradigms–the patch dynamic, the species sorting, the mass effects and the neutral model–local and regional processes in an inclusive framework for understanding community dynamics (Leibold et al. 2004). These models differ mainly in the assumption of whether dispersal is high enough to alter local population abundances and whether patches' environmental conditions are homogeneous (Holyoak et al. 2005). In other words, they can be viewed as a continuum, where at one extreme, metacommunity structure is determined mainly by dispersal limitation (the neutral model), and at the other extreme, it is determined by species responses to environmental factors (Leibold and McPeek 2006). A number of metacommunity studies have advanced the understanding of community assembly processes by explaining how environmental and spatial processes interact to affect variation in community composition of actual, observed communities (e.g., Cottenie 2005; Vanormelingen et al. 2008; Davies et al. 2009). Despite this parallel between the common versus rare species debate and the metacommunity theory, no study has investigated how common and rare species are affected by environmental and spatial processes at the metacommunity scale.

Besides these theoretical reasons and associated analytical tools for using a metacommunity approach to address questions related to the nature of commonness and rarity, the metacommunity framework can also provide important information for conservation strategies (Mouillot 2007), which can be worthwhile for both common and rare species. For instance, whereas rare species are expected to be at higher risk of extinction (Purvis et al. 2000), common species constitute much of structure, function and service provision of ecosystems (Gaston and Fuller 2008). Therefore, knowing which processes are more important for each group of species can aid in the way conservationists set priorities for conserving total biological diversity.

In this study we investigate the responses of sets of common and rare species to environmental and spatial processes at the metacommunity scale. We address two questions here: Do common and rare species respond differently to environmental and dispersal processes?; how does the composition of common and of rare species form? Therefore, the main hypothesis we test is that common and rare species respond differently to environmental and spatial processes. Common and rare species may be biologically distinguishable in a number of ways, e.g., dispersal and life-history strategies (Kunin and Gaston 1993, Kunin and Shimida 1997), and environmental preferences (Magurran and Henderson 2003), which would hence make them different in the way they are affected by these processes. We refine this main hypothesis and construct two, more specific, competing hypotheses with different predictions based on two sets of theories: metacommunity theory, and previous findings regarding the common versus rare species debate. We use 10 datasets on tropical aquatic invertebrate metacommunities to test the generality of our predictions.

The first specific hypothesis is based mainly on observational evidence from metacommunity studies. Natural communities do not conform solely to any one of the four metacommunity models, i.e., niche-assembly and dispersal-assembly models are not mutually exclusive in explaining community patterns (Chave et al. 2002; Mouquet and Loreau 2002). A meta-analysis by Cottenie (2005), however, revealed the predominance of species sorting and associated environmental heterogeneity over spatial processes in explaining variation in community composition of 158 metacommunities. We reason that this general pattern is mainly produced by common species, because rare species, by definition, occur in low numbers in any analyzed matrix and would have less of an influence on multivariate patterns. In addition, Chase et al. (2005) suggested that rare species may be more affected by demographic stochasticity (neutral model). So, following this reasoning, we hypothesize (H1) that common species composition is mainly determined by environmental processes and rare species composition by spatial processes (Fig. 1). If this is the case, we predict that environment will play a major role in explaining total variation in composition of common metacommunity species in most data sets. We also predict that variation in the composition of rare metacommunity species will be less affected by environmental heterogeneity and, due to their possible poorer dispersal abilities, more related to space, displaying more small scale spatial clustering.

In our second competing hypothesis (H2) we make completely opposite predictions compared to the the previous one. Of the many explanations for commonness and rarity from classical ecological theory, one of the most discussed is that rare taxa have a higher level of environmental specialization than common ones. Because environmental factors vary in space, generalists would be able to occupy more sites and attain higher abundances than specialists within the landscape (Brown 1984). In sites where environmental conditions are coincidentally favorable for a more specialized species, this species would be abundant at this site (Brown et al. 1995), but still rare within the metacommunity. A recent empirical extension to the metacommunity framework has shown that these habitat specialists respond primarily to environmental factors whereas habitat generalists respond mainly to spatial factors (Pandit et al. 2009). By combining these two theories, we hypothesize (H2) that common species are more influenced by spatial processes and rare species more by environmental processes (Fig. 1). If this is the case, variation in composition of common metacommunity species will be explained mainly by spatial variables in most data sets whereas environment will explain most of the variation in composition of rare metacommunity species. In this last case, for rare species, environment includes both abiotic and biotic (abundance of common species) factors. That is because competitive interactions between species could cause the dominant species to be numerically abundant and the subordinate species to be numerically scarce. By testing these two competing hypotheses we also attempt to answer a third question: Why are some species rare and others common?

Finally, we must also consider that there is a transition zone between abundant and rare species in most communities. This intermediate abundance class is characterized by species that suffer stochastic changes in their abundances, shifting from common or rare to intermediate abundances (Hubbell 2001). The intermediate hypothesis (H3) is related to a transitional situation regarding the previous hypotheses. We predict that intermediate species will lie somewhere between the endpoints of a continuum defined by niche-assembly and dispersal-assembly rules. Also, we expect common and intermediate species to show more similar responses to environmental and spatial processes than common and rare or intermediate and rare. By making an explicit hypothesis to intermediate abundant species, we also guarantee that the general and specific hypotheses were really directed to the most common and rare species within each metacommunity.

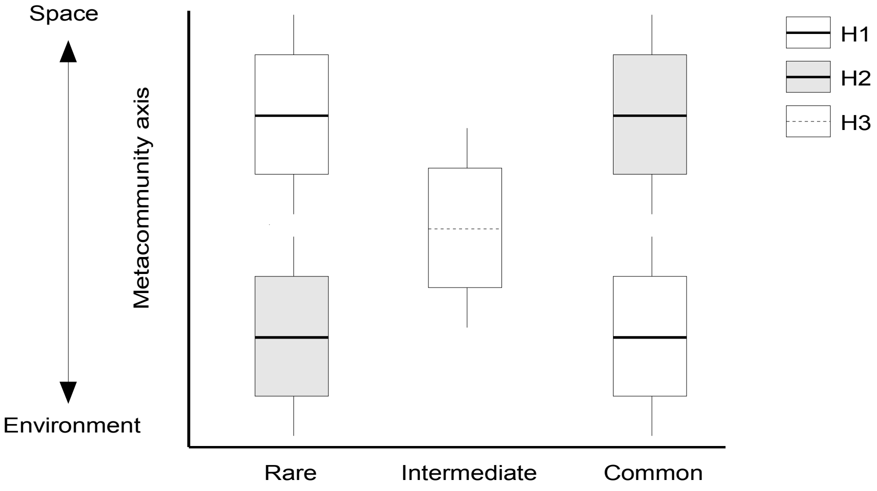

Fig 1. Graphical representation of the two competing hypotheses (H1, H2) and the intermediate hypothesis (H3).

Material and methods

We analyzed 10 data sets on macroinvertebrates collected in distinct types of freshwater environments located in different regions of Brazil. Each data set comprised a distinct metacommunity with information on community composition, environmental variables relevant for structuring that particular metacommunity, and spatial position of the sampled sites. Three data sets were identified to species level and seven to genus level, which does not seem to impose any bias in the study of rarity (Edwards 1998). For a summarized description of the different data sets see Table 1.

Table 1. Summarized description of the data sets analyzed. *S* refers to the number of taxa and *n* to the number of sites. C, I and R refer to common, intermediate and rare respectively. Env. (n) refers to the number of environmental variables in each data set.

Data set	**Habitat (*n*)**	***S* (C)**	***S* (I)**	***S* (R)**	**% of R**	**Env. (*n*)**
1- Black-flies inventory	Streams (136)	4	7	29	72.5	8
2- Central Amazon	Streams (65)	6	26	120	78.9	11
3- Atlantic Rain Forest	Streams (47)	6	9	38	71.7	26
4- Northeastern Brazil	Streams (41)	9	18	80	74.8	8
5- Northeastern Brazil II	Streams (50)	3	-	17	85.0	9
6- Southeastern Brazil	Streams (39)	10	6	250	94.0	17
7- Southeastern Brazil II	Streams (61)	6	16	40	64.5	26
8- Southeastern Brazil III	Lakes (17)	3	7	34	77.3	11
9- Southeastern Brazil IV	Inselbergs (19)	4	13	54	76.1	8
10- Western Amazon	Streams (20)	7	33	94	70.1	10

A number of different methods for defining commonness and rarity can be found in the ecological literature (see Gaston 1994 for a review). Here, we ranked taxa in each data set from the most abundant to the least abundant (for the eight data sets containing abundance information) and from the most widespread to the most restricted (for the two data sets containing presence-absence information) within the metacommunity. We then generated rank-abundance and “rank-occupancy” curves, respectively. Our objective was not to fit the best theoretical model for species abundance distribution (e.g., log-normal, log-series; see McGill et al. 2007), but to determine the general shape of each curve. All curves were characterized by a small number of abundant (or widespread) taxa, some intermediate abundance (or occupancy) taxa, and a large number of rare (or restricted) taxa. From these curves we visually inspected the inflection points and determined groups of common, intermediate and rare species for each data set. Hereafter, common species refers to highly abundant or widely distributed taxa at the metacommunity scale, with the same manner of categorization used for intermediate and rare taxa.

We tested the predictions associated with the competing hypotheses H1 and H2 and intermediate hypothesis H3 by using different groups of analyses. First, we assessed the role of environmental and spatial processes in explaining the composition of common, intermediate abundant and rare metacommunity species through a redundancy analysis (RDA) coupled with a forward selection (Blanchet et al. 2008), and a variation partitioning procedure (Borcard et al. 1992). Response variables were the compositional matrices (taxonomic composition and abundances of species) of common, intermediate and rare species whereas explanatory groups of variables were environmental and spatial variables. We transformed common and intermediate species matrices using Hellinger transformations (Legendre and Gallagher 2001) prior to analyses. Due to the high number of zeros in the rare species matrices, which generally cause bias in multivariate analysis (Legendre and Legendre 1998), we first transformed them into distance matrices by using the Jaccard index, and then submitted them to a classical multidimensional scaling procedure. The first two vectors extracted from the multidimensional scaling represented the rare species matrices. Therefore, matrices of common, intermediate abundant and rare species used in all analyses represented the structure of taxonomic composition of these sets of species. To represent spatial processes, we created spatial variables following the approach–Principal Coordinates of Neighbor Matrices (PCNM)– proposed by Borcard and Legendre (2002) where eigenvectors with positive eigenvalues were extracted from a spatial matrix consisting of the distances between all sites within each matrix. PCNM variables represent spatial structures generated by two independent processes–

environmental autocorrelation and biotic processes such as colonization and dispersal (Dray et al. 2006).

Following Blanchet et al. (2008), we ran a global RDA with the two sets of explanatory variables to model the response variable for each matrix. If the global test was significant for a given set of variables (environmental or spatial), we selected the most important variables for explaining total variation within the matrix and used them as predictor variables in variation partitioning. We used variation partitioning to decompose the total variation in abundance within common, intermediate and rare matrices into unique environmental and spatial components with corresponding R^2 and *P*-values. This analysis measures the amount of variation that can be attributed exclusively to one or the other set of explanatory environmental, E, or spatial, S, variables. The different components of explanation are: total explained variation [T], environmental variation [E], spatial variation [S], environmental variation without a spatial component [E|S], spatial variation without the environmental component [S|E] (for details see Peres-Neto et al. 2006). Note that [S|E] include not only biotic processes like dispersal but may also include potential important non-measured environmental variables. Finally, we conducted the same procedure for rare species matrices but including the abundances of common species as a additional explanatory matrix. Results of variation partitioning were based on adjusted fractions of variation (Peres-Neto et al. 2006). Significance (at a level of $\alpha \leq 0.05$) was computed by permutation tests (n = 9,999; Legendre and Legendre 1998). We interpreted the different components and associated *P*-values as estimates for the observational evidence that a given process (environmental, spatial, or a combination of both) is important in determining community structure (Cottenie 2005).

Using the results from RDA and variation partitioning we constructed a metacommunity axis through linear discriminant analysis (Legendre and Legendre 1998). We tested whether the four variation components [E], [S], [E|S], and [S|E] could discriminate between environmental and spatial processes for common, intermediate and rare species matrices. The idea is that this metacommunity axis would represent the relative importance of environmental versus spatial processes for shaping the analyzed metacommunities. To this end, we plotted the first linear discriminant axis (metacommunity axis), and the position of all analyzed matrices (scores).

Finally, we compared the way common, intermediate and rare species responded to ecological processes (environmental, dispersal, or a combination of both) by using Procrustes rotation analysis (see Peres-Neto and Jackson 2001). For this, we used ordination scores and variable loadings extracted from the RDAs between common, intermediate and rare species, and environmental and spatial variables within each data set and submitted them to a Procrustes rotation. For example, for comparing environmental responses of common vs. rare species: ordination scores extracted from the RDA between common species matrix and environmental variables vs. ordination scores extracted from the RDA between rare species matrix and environmental variables. Our aim here was to verify if common, intermediate and rare species were affected by environmental and/or spatial processes in a different manner. Statistical significance of the Procrustes concordance (at a level of $\alpha \leq 0.05$) was determined by randomization tests ($n = 9,999$). Analyses were performed in the R-language environment (R Development Core Team 2006) using the packages “spacemakeR” (Dray et al. 2006) for generating PCNM variables, “vegan” (Oksanen et al. 2007) for RDA and variation partitioning, “packfor” (Dray 2005) for the forward selection procedure, and ade4 (Dray and Dufour 2007) for Procrustean analysis.

Results

Our analyses revealed similar patterns of variation within most data sets. The mean percentage of species considered rare according to our criteria was 76.5% (varying from 64.5 to 95%), which corresponds to the limit of rare species that has been used in many studies (see Kunin and Gaston 1997). We found that the total explained variation in 55 % of the analyzed matrices was related to both environmental ([E] or [E|S]) and spatial components ([S] or [S|E]) and in some (37.9%) to environmental components only (Table 2). In none of the matrices, the spatial component explained solely variation in composition. In one rare and one intermediate species matrix neither environment nor space explained a significant amount of the total variation. The amount of total variation explained by environmental components ([E] or [E|S]) was higher than that explained by spatial components ([S] or [S|E]) in most common, intermediate and rare matrices (Table 2). We found that the composition of common species significantly explained variation in only one rare species matrix, which suggests competitive interactions between common and rare species are not a major factor affecting these metacommunities.

The first linear discriminant axis significantly discriminated the two main processes affecting the analyzed metacommunities–a combination of environmental and spatial processes (E+S) and environmental processes alone (E). However, most sets of species were affected mainly by E+S (Fig. 2). Common, intermediate and rare matrices were positioned mainly in a similar transition zone along the metacommunity axis, where species matrices mainly affected by environment plus space were associated with positive scores and species sets mainly affected by environment alone with negative scores (Fig. 3). Note, however, that because space alone did not explain variation in composition in any matrix, we did not reach the region in the metacommunity axis that would represent pure spatial processes (Fig. 3). These results provide us evidence to reject completely the hypothesis H2, and support part of the predictions of hypothesis H1.

Table 2. Total amount of variation explained by each component: environmental variation [E], spatial variation [S], environmental variation without a spatial component [E|S], spatial variation without the environmental component [S|E], and main ecological process represented according to the significance of the component for each analyzed matrix; zeros represent non-significant components. “E” refers to environmental and “S” to spatial. C, I and R refer to common, intermediate and rare respectively while the numbers correspond to the data set (Table 1).

Matrix	***Explained variation ($R^2_{adj.}$)***				***Process***		***Explained variation ($R^2_{adj.}$)***				***Process***
	[E]	**[S]**	**[E/S]**	**[S/E]**			**[E]**	**[S]**	**[E/S]**	**[S/E]**	
C-1	0.45	0.50	0.00	0.06	E+S	*I-6*	0.22	0.13	0.14	0.05	E+S
I-1	0.26	0.26	0.00	0.00	E+S	*R-6*	0.31	0.00	0.24	0.00	E
R-1	0.20	0.35	0.00	0.00	E+S	*C-7*	0.35	0.03	0.31	0.00	E+S
C-2	0.33	0.12	0.29	0.07	E+S	*I-7*	0.19	0.02	0.18	0.00	E+S
I-2	0.34	0.12	0.28	0.06	E+S	*R-7*	0.22	0.00	0.23	0.00	E
R-2	0.85	0.40	0.48	0.03	E+S	*C-8*	0.42	0.00	0.33	0.00	E
C-3	0.00	0.00	0.17	0.16	E+S	*I-8*	0.30	0.00	0.30	0.00	E
I-3	0.00	0.00	0.00	0.00	None	*R-8*	0.00	0.00	0.00	0.00	None
R-3	0.28	0.09	0.26	0.01	E+S	*C-9*	0.47	0.00	0.60	0.00	E
C-4	0.21	0.14	0.12	0.05	E+S	*I-9*	0.01	0.01	0.00	0.00	E+S
R-4	0.29	0.00	0.20	0.00	E	*R-9*	0.24	0.24	0.25	0.25	E+S
C-5	0.15	0.00	0.17	0.00	E	*C-10*	0.08	0.19	0.00	0.11	E+S
I-5	0.14	0.00	0.14	0.00	E	*I-10*	0.11	0.00	0.05	0.00	E
R-5	0.27	0.00	0.12	0.00	E	*R-10*	0.24	0.00	0.00	0.00	E
C-6	0.13	0.11	0.08	0.06	E+S						

Because space alone did not explain variation in composition in any matrix, procrustes rotation analysis was only used to compare the responses of common, intermediate and rare species to environmental processes. We found significant and surprisingly high correlations in most comparisons between common vs. intermediate, intermediate vs. rare, and between rare vs. common species (Table 3), suggesting that the way environment affects these sets of species, regardless of they are common or rare, is very similar. The mean observed correlation decreased from common vs. intermediate to rare vs. common when considering both site scores and variable scores (Table 3). This last result is in accordance with our intermediate hypothesis (H3).

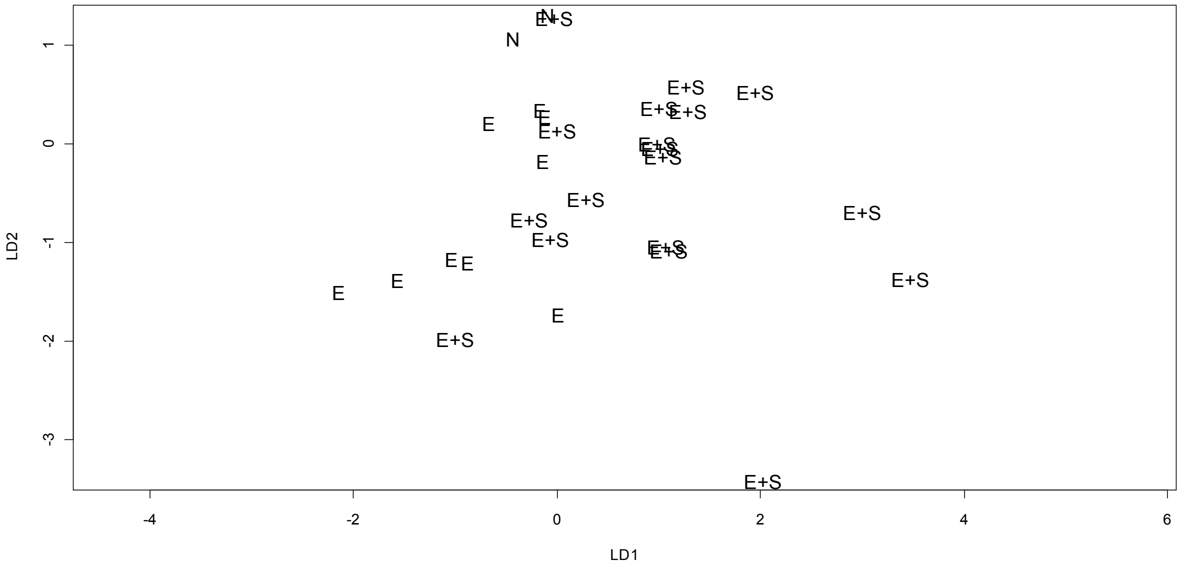

Fig 2. Position of each analyzed matrix in the first two linear discriminant axes (LD1 and LD2). according to the main ecological process affecting them. E+S refers to a combination of environmental and spatial variables, E to environmental process alone and N to none. LD1 represents the metacommunity axis.

Due to the high number of significant correlations between common and rare species we found in Procrustes analysis, 60-70% of the comparisons were significant and most correlations were higher than 0.50, we decided to examine which environmental variables were selected through the forward selection procedure. Selected variables for explaining variation in composition were similar for common and rare species matrices within each data set where the

Procrustes rotation was significant. Even when different environmental variables were selected for explaining variation in composition of a given matrix (e.g., percentage of sand in the stream bed for common species and percentage of mud in the stream bed for rare species), they belonged to the same category of variable, in this example, substratum type.

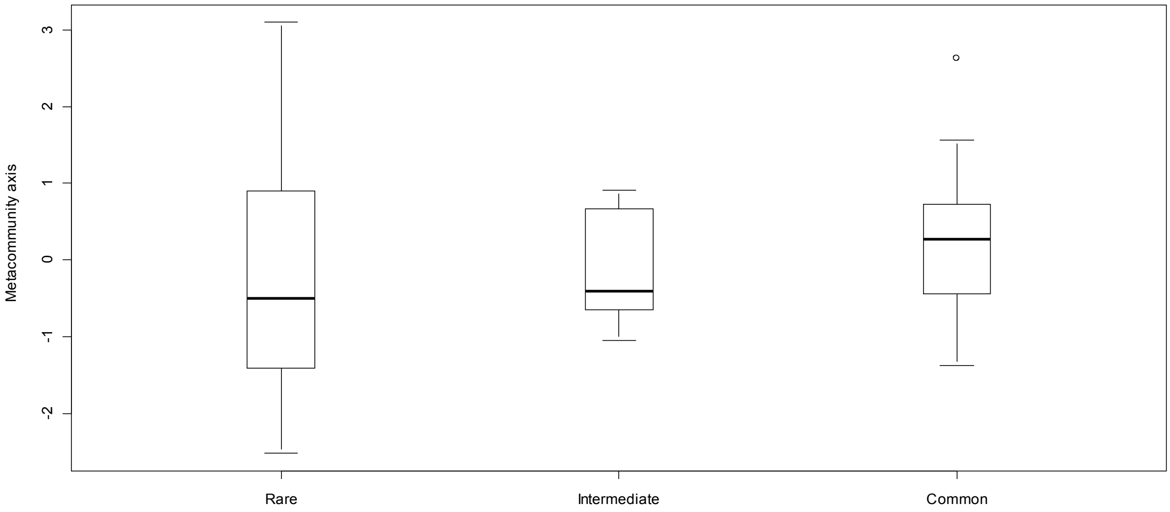

Fig 3. Distribution of rare, intermediate and common species matrices along the first linear discriminant axis. This axis significantly explained the differences between the two main processes affecting these sets of species, in which negative values represent the importance of environmental processes and positive values of spatial processes. The boxes represent the 25, 50 and 75 quartiles, the whiskers the minimum and maximum values excluding the outliers, values outside 1.5 times the interquartile range.

The environmental variables that best explained total variation in common, intermediate and rare matrices included: substratum type (e.g., % of sand), water variables (e.g., pH), habitat size (e.g., stream width) landscape characteristics (e.g., area cover by forest), topography (e.g., altitude) and climatic variables (e.g., mean annual temperature). These are the groups of environmental variables that have usually been recognized as determinants of the structure of aquatic macroinvertebrate communities (Vinson and Hawkins 1998). For those comparisons between common and rare species where the Procrustes rotation was not significant (40% of all comparisons), selected environmental variables were different. For instance, within the Atlantic Rain Forest data set, variation in composition of common species was best explained by the predominant type of substratum in the stream bed whereas for rare species variation was best explained by rainfall and the amount of preserved forest in the surrounding landscape.

Table 3. Results of Procrustes comparisons among common vs. rare, intermediate vs. common and rare vs. intermediate metacommunities regarding their responses to environment. C = common species; I = intermediate abundant species; R = rare species, *r* = correlation; *n* = number of data sets.

	Significant correlation (%)		**Mean correlation–*r* (range)**	
Comparison	*site scores*	*variable scores*	*site scores*	*variable scores*
C vs. I (n = 9)	88.89	88.89	0.62 (0.40-0.84)	0.86 (0.59-0.94)
I vs. R (n = 9)	66.67	55.56	0.60 (0.38-0.94)	0.84 (0.66-0.99)
R vs. C (n = 10)	70	60	0.50 (0.29-0.72)	0.78 (0.62-0.90)

Regarding spatial variables, the scale of selected PCNM variables was also similar for all common and intermediate species matrices (large scale PCNM variables) within each data set. We found, however, that variation in most of the rare species matrices was explained by small scale PCNM variables. This result indicates that common and rare species are affected by spatial processes in a different way, which partially supports our prediction (hypothesis H1) that rare metacommunity species would display more small scale spatial clustering.

Discussion

Recent rates of biodiversity loss have intensified the need to understand how communities are structured within regions. We found strong evidence supporting the idea that common, intermediate and rare species are mainly affected by environmental and to a lesser extent also by spatial processes. The most surprising aspect of our study, however, was the similarity in patterns between the sets of common and rare species. Contrary to our expectation, variation in composition of common and rare species matrices was best explained by the same set of environmental variables within each data set, and the responses of these sets of species to environmental processes were very similar.

We have also found strong evidence supporting the predictions related to our intermediate hypothesis. In general, common and intermediate species were more similar in their responses to environment, followed by intermediate and rare, and common and rare. Intermediately abundant species does not seem to be an artificial category in the analyzed data sets. This last result also confirms that we were really dealing with the more abundant and rarer species in our analyses.

Studies on the relative importance of niche and dispersal processes in structuring communities have shown that habitat heterogeneity and associated species sorting dynamics are dominant in most systems (see Cottenie 2005). We extended this view here for different species abundance categories by showing that environmental components were significant in almost all common, intermediate and rare species matrices whereas spatial components were significant in fewer cases. Additionally, we found that environmental components explained higher amounts of total variation than spatial components in most analyses. Together these results indicate that environmental gradients within landscapes are the main factor affecting species, whether they are highly abundant or rare.

Environmental heterogeneity was not, however, the only factor affecting common, intermediate and rare species. Spatial processes also played a role in structuring some of the analyzed metacommunities. When spatial components were significant, common and intermediate species responded to the same large scale spatial variables within each data set, whereas rare species responded to small scale variables in some data sets and to large scale in others. This indicates that the composition of common species only changes in sites that are distant to each other whereas rare species tend to have different compositional patterns even at sites that are close to each other. In other words, common and intermediate species have broad spatial clusters of species with high dispersing populations whereas rare species have small spatial clusters of species with probably poorer dispersal abilities or populations under source-sink dynamics (Amarasekare and Nisbet 2001). In this scenario, rare species are rare at the metacommunity scale but abundant in a few sites. From these, they disperse at high rates to nearby sites, maintaining their populations, but at low levels. However, due to their poor dispersal ability in traveling too far, they are restricted to some small clusters of habitats.

Cottenie (2005) suggested that when both environmental and spatial components are significant, metacommunities are structured by a combination of species sorting and mass effects dynamics. Species sorting dynamics emphasizes the importance of the local environment, assuming that with moderate dispersal (Fuentes 2002), species will be assorted along local resource gradients (Chave et al. 2002). Mass effects describe a process of dispersal in heterogeneous environments high enough to change population abundances (Holt 1993). However, significant spatial components can result from both high and limiting dispersal (Ng et al. 2009). So, it is not guaranteed that mass effects dynamics are present only by finding a significant spatial component. This brings to discussion the difficulty in inferring the role of dispersal in metacommunity dynamics, especially through observational studies. As we explained before (see methods), PCNM variables were used as a proxy for representing spatial processes. It is likely that dispersal is represented by these variables, but other processes that were not represented by the measured environmental variables can also be present. It is urgent then that ecologists produce more detailed information about species dispersal abilities at the metacommunity scale. This could help elucidate if species abundance is a function of immigration rate (Hubbell 2001, Magurran and Henderson 2003).

So what do the above evidences tell us about the causes of commonness and rarity? If common and rare species differ in their environmental preferences (Brown 1984, Brown et al. 1995, Magurran and Henderson 2003), one would expect them to show different responses to habitat environmental gradients in a landscape. Our findings do not support this hypothesis. Not only were common and rare species located at a similar position at the metacommunity axis (Fig. 3), but their responses to environmental gradients were also very similar. Environmental variation within the landscape alone thus appears an unlikely sole factor for generating patterns of commonness and rarity in nature. Note, however, that we are not implying that niche assembly does not play a role in determining community patterns, or that competing species in a community have no niche differences at all. Rather, we suggest that common and rare species do not differ substantially in the way they are influenced by environmental heterogeneity (i.e., range of abiotic variables of the environment). This view was also confirmed by the lack of influence of competitive interactions between common and rare species. Although competition is claimed to be an important cause of rarity (Kunin and Gaston 1997), evidence from pairwise experimental comparisons have given contrasting results (e.g., Rabinowitz et al. 1984, Walck et al. 1999). We speculate that, at the metacommunity scale, competition through direct interactions between species is not a major cause for patterns of rarity. The only differences we found here between common and rare species, although subtle and subject to some uncertainty, were the way they were affected by space and by factors not included in the analysis (i.e., unexplained variation). In this sense, the existence of small scale spatial structures within rare metacommunities indicates that rare species may really have poorer dispersal abilities compared with common species, as suggested by previous studies (e.g., McCreadie and Adler 2008).

Our results have some implications for conservation strategies. Because rare species are believed to be at greater risk of extinction (Purvis et al. 2000), they usually dominate lists of species of conservation priority and, consequently, are the main focus of conservation biologists (Baillie et al. 2004). In this vein, Gaston and Fuller (2008) have brought to discussion that common species may also be at great risk because they usually receive much less attention by conservationists. This is despite the fact that, due to practical reasons, the amount of available information on the abundance and spatial distribution of common species is generally higher than of rare species. If our findings are general and species sorting is really the main process driving community structure in nature (Cottenie 2005), then it should not matter if a reserve network is designed to protect common or rare species. By setting the more extinction prone rare species as the main conservation target within the reserve landscape, we would also protect the common ones. Alternatively, if high quality information is available only for common species, they could be used as targets and by extension, rare species would also be included in the conservation area scheme. Actually, there has been a recent attempt to pay more attention to common species (Gaston and Fuller 2008; Scarano 2009). This is justified by a number of reasons, including the importance of common species for natural ecosystem structure and function (Gaston 2008), and by the growing body of knowledge showing that common species might contribute more to patterns of species richness (e.g., Jetz and Rahbek 2002; Lennon et al. 2004). Of course, the implication of our findings for conservation depends on the approach being adopted for setting the priorities. If instead of rarity, other approaches are also to be considered (e.g., keystone or umbrella species, species or phylogenetic diversity), then our findings may not apply completely. We must also bear in mind the implications of our results regarding dispersal processes. As already noted, a requisite of the species sorting concept is that species are able to reach all habitat patches through moderate dispersal. This, combined with the evidence of spatial structures at different scales in common and rare species, reinforces the view that reserve networks, with high habitat quality and connected patches, should be targeted for conservation management (Thomas and Hanski 1997, Williams et al. 1996). Finally, we consider that commonness and rarity cannot be analyzed at the local scale–communities are not isolated units–nor with pairwise comparisons. Local communities are embedded in a dynamic landscape and connected with other communities through dispersal (Leibold et al. 2004). Therefore, future studies on this important and complicated issue would benefit from adopting a metacommunity perspective. In this sense, we must advance in the way we represent dispersal processes into the dynamics of ecological systems.

Acknowledgements

This study was partly financed by a CNPq Sandwich Program Scholarship to TS while he was an international visiting student at the University of Guelph and by a FAPESP Research Grant to ST and FOR. Additional funding for this study was provided by an NSERC Discovery Grant to KC. We thank Ingrid Ng for helpful comments on an early version of this manuscript and Victor Landeiro and Marcia Suriano for providing some of the data sets.

References

Amarasekare, P. and Nisbet, R.M. (2001). Spatial Heterogeneity, Source-Sink Dynamics, and the Local Coexistence of Competing Species. *Am. Nat.*, 158, 572-584.

Blanchet, F.G., Legendre, P. and Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, 89, 2623-2632.

Borcard, D. and Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.*, 153, 51-68.

Borcard. D., Legendre, P. and Drapeau, P. (1992). Partialling out the Spatial Component of Ecological Variation. *Ecology*, 73, 1045-1055.

Brown, J.H. (1984). On the Relationship between Abundance and Distribution of Species. *Am. Nat.*, 124, 255-279.

Brown J.H., Mehlman D.W. and Stevens G.C. (1995). Spatial Variation in Abundance. *Ecology*, 76, 2028-2043.

Cao, Y., Williams, D.D. and Williams, N.E. (1998). How important are rare species in aquatic community ecology and bioassessment? *Limnol. Oceanogr.*, 43, 1403-1409.

Chase, J.M., Amarasekeare, P., Cottenie, K., Gonzalez, A., Holt, et al. (2005) Competing theories for competitive metacommunities. In: *Metacommunities. Spatial Dynamics and Ecological Communities* (eds. M. Holyoak, M. Leibold and R. Holt). Univ. of Chicago Press, Chicago, pp. 335-354.

Chave, J., Muller-Landau, H.C. and Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1-23.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.*, 8, 1175-1182.

Davies, K.F., Holyoak, M., Preston, K.A., Offeman, V.A. and Lum Q. (2009). Factors controlling community structure in heterogeneous metacommunities. *J. Anim. Ecol.*, 78, 937-944.

Dray, S. (2005). packfor: forward selection with multivariate Y by permutation under reduced model. Laboratoire Biométrie et Biologie Évolutive, Lyon. URL http://biomserv.univ-lyon1.fr/~dray/software.php

Dray, S. and Dufour, A.B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.*, 22, 6.

Dray, S., Legendre, P. and Peres-Neto, P.R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.*, 196, 483-493.

Duncan, R.P. and Young, J.R. (2000). Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology,* 81, 3048-3061.

Edwards, W. (1998). Rarity within taxonomic lineages and the use of taxa above the level of species. *Ecography*, 21, 625-629.

Gaston, K. (1994). *Rarity.* Chapman and Hall, London.

Gaston, K.J. (2008). Biodiversity and extinction: the importance of being common. *Prog. Phys. Geog.*, 32, 73-79.

Gaston, K.J. and Fuller, R.A. (2008). Commonness, population depletion and conservation biology. *Trends Ecol. Evol.* 23, 14-19.

Holt, R.D. (1993). Ecology at the mesoscale: the influence of regional processes on local communities. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds. Ricklefs, R.E. and Schluter, D.) Univ. of Chicago Press, Chicago, pp. 77-88.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton Univ. Press, Princeton, Oxford.

Jetz, W. and Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science* 297:1548-1551.

Johnson, R., Furse, M., Hering, D. and Sandin, L. (2007). Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. *Freshwater Biol.*, 52, 939-958.

Kunin, W.E. and Gaston, K.J. (1997). *The biology of rarity: cause and consequences of rare-common differences*. Chapman and Hall, London.

Kunin, W.E. and Shmida, A. (1997). Plant reproductive traits as a function of local, regional, and global abundance. *Conserv. Biol.*, 11, 183-192.

Legendre, L. and Legendre, P. (1998). *Numerical Ecology.* Elsevier, Amsterdam.

Legendre, P. and Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601-613.

Leibold, M. A., and M. A. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. and Gaston, K.J. (2004). Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.*, 7, 81-87.

Magurran A.E. and Henderson P.A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, 422, 714-716.

McCreadie, J.W. and Adler, P. (2008). Spatial distribution of rare species in lotic habitats. *Insect Conserv. Diver.*, 1, 127-134.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., et al. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995-1015.

Mouillot, D. (2007). Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *J. Appl. Ecology*, 44, 760-767.

Mouquet, N. and Loreau, M. (2002). Coexistence in Metacommunities: The Regional Similarity Hypothesis. *Am. Nat.* 159, 420-426.

Ng, I.S.Y., Carr, C.M. and Cottenie, K. (2009). Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia*, 619, 133-143.

Oksanen, J., Kindt, R., Legendre, P. and O'Hara, R.B. (2007). Vegan: Community Ecology Package, Version 1.8-6. URL http://cran.r-project.org.

Pandit, S.N., Kolasa, J. and Cottenie, K. (2009). Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, 90, 2253-2262.

Peres-Neto, P.R. and Jackson, D.A. (2001). How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, 129, 169-178.

Peres-Neto, P.R., Legendre, P., Dray, S. and Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, 87, 2614-2625.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. and Gibbons, D.W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, 365, 335-337.

Purvis, A., Agapow, P., Gittleman, J.L. and Mace, G.M. (2000). Nonrandom Extinction and the Loss of Evolutionary History. *Science*, 288, 328-330.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna.

Rabinowitz, D. and Rapp, J.K. (1985). Colonization and Establishment of Missouri Prairie Plants on Artificial Soil Disturbances. III. Species Abundance Distributions, Survivorship, and Rarity. *Am. J. Bot.*, 72, 1635-1640.

Rabinowitz, D., Rapp, J.K. and Dixon, P.M. (1984). Competitive Abilities of Sparse Grass Species: Means of Persistence or Cause of Abundance. *Ecology*, 65, 1144-1154.

Resh, V.H., Bêche, L.A. and McElravy, E.P. (2005) How common are rare taxa in long-term benthic macroinvertebrate surveys? *J. N. Am. Benthol. Soc.*, 24, 976-989.

Thomas, C.D. and Hanski, I. (1997). Butterfly metapopulations. In: *Metapopulation Biology: Ecology, Genetics and Evolution* (eds. Hanski, I and Gilpin, M.E.). Academic Press, London, pp. 359-386.

Vinson, M.R. and Hawkins, C.P. (1998). Biodiversity of Stream Insects: Variation at Local, Basin, and Regional Scales 1. *Annu. Rev. Entomol.*, 43:271-293.

Walck, J.L., Baskin, J.M. and Baskin, C.C. (1999). Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (Asteraceae). *Am. J. Bot.*, 86, 820-828.

7. Capítulo III

Este capítulo foi publicado na forma de artigo científico no periódico Freshwater Biology. Apesar de não ser o primeiro autor, contribui igualmente em todas as etapadas do processo de desenvolvimento e submissão do estudo.

Roque, F. O., Siqueira, T., Bini, L. M., Ribeiro, M. C., Tambosi, L. R., Ciocheti, G. & Trivinho-Strixino, S. (2010). Untangling associations between chironomid taxa in Neotropical streams using local and landscape filters. *Freshwater Biology*, 55, 847-865.

Untangling chironomid taxon associations in Neotropical streams using local and landscape filters

FABIO O. ROQUE[1], TADEU SIQUEIRA[2,3], LUIS M. BINI[3] , MILTON C. RIBEIRO[4,5], LEANDRO R. TAMBOSI[4], GIORDANO CIOCHETI[4] & SUSANA TRIVINHO-STRIXINO[6]

[1]*Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados,, 79825-070, Dourados, MS, Brazil;* [2]*Programa de Pós-graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, SP, Brazil;* [3]*Laboratório de Ecologia Teórica e Síntese, Universidade Federal de Goiás, GO, Brazil;* [4]*Laboratório de Ecologia da Paisagem e Conservação, Universidade de São Paulo, SP, Brazil;* [5]*Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, ON, Canada;* [6]*Laboratório de Entomologia Aquática, Universidade Federal de São Carlos, SP, Brazil*

Correspondence: Fabio Oliveira Roque, Universidade Federal da Grande Dourados, Faculdade de Ciências Biológicas e Ambientais, Dourados, CEP 79825-070, MS, Brazil
e-mail: roque.eco@gmail.com, phone: 55 6734113895

Abbreviated title: Untangling taxon associations in streams using local and landscape filters

Keywords: Atlantic Forest, aquatic insects, landscape ecology, model selection, spatial eigenvectors

SUMMARY

1. Analyses of species association have major implications for selecting indicators for freshwater biomonitoring and conservation because they allow for the elimination of redundant information and focus on taxa that can be easily handled and identified. These analyses are particularly relevant in the debate about using speciose groups (such as the Chironomidae) as indicators in the tropics, because they require difficult and time-consuming analysis and their responses to environmental gradients, including anthropogenic stressors, are poorly known.

2. Our objective was to show whether chironomid assemblages in Neotropical streams have clear taxon associations and, if so, how well these associations could be explained by a set of models containing information from different spatial scales. For this, we formulated *a priori* models that allowed for the influence of local, landscape and spatial factors on chironomid taxon associations (CTA). These models represented biological hypotheses capable of explaining associations between chironomid taxa. For instance, CTA could be best explained by local variables (e.g., pH, conductivity and water temperature) or by processes acting at wider landscape scales (e.g., percentage of forest cover).

3. Biological data were taken from 61 streams in southeastern Brazil, 47 of which were in well-preserved regions, and 14 of which drained areas severely affected by anthropogenic activities. We adopted a model selection procedure using Akaike's information criterion to determine the most parsimonious models for explaining chironomid taxon associations.

4. Applying Kendall's coefficient of concordance, seven genera (*Tanytarsus*/*Caladomyia*, *Ablabesmyia*, *Parametriocnemus, Pentaneura, Nanocladius, Polypedilum* and *Rheotanytarsus*) were identified as associated taxa. The best-supported model explained 42.6% of the total variance in the abundance of associated taxa. This model combined local and landscape environmental filters, and spatial variables (which were derived from eigenfunction analysis).

However, the model with local filters and spatial variables also had a good chance of being selected as the best model.

5. Standardized partial regression coefficients of local and landscape filters, including spatial variables, derived from model averaging allowed an estimation of which variables were best correlated with the abundance of associated taxa. In general, the abundance of the associated genera tended to be lower in streams characterized by a high percentage of forest cover (landscape scale), lower proportion of muddy substrata and high values of pH and conductivity (local scale).

6. Overall, our main result adds to the increasing number of studies that have indicated the importance of local and landscape variables, as well as the spatial relationships among sampling sites, for explaining aquatic insect community patterns in streams. Furthermore, our findings open new possibilities for the elimination of redundant data in the assessment of anthropogenic impacts on tropical streams.

Introduction

A long-standing goal in stream ecology has been to relate species distributions to key environmental factors (Thienemann, 1954; Hynes, 1970; Townsend & Hildrew, 1994; Statzner, Hildrew & Resh, 2001; Poff *et al*., 2006). The ability to track how patterns of biodiversity change in response to environmental factors is important in the development of strategies for monitoring biodiversity. This goal has proved challenging, not only because of taxonomic impediments, but also because lotic communities are controlled by a number of factors that are in turn, influenced by the characteristics of the catchment (Allan, 1995; Wiens, 2002; Townsend *et al*., 2003). Nevertheless, the way the local environment interacts with the wider and dynamic landscape remains poorly understood (Bengtsson *et al*., 2002).

The ‘species association’ concept stems from the classic debate about biotic communities as discrete entities (Clements’ ideas) or as coincident groups of individualistic species (Gleason’s ideas) (Odum, 1971). Although in recent years this dichotomy has been substituted by a combination of both views (Heino *et al*., 2003), applied ecologists are interested in taxon associations, i.e., groups of taxa recognized as clusters following the application of a clearly stated set of rules (Legendre, 2005). When an association has been identified, one can then concentrate on finding the ecological requirements common to most or all members of the group rather than describing the biology and habitat of each species. Conversely, species associations may be used to predict environmental characteristics (Legendre, 2005). Clearly this approach has major implications for the selection of indicators for freshwater biomonitoring and conservation because it allows for a reduction in redundant information and focuses on taxa that can be easily handled in the field, and are suitable for rapid identification. Furthermore, in times of great concern about the effects of climate change, nations must follow the requirements of international conventions (UNFCCC, 1992) and initiate research programmes aimed at identifying species indicating large-scale environmental change. In this context, it would be highly desirable to find a relationship between groups of associated taxa and more easily measured predictor variables such as, for instance, landscape metrics (Williams, Margules & Hilbert, 2002; Metzger, 2008).

The dipteran family Chironomidae is a potentially useful group for exploring species associations because of its ecological importance and applied significance. In the tropics it represents one of the most speciose groups in any aquatic environment. Their larvae feed in a variety of ways and occupy different habitats (Ferrington Jr, 2008). Furthermore, Chironomidae species have wide-ranging life-histories, modes of locomotion and tolerance to oxygen deficit (Pinder, 1986). They are also considered to be a group requiring difficult and time-consuming analysis for identification to the genus level or lower, and there is much debate on the importance of including chironomid data in biomonitoring and conservation programmes (Rosenberg, 1992; Cranston, 2000; Hawkins & Norris, 2000; Rabeni & Wang, 2001; Nijboer, Verdonschot & Van Der Werf, 2005). Thus, the species association approach is relevant on the debate about using chironomids in biomonitoring programmes in the tropics. This is because, if a group of taxa exhibit similar responses to major environmental factors, particularly anthropogenic stressors, then one could select members of that group that are easily collected and identified as a surrogate for the others. Such an approach could be a way of monitoring biodiversity in freshwater ecosystems, in situations where reliable species-abundance lists are lacking.

The problem of explaining chironomid taxon association based on environmental variables is a typical problem of model selection (see Stephens, Buskirk & del Rio, 2007). For this reason, the null hypothesis significance testing approach may be inappropriate and an alternative is preferable. Here we use a model selection approach based on Akaike´s Information Criteria (AIC; see Burnham & Anderson, 2002) to analyse chironomid taxon association patterns. As the ecological processes interact dynamically at multiple spatial scales (Levin, 1992; Wagner & Fortin, 2005), we used local, landscape and spatial variables as predictors in our analyses. Specifically, our objectives here were two-fold. First, we wanted to know whether chironomid assemblages in Neotropical streams have clear taxon associations (are there groups of concordant taxa that respond similarly to environmental gradients?). Second, if so, how well can these associations be explained by a set of models containing information from multiple spatial scales (local, landscape and spatial variables)? We used the idea of multiple filters, in which to establish a viable population in a particular site each species has to pass through several environmental filters operating at different spatial scales (Poff, 1997). We expected that the filtering processes could act on taxon characteristics, and only groups of concordant species that possess suitable traits can pass the filter at each scale. We then considered the implications of our findings for the biomonitoring and conservation of Neotropical streams.

Methods

Study area and selection of streams

São Paulo state has an area of approximately 248,800 km^2, and a human population of about 40 million (22% of the Brazilian population). The region is composed of four major vegetation types, the coastal forest or Atlantic Rain Forest, the tropical seasonal forest or Atlantic semi-deciduous forest, the Mixed Atlantic Rain Forest, and Cerrado (Brazilian savanna). The Atlantic Rain Forest grows at low to medium altitude (< 1,000 m a.s.l.) on the eastern slopes of mountain chains running close to the coastline from southern to northeastern Brazil. The Atlantic semi-deciduous forest and Cerrado extend across the plateau (usually > 600 m a.s.l.) in the central and southeastern parts of the country. The climate of São Paulo varies from tropical to subtropical. The Atlantic Rain Forest and the Mixed Atlantic Rain Forest have a warm and wet climate without a dry season, while the Atlantic semi-deciduous forest and Cerrado have a more seasonal climate with a comparatively severe dry season, generally from April to September. The Atlantic Forest is among the most threatened tropical forests in the world, having been reduced to 7% of their original cover in the interior region of São Paulo state, although the coastal region retains more than 30% of its original cover (Ribeiro *et al.*, 2009). Most remnants are found on sheltered, steep mountain slopes, and are <50 ha in size (Ribeiro *et al.*, 2009).

The present study was conducted in 61 first- and second-order streams across the São Paulo state (Fig. 1). Of these, 47 were located in protected conservation areas, and 14 drained an impacted landscape. The streams from well-preserved regions are typical of Brazilian forested headwater streams, with water depth less than 50 cm, tree canopy coverage exceeding

70% of the channel, an absence of macrophytes, high dissolved oxygen concentration, low conductivity, and slightly alkaline to acid water. Water temperature typically ranges from 15 to 23ºC. The riparian vegetation along all streams is well-preserved. The fourteen impacted streams lay in three of the most common land uses in the São Paulo state: *Eucalyptus* plantation (*n*=4), sugar-cane plantation (*n*=5) and pasture (*n*=5).

Chironomid sampling and identification

We used data on chironomid larvae distribution extracted from the "Macroinvertebrates database" compiled by the research group of the "Laboratório de Entomologia Aquática da Universidade Federal de São Carlos (SP)". These data were collected during the dry seasons of 2001 (three streams), 2005 (24 streams), and 2006 (34 streams) using a Surber sampler (0.1 m^2 area and 250 µm mesh size). Our group has been continually visiting all sampling areas since 2001 and has not noticed any drastic change in land use during this period, particularly with regard to forested streams, which are in protected conservation areas.

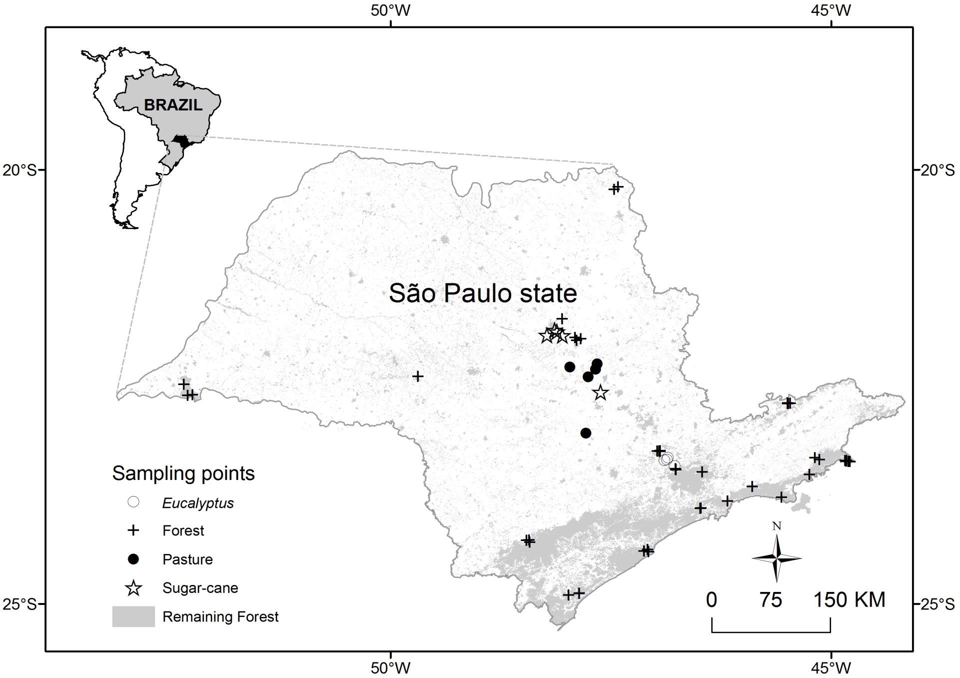

Figure 1. The location of the study sites in São Paulo state, Brazil. The dominant land use for each sampling point is indicated by symbols.

Samples were taken at each stream on one occasion; six samples (three samples in pools and three in riffle sites) were taken randomly along a 100 m stretch of each stream. All specimens were counted and identified to the genus level, bearing in mind the limited knowledge available for Neotropical fauna. The specimens have been deposited in the collection of the "Laboratório de Entomologia Aquática da Universidade Federal de São Carlos (SP)". Illustrations of most taxa can be obtained from the senior author.

Chironomid taxon association response variables

We applied Kendall's coefficient of concordance (*W*), following Legendre (2005), to identify significantly associated groups of genera. This coefficient is a measure of the concurrence among several judges who are evaluating a given set of objects (Legendre, 2005). In our case, the ‘judges’ are chironomid genera. Firstly, we conducted an overall global test of independence using the Hellinger-transformed abundance of all taxa collected (for details about Hellinger transformation, see Legendre & Gallagher, 2001). In this first test, the rank values in all genera are permuted at random, independently from genus to genus. Secondly, if the null hypothesis (independent rankings of the genera) was rejected, we performed an *a posteriori* analysis of concordance using the modified form of the permutation test to identify the genera that were significantly associated. Here, the null hypothesis is the independence of the genus subjected to the test, with respect to all the other genera. The modified test differs from the overall test in the sense that only the genus under test is permuted. If a genus is concordant with one or several other genera, shuffling its values at random should break the concordance and have a conspicuous influence on the W statistics (Legendre, 2005). Subsequently, we explored through a principal component analysis the possibility of more than one group of concordant taxa, and we eliminated taxa that occurred at low abundance and frequency and showed distinct patterns in the PCA plot (isolated groups). Finally, we used the sum of the abundances of the significantly associated genera (log [x + 1]) as the response variable representing ‘chironomid taxon association’ (hereafter CTA).

Local variables

Conductivity and pH were measured at three different sections of each stream using a Horiba U-10 or a Yellow Springs-556 water checker equipped with multiple probes. We used the mean of these measures in the statistical analyses. Predominant substrata were estimated visually as the proportion of the stream bottom covered by boulder and cobble (>256 mm), gravel (2-255 mm), sand (0.125-2 mm) and mud (<0.125 mm). To assess physical and biological conditions in the riparian zone and stream channel morphology at the local scale, seven metrics and their respective scores from RCE - the “Riparian Channel and Environmental Inventory” for small streams (Petersen Jr., 1992) were applied to each sampling site (consisting of 100 m of stream). These metrics were: 1, land-use pattern beyond the immediate riparian zone; 2, width of riparian zone from stream edge to field; 3, completeness of riparian zone; 4, vegetation of riparian zone within 10 m of channel; 5, retention devices; 6, channel sediments; and 7, stream-bank structure. Thus, our RCE final score for each stream refers to the sum of the scores of these seven metrics.

Landscape metrics and macro-regional variables

Landscape ecology has been recognized as an important approach for understanding biodiversity patterns and the underlying processes and mechanisms in aquatic systems (Wiens, 2002). Part of its importance comes from the potential to provide data about landscape modification that can directly impact management efforts (Johnson, 2007). In this study, we incorporated compositional and configuration landscape metrics as potential predictors of CTA.

To compute the landscape metrics, we delineated a circular buffer area (500 m radius, ca 78.5 ha) around a point located in the center of the stream channel of each of the 61 sampling sites (see Umetsu *et al.*, 2008; for application of landscape metrics based on buffers of varying width). Buffers of different width were also delineated, but added no new significant information relative to the metrics derived from 500 m buffer. Some of our landscape metrics were derived from a land cover map at a scale of 1:50,000 from the Forestry Institute of São Paulo (Kronka, 2005; Metzger *et al.*, 2008). Macro-regional climatic variables, derived from coarse-scale maps were also included in this set of variables. Landscape metrics derived from the land cover map were the land use cover, the total edge contrast index, and the edge density (see below for explanation). The macro-regional variables were the enhanced vegetation index (EVI), the rainfall and the irradiance, all of which are indicators of primary production and biomass accumulation. We also included a measure of altitude in our set of landscape metrics. A description of the metrics presented above is given below:

1- Land use cover. Area of forest, area of *Eucalyptus* plantation, area of agriculture, area of sugar cane plantation, and area of urban areas. These metrics represent the total area cover by a land use within the buffer. This information was provided by the Forestry Institute of São Paulo for the year 2005. The cover classes were obtained by visual inspection of Landsat images, on a scale of 1:50,000 and with a spatial resolution of 30 m.

2- Total edge contrast index (TECI). This metric represents a comparison of all the edges of a particular patch across the entire buffer according to an 'edge contrast weight' (e.g., forest to forest =0, forest to *Eucalyptus* plantation = 0.5, forest to agriculture = 0.7, forest to sugar-cane plantation = 0.8 and forest to urban areas = 1).

3- Edge density (LED). This metric represents the total edge length divided by the total landscape area. LED = (E/A)10000, where E is the total length (m) of edge in the landscape area and A is the total landscape area (m^2).

4 - Enhanced vegetation index (EVI). This is a general measure of foliar biomass. The index is derived from the MODIS sensor (Bagan *et al*., 2005) and was developed to optimize the vegetation signal with improved sensitivity in high biomass regions, and to improve vegetation monitoring through decoupling of the canopy background signal and a reduction in atmospheric influences. We included four variables based on EVI measures: the EVI for the autumn (EVI AR) and for the winter (EVI AM), and both the range (EVI WR) and mean (EVI WM) between the two seasonal variables.

5 - Rainfall was obtained from the São Paulo state Rainfall database.

6- Irradiance was obtained from the Brazilian Irradiation Atlas. We used mean values of the irradiation bands of São Paulo state.

7 - Altitude was calculated using the mean value of the altitude in a circle of 500-m radius around each sampling site. We used the Digital Elevation Model provided by the Shuttle Radar Topography Mission (SRTM/NASA; http://www2.jpl.nasa.gov/srtm).

The cover area, TECI and LED metrics were calculated using FRAGSTATS 3.3 (McGarigal *et al*., 2002). The EVI and altitude values were calculated using the Zonal statistics tool in ArcGis 9.

Spatial variables

Geographic space can be considered either as a factor responsible for ecological structures, or as a confounding variable that introduces biases when it is ignored in a spatial analysis (see Legendre, 1993). In the second case, a correlation between pairs of observations (spatial autocorrelation) is commonly found in ecological data. Thus, more complex strategies for data analyses are required (Diniz-Filho, Bini & Hawkins, 2003).

We created spatial variables following the approach proposed by Borcard & Legendre (2002), where eigenvectors with positive eigenvalues were extracted from a spatial matrix consisting of the distances between all pairs of streams (see also Thioulouse, Chessel & Champely, 1995 for an early use of this approach). These spatial eigenvectors can be considered as independent schemes of how streams are geographically related to each other, expressed as a set of new variables indicating the spatial relationships (i.e., spatial structure) among them (Borcard *et al*., 2004; Diniz-Filho & Bini, 2005; Griffith & Peres-Neto, 2006).

Recently Diniz-Filho, Rangel & Bini (2008) stressed that shifting from a classical significance testing of a null hypothesis to an information theoretical approach does not guarantee a solution to the problem of spatial autocorrelation. The inclusion of spatial eigenvectors is a further safeguard against the problems caused by the presence of spatial structure in the model residuals in information theoretic approaches, just as much as in classical null hypothesis testing. Furthermore, spatial eigenvectors can account for the inability to measure an environmental variable that is spatially structured. We selected eigenvectors with significant patterns of spatial autocorrelation. We evaluated these patterns by using Moran's *I* based correlograms with 10 distance class intervals, established in such a way that the number of pairs of sites compared at each distance class tends to be the same. A correlogram allows one to evaluate the level of autocorrelation as a function of spatial distance, thus providing a description of the level of spatial dependence in the data and, at the same time, is useful for examining the nature of the spatial structure (e.g., gradients or patches) displayed by each variable (eigenvectors in our case). We assessed the significance level of each Moran's *I* coefficient with 999 permutations (Sokal & Oden, 1978a, b), and a correlogram as a whole was considered to be significant (at a significance level of $P \leq 0.05$) if at least one of the Moran's *I* coefficients was significant at P/k, where k is the number of distance classes used (following the Bonferroni criterion; see Oden, 1984).

It is important to note that a spatial eigenvector is not a variable with ecological meaning, it is a mathematical construction. The amount of variation attributed to spatial variables is probably related to an "unexplored" variable (e.g., dispersal) that could generate the observed pattern. Although there is an increasing number of studies on chironomids in the Neotropical region (Fittkau, 2001), and some information on dispersal patterns of adults and larvae in other regions (e.g., Delettre & Morvan, 2000; Silver, Wooster & Palmer, 2004), to date no study has examined specifically the ability of chironomids to disperse in heterogeneous landscapes as those sampled in our studied. Thus, given the absence of specific information we consider our exploratory approach, including all distances among the sites, as the best option.

Data analyses

For each group of variables (i.e., local and regional-scale variables) we used a principal component analysis (PCA) to reduce data dimensionality. Subsequently, we applied a randomization procedure based on eigenvalues to determine the number of non-trivial axes to be used as local and landscape-scale predictors of CTA abundance. This method is based on the randomization of the values within variables and the subsequent recalculation of the correlation matrix and associated eigenvalues. After repeating this process many times, a null distribution is generated for comparison with the observed eigenvalues. The *P*-value associated with the *i*-th eigenvalue is calculated as the number of random eigenvalues (which were obtained after reshuffling the data) that were equal to or larger than the observed (plus one) divided by the number of randomizations (plus one; see Peres-Neto, Jackson & Somers, 2005). We used 999 randomizations to assess the significance level of the eigenvalues. For each PCA, a method based on the broken-stick model (see Peres-Neto, Jackson & Somers, 2003) was used to determine which original variables were significantly correlated with the selected axes. As principal component axes scores are new orthogonal variables, their use in multiple regression analysis, as explanatory variables summarizing each multidimensional dataset, can minimize the problems caused by multicollinearity (King & Jackson, 1999). Due to the reduced number of variables (non-trivial axes) over-parametrization problems are also minimized, avoiding the Freedman's paradox, i.e., too many variables with a small sample size (see Burnham & Anderson, 2002).

Following the recommendations of Burnham & Anderson (2002), we formulated *a priori* models containing different explanatory variables (local, landscape and spatial variables) representing biological hypotheses that could explain CTA. Model 1: CTA can be best explained by principal component axes representing the main patterns of local variables, such as pH, conductivity and substratum characteristics; Model 2: processes acting on wider landscape scales (e.g., the landscape structure) are responsible for shaping CTA, so it can be best explained by principal component axes representing the main patterns of landscape variables, such as land cover, edge density and rainfall; Model 3: there may be a spatially structured missing variable that influences the CTA (e.g., dispersal), so it can be best explained by spatial eigenvectors indicating the spatial relationships among streams. Nevertheless, it could be that CTA can be better explained by more than one model. So, based on the combination of these previous three models and using these parameters (local and landscape PCAs, and spatial eigenvectors) we constructed four additional hypothetical models (Table 1), totaling seven models.

The minimum adequate model was selected using the Akaike Information Criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002). For each model, we calculated the Akaike Information Criterion (AIC) using the modified index for small sample sizes (AIC_c). The best models are those with the lowest AIC_c values, which are computed by:

$$AIC_c = n \log(\Sigma\, e_i^2/n) + 2\mathrm{K} + [2K(K+1)/(n-K-1)] \quad \text{(eq. 1)}$$

where e_i is the residual of the i-th observation for a candidate model, K is the number of parameters in the model, and n is the sample size.

Each model was represented by the entire set of explanatory variables, i.e., all selected PCA axes representing the local filters, all selected PCA axes representing the landscape filters, and spatial variables representing geographical relationships between sampling sites. For example, model 1 (local filters alone) was represented by:

$$E(y)=\beta_0+\beta_1 PCA1+\beta_2 PCA2 \quad \text{(eq. 2)}$$

where β_0 is the intercept and β_i is the partial regression coefficient, estimated by ordinary least squares (OLS).

We first calculated AIC_c values for each model using the Spatial Analysis in Macroecology (SAM) software v.3 (Rangel, Diniz-Filho & Bini, 2006). After calculating AIC_c values for all models, we used the model with the lowest AIC_c value (the best model) and derived other metrics from it (Burnham & Anderson, 2002). We used the AIC_c of each model i to calculate the Δ_i value, which is the difference between AIC_{ci} and the minimum AIC_c found for the set of models analysed. Values of Δ_i higher than seven indicate models that have poor fit relative to the best model, whereas values less than two indicate models that are equivalent to the minimum AIC_c model (Burnham & Anderson, 2002). These cut-off values are arbitrary but, more importantly, Δ_i can also be used to compute the Akaike weight of each model (w_i), which is a measure of the chance that a model is the best one. These weights can be calculated by:

$$w_i = \exp(-1/2\Delta_i)/\Sigma_i[\exp(-1/2\Delta_i)] \qquad \text{(eq. 3)}$$

where $\exp(-1/2\Delta_i)$ approximates the likelihood of the model. w_i values were normalized across the set of candidate models to sum to one, and interpreted as probabilities (Johnson & Omland, 2004).

When no single model is clearly superior to the others in the set (i.e., $w_{\text{best}} < 0.9$), then model averaging is recommended (Johnson & Omland, 2004). This is usually done in order to obtain robust estimates of linear regression coefficients and to reduce the extent of bias that would arise if one uses only one model to make conclusions. In model averaging it is possible to average the estimated coefficients of the explanatory variables across all models in which they are present, but weighting this average according to the w_i value of the model. Burnham & Anderson (2002) advise that, when possible, one should use inference based on more than one model, via model averaging. Thus, when necessary, we estimated new linear regression coefficients by averaging each coefficient across all models in which it was present (see details in Burnham & Anderson, 2002). For example, $\beta_1$localPC1 would be the average of the coefficients found in models 1, 4, 5 and 7, whereas $\beta_2$landPC2 would be the average of the coefficients found in models 2, 4, 6 and 7 (see Table 1).

Table 1. A set of *a priori* candidate models reflecting our hypotheses relating local variables, landscape metrics and spatial filters to chironomid taxon association; n=61 in all cases. The number of parameters to be estimated in each model is also shown. Notice that the maximum number of parameters (12) was estimated for the seventh model because we extracted two non-trivial principal components (PCs) from local variables, three PC from landscape metrics and seven eigenvectors with significant spatial structures (see Results).

Model code	Model	Number of parameters
1	Local variables	2 (PCs)
2	Landscape variables	3 (PCs)
3	Spatial variables	7 (Spatial eigenvectors)
4	Local + Landscape variables	5
5	Local + Spatial variables	9
6	Landscape + Spatial variables	10
7	Local + Landscape + Spatial variables	12

Results

Local variables

The first two principal component axes (PC1 and PC2) were significant ($P < 0.001$) according to the randomization procedure based on the eigenvalues (Table 2). The first principal component (explaining 37.1 % of the total variability) tended to segregate “forested streams”, mostly characterized by high values for RCE, cobble and gravel, from “impacted streams" or lowland streams, mostly covered by *Eucalyptus* plantation and dominated by mud (Table 2; Fig. 2). Most sites with low and positive scores on PC1 were in the Atlantic forest mountain range (eastern coast) while those with higher and negative PC1 values were in the non-mountainous areas of the state (western part; Fig. 2). The second principal component (22.9%) was positively correlated with pH and conductivity and negatively correlated with dissolved oxygen concentration, clearly separating streams located in karstic regions and some anthropogenically impacted streams (with high pH and conductivity values and low dissolved oxygen concentrations) from the others (Table 2; Fig. 2).

Table 2. Loadings of the local environmental variables on the first three principal component axes. (Cond: Conductivity, DO: dissolved oxygen, RCE: Riparian Channel Environmental Protocol). Significant loadings (according to the broken-stick criterion) are indicated in bold. The eigenvalues associated with the non-significant axes (third up to eighth) were: 1.13, 0.81, 0.62, 0.34, 0.30 and 0.01.

	Axes	
Variables	1	2
pH	0.40	**0.76**
Cond	-0.21	**0.75**
DO	0.20	**-0.69**
RCE	**0.87**	0.03
% cobble	**0.54**	**0.36**
% gravel	**0.72**	-0.12
% sand	**0.47**	-0.27
% mud	**-0.97**	0.02
Eigenvalues	2.97	1.83
% of variance	37.08	22.9
P	< 0.001	< 0.001

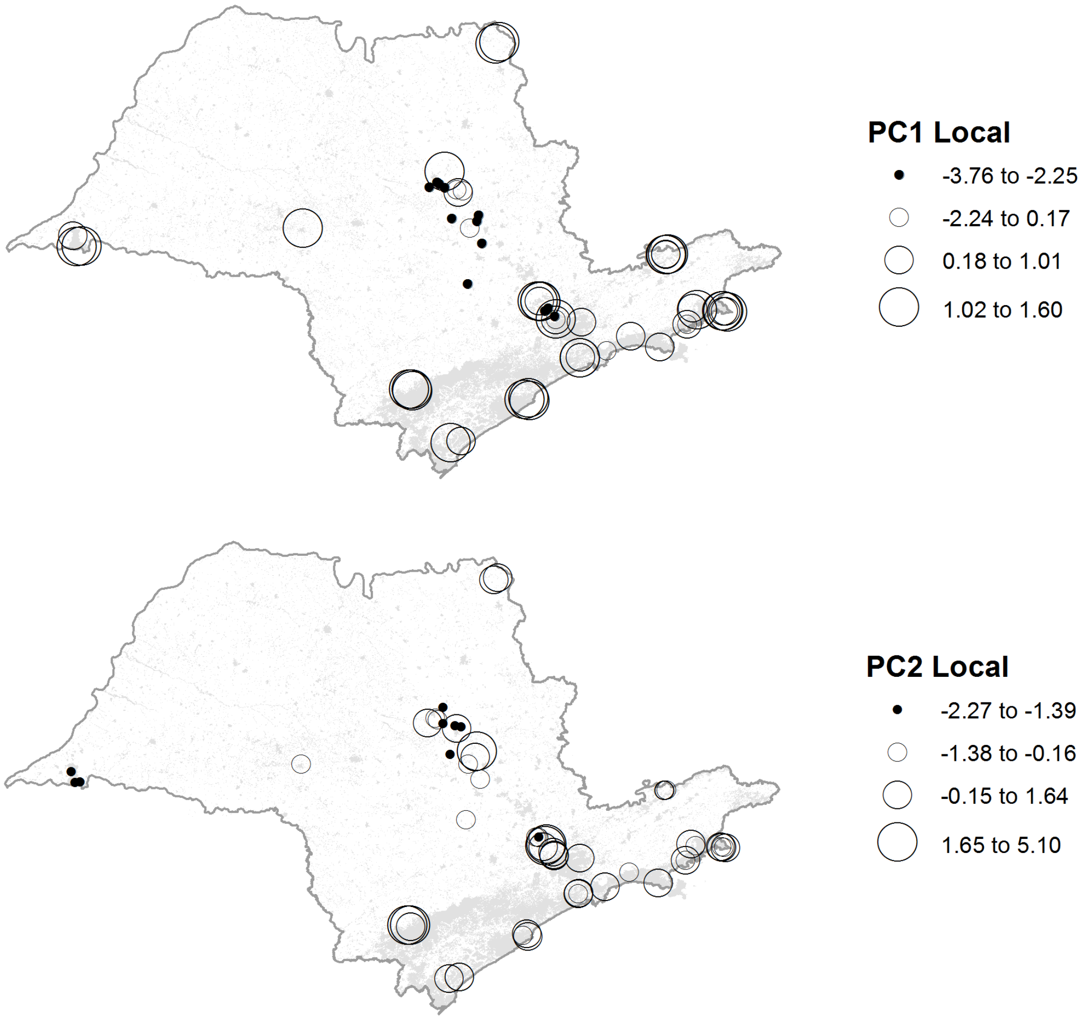

Figure 2. Geographical patterns of principal component scores generated from local environmental variables.

Landscape metrics and macro-regional variables

The first three axes selected based on landscape metrics accounted for 52.9% of the total variability (Table 3). The first axis expressed a gradient of land use; most sites in areas dominated by agriculture and sugar-cane had high negative scores. Streams in areas dominated by *Eucalyptus* plantations had intermediate scores, whereas streams in forested areas had high positive scores (eastern coastal region). The second axis was related to plant biomass around the streams (EVI measures) and urban areas; it also roughly differentiated streams in forested areas and *Eucalyptus* plantations from those in other land uses. The third axis was most closely related to agriculture, *Eucalyptus*, rainfall and altitude, which approximately corresponds to the dominant landscape gradient at the state scale. The western part of São Paulo state is located on a plateau with a continental climate and has areas historically dominated by agriculture, whereas the eastern coastal part is mountainous with higher precipitation (Fig. 3).

Spatial variables

Out of the eight eigenvalues extracted from the geographic distance matrix among sampling sites, seven presented significant ($P \leq 0.005$) patterns of spatial autocorrelation (i.e., at least one Moran's I coefficient of the correlogram was significant at the Bonferroni corrected level of probability). Specifically, the seventh eigenvector was discarded. The first eigenvector accounted for the highest level of spatial autocorrelation, representing a pattern with two major groups of similar values: one group with relatively high values and the other with relatively low values (Fig. 4). The other eigenvectors represented spatial patterns at more local scales. In these cases, significant autocorrelations coefficients were, in general, detected for only a few distance classes (detailed results not shown).

Table 3. Loadings of the landscape variables on the first three principal component axes. EVI, enhanced vegetation index; WR, winter range; WM, winter mean; AR, autumn range; AM, autumn mean; ED, Edge Density; TECI, Total Edge Contrast Index. Significant loadings (according to the broken-stick criterion) are indicated in bold. The eigenvalues associated with the non-significant axes (fourth up to fourteenth) were: 1.44, 1.33, 1.09, 0.76, 0.73, 0.48, 0.34, 0.20, 0.13, 0.11 and 0.00.

	Axes		
Variable	1	2	3
Area of agriculture	**-0.46**	-0.06	**0.59**
Area of sugar cane	**-0.51**	0.31	0.36
Area of *Eucalyptus*	-0.27	**-0.45**	**-0.58**
Area of forest	**0.80**	0.03	-0.16
Urban area	-0.06	**0.47**	**-0.41**
Landscape ED	**-0.45**	-0.26	0.30
Landscape TECI	0.47	**-0.44**	0.08
EVI WR	**0.71**	0.14	-0.07
EVI WM	**0.53**	**-0.67**	0.07
EVI AR	0.00	0.24	-0.14
EVI AM	0.16	**-0.62**	**0.47**
Altitude	**-0.54**	**-0.49**	**-0.45**
Irradiance	**-0.72**	0.06	0.01
Rainfall	**0.65**	0.38	0.33
Eigenvalues	3.66	2.09	1.66
% of variance	26.13	14.92	11.88
P	<0.001	<0.001	0.014

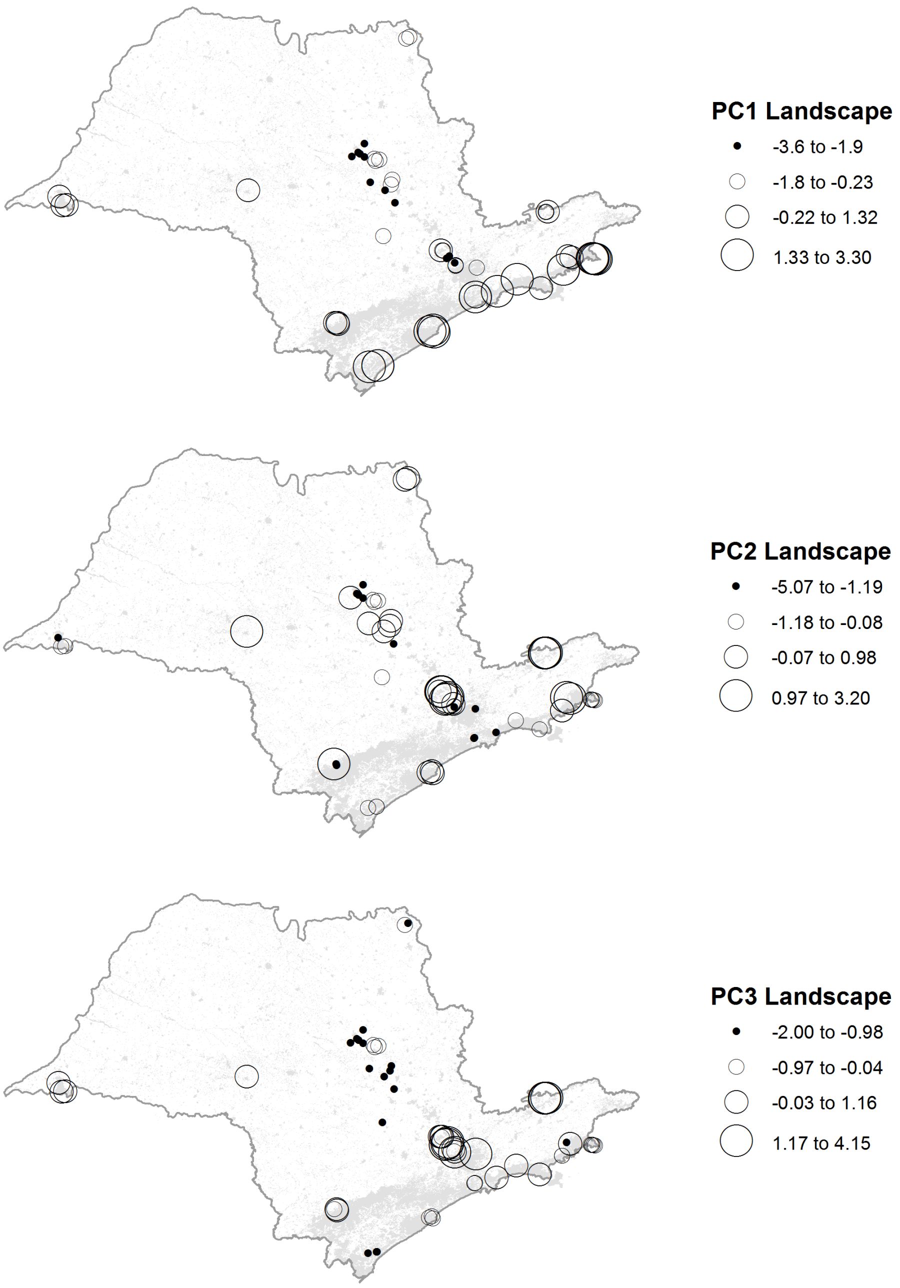

Figure 3. Geographical patterns of principal component scores generated from local landscape variables.

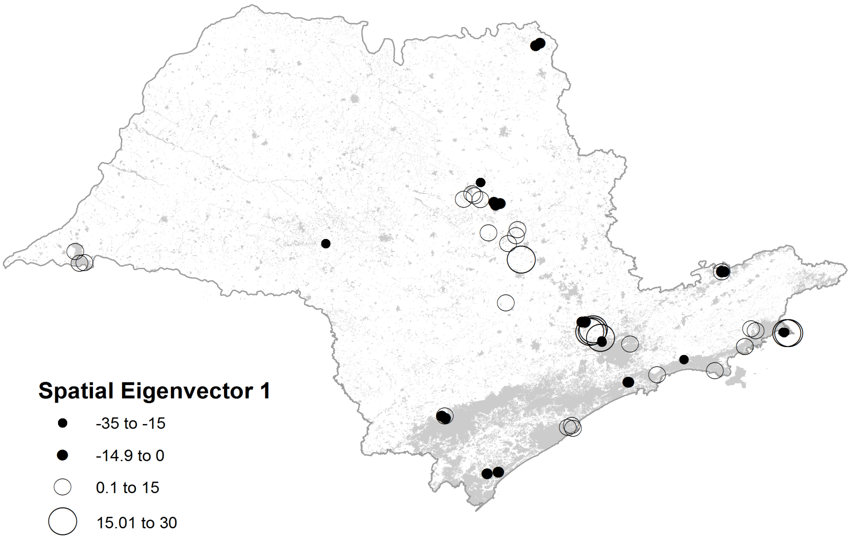

Figure 4. Patterns depicted by spatial eigenvector 1, showing the relationship among streams. Open symbols refer to positive values and closed to negative.

Chironomid assemblage descriptors: associated taxa

We detected a significant level of concordance in the first step of the Kendall's concordance analysis involving the 50 chironomid taxa collected in our study ($W = 0.09991$; $P = 0.001$ after 9,999 permutations). *Tanytarsus*/*Caladomyia*, *Ablabesmyia*, *Tanypus*, *Parametriocnemus*, *Pentaneura*, Orthocladiinae gen. 2, *Nanocladius, Beardius*, *Cricotopus*, *Polypedilum*, and *Rheotanytarsus* were identified as concordant taxa (Table 4). After applying a PCA to this group, we found that *Beardius*, *Cricotopus*, Orthocladiinae gen. 2, and *Tanypus* seemed to be unrelated to the others and, as they were also scarce, we excluded them from the concordant group. It is highly probable that *Beardius*, *Cricotopus*, Orthocladiinae gen. 2 and *Tanypus* were grouped as concordant due to their absence from most sampling areas. The summed abundances of the seven remaining taxa (representing 63.95% of total abundance) was the response variable, i.e., the chironomid taxon association (CTA), used in the models described below (Fig. 5). In general, associated genera were less abundant in streams located in the Atlantic Forest region in the eastern part of São Paulo state (Fig. 6).

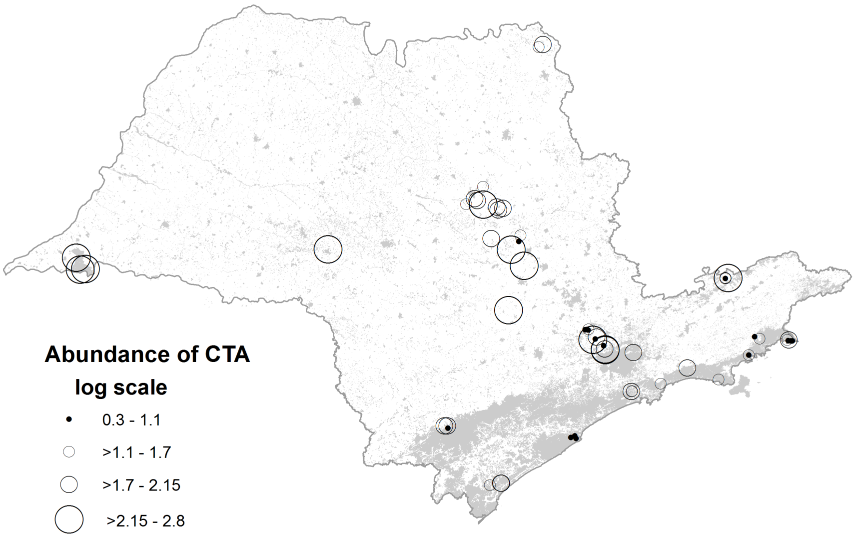

Figure 5. Geographical distribution of chironomid taxon association (CTA) across São Paulo state.

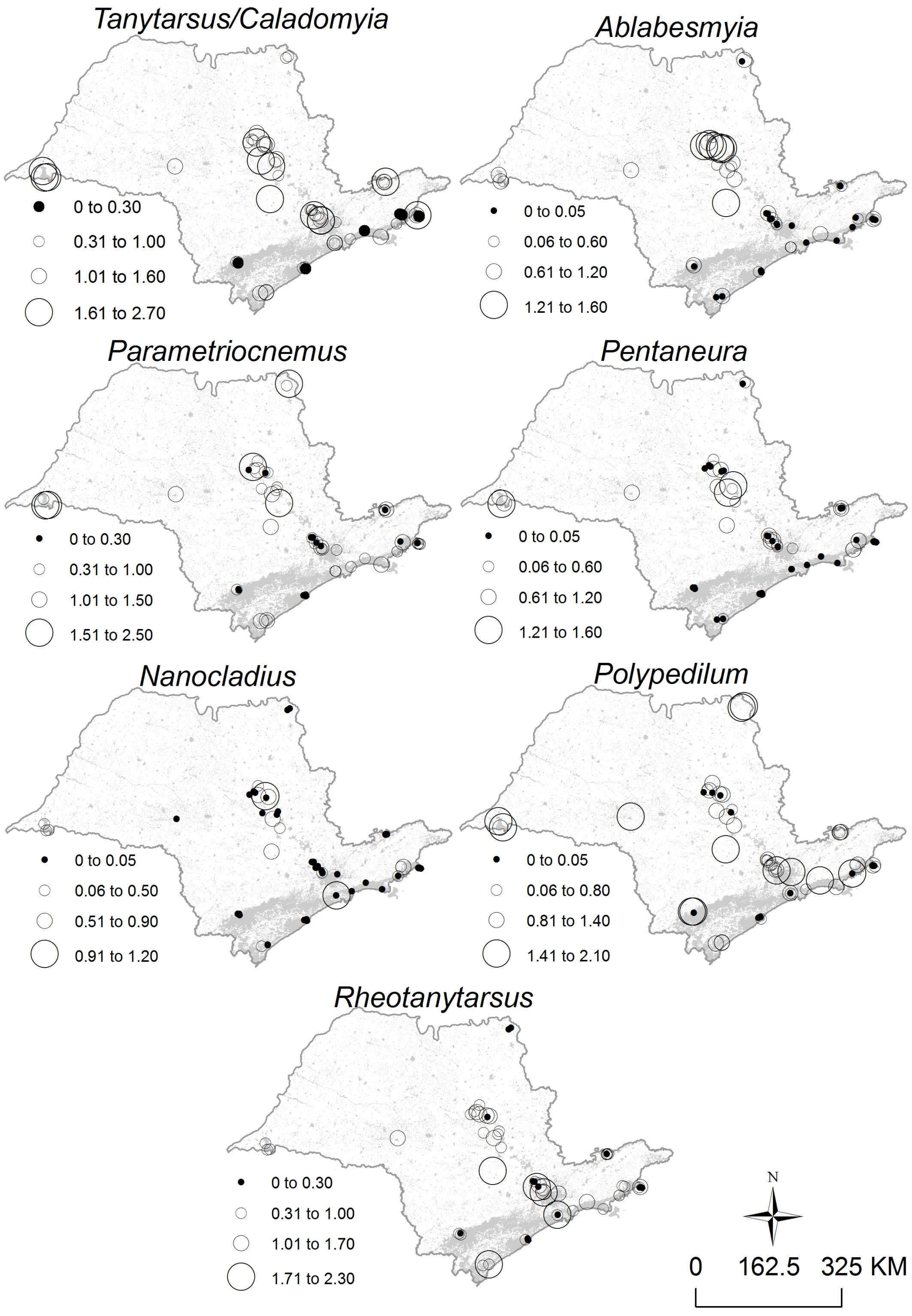

Figure 6. Spatial patterns of chironomid associated genera across São Paulo state. Symbols refer to classes of abundance (log scale).

Relationships between chironomid taxon association and filters: the minimum adequate model

The best-supported model according to the AIC_c criterion was the global model (Model 7: Table 5), which represented local and landscape environmental filters, and spatial eigenvectors. This model explained 42.6% (adjusted R^2) of the variance in the CTA (Table 5) and had about a 49.4% probability of being the best model according to the Akaike weights (w_i). However, model 5 (local environmental filters and spatial eigenvectors) had a Δ_i value less than 2, with a 26.4% probability of being the best (Table 5), and also seemed to provide support for explaining CTA. Because of this uncertainty, a model averaging procedure based on all models was necessary (see Methods). The third ($\Delta_i = 2.77$) and fourth ($\Delta_i = 4.62$) best models had w_i values of 0.124 and 0.049 respectively, whereas the summed weights for the models ranked 5-7 was 0.069.

Standardized partial regression coefficients of local and landscape filters, including seven spatial eigenvectors derived from model averaging, allowed an estimation of which axes were most strongly correlated with taxon associations, independently of spatial autocorrelation at distinct scales. CTA was negatively related to local PC1 (proportion of mud in the stream bed; standardized regression coefficient, $b' = -0.46$) and PC2 (pH and conductivity; $b' = -0.20$) as well as to landscape PC1 (area covered by forest; $b' = -0.43$) and PC2 (area covered by urban areas; $b' = -0.11$), and positively related to landscape PC3 (area covered by in *Eucalyptus* plantations; $b' = 0.11$). The comparison among the standardized regression coefficients (b') indicates that variation in CTA was better explained by local PC1 and landscape PC1.

Table 4. Results of the *a posteriori* test of concordance involving all chironomid larvae collected. The 50 taxa were ordered by the values of the partial concordance statistics, r_j and W_j, to facilitate interpretation. *P* = permutational probability based upon 9,999 random permutations. *P*H = probability after Holm adjustment. H_0: This species is not concordant with most of the others - Reject H_0 at $\alpha = .05$.

Taxa	**Total abundance**	**Mean abundance (SD)**	r_j	W_j	***P***	***P*H**
Tanytarsus/Caladomyia	2307	37.81 (74.45)	0.176	0.192	0.000	0.005
Ablabesmyia	311	5.09 (9.99)	0.163	0.180	0.000	0.005
Tanypus	2	0.03 (0.17)	0.162	0.178	0.001	0.033
Parametriocnemus	1035	16.96 (46.71)	0.157	0.174	0.000	0.005
Pentaneura	178	2.91 (6.49)	0.154	0.171	0.000	0.005
Orthocladiinae gen. 2	3	0.04 (0.38)	0.149	0.166	0.001	0.025
Nanocladius	54	0.88 (2.10)	0.149	0.166	0.000	0.005
Orthocladiinae gen. 3	183	3 (19.5)	0.141	0.158	0.016	0.470
Beardius	18	0.29 (0.92)	0.139	0.156	0.000	0.013
Cricotopus	195	13.19 (13.30)	0.128	0.146	0.000	0.017
Parachironomus	33	0.54 (3.33)	0.126	0.143	0.008	0.269
Polypedilum	905	14.83 (20.43)	0.125	0.143	0.000	0.005
Pelomus	31	0.50 (1.44)	0.122	0.139	0.002	0.062
Clinotanypus	30	0.49 (1.51)	0.121	0.139	0.005	0.153
Rheotanytarsus	952	15.60 (32.87)	0.121	0.138	0.001	0.033
Onconeura	80	1.31 (3.76)	0.106	0.124	0.002	0.089
Coelotanypus	32	0.52 (3.19)	0.105	0.123	0.005	0.165
Labrundinia	65	1.06 (2.03)	0.105	0.123	0.004	0.137
Cryptochironomus	66	1.08 (2.82)	0.103	0.121	0.004	0.133
Stenochironomus	135	2.21 (4.68)	0.101	0.119	0.002	0.080
Pseudochironomini gen.3	223	3.65 (18.75)	0.094	0.112	0.010	0.319
Larsia	509	8.34 (29.56)	0.093	0.111	0.013	0.375
Pseudochironomini gen. 2	4	0.06 (0.30)	0.090	0.108	0.043	1.022
Zavreliella	14	0.22 (1.01)	0.086	0.105	0.017	0.476
Fittkauimyia	20	0.32 (1.05)	0.078	0.096	0.046	1.060
Dicrotendipes	5	0.08 (0.27)	0.073	0.092	0.080	1.670

Stempellinella	88	1.44 (5.01)	0.066	0.085	0.036	0.578
Thienenanimyia	11	0.18 (0.73)	0.065	0.084	0.036	0.936
Cladotanytarsus	4	0.06 (0.39)	0.065	0.084	0.036	0.990
Harnischia gen. 2	8	0.13 (0.66)	0.064	0.083	0.086	1.670
Djalmabatista	199	3.26 (7.95)	0.063	0.082	0.092	1.670
Thienemanniella	149	2.44 (8.65)	0.061	0.079	0.064	1.404
Stempellina	8	0.13 (0.68)	0.052	0.071	0.082	1.670
Paratendipes	114	1.86 (5.57)	0.051	0.070	0.082	1.670
Rheocricotopus	16	0.26 (1.19)	0.049	0.068	0.169	2.535
Corynoneura	114	1.86 (4.56)	0.043	0.063	0.106	1.702
Procladius	22	0.36 (1.66)	0.024	0.043	0.221	3.088
Lauterborniella	4	0.06 (0.50)	0.019	0.039	0.247	3.208
Chironomus	212	3.47 (11.38)	0.014	0.034	0.385	4.411
Paraphaenocladius	3	0.04 (0.38)	0.005	0.025	0.421	4.411
Harnischia gen. 1	4	0.06 (0.30)	0.003	0.023	0.368	4.411
Lopescladius	49	0.80 (2.14)	0.001	0.021	0.407	4.411
Macropelopini	2	0.03 (0.17)	-0.005	0.015	0.425	4.411
Aff. *Stackelbergina*	3	0.04 (0.28)	-0.006	0.014	0.487	4.411
Gymnometriocnemus	2	0.03 (0.17)	-0.007	0.013	0.452	4.411
Endotribelos	550	9.01 (16.45)	-0.014	0.006	0.430	4.411
Fissimentum	7	0.11 (0.40)	-0.014	0.006	0.605	4.411
Zavrelimyia	5	0.08 (0.41)	-0.018	0.002	0.593	4.411
Psedouchironomini gen.1	3	0.04 (0.21)	-0.029	-0.008	0.687	4.411
Orthocladiinae gen. 1	11	0.18 (0.91)	-0.049	-0.028	0.947	4.411

Table 5. Models of chironomid taxon association in the studied streams, built with different sets of explanatory variables, with their relative weights (w_i) derived from the Akaike information criterion (AIC_c) and adjusted R^2. Δ_i = difference between AIC_c-i and the minimum AIC_c found for the set of models compared.

Model code	Model	R^2-adjus.	AIC_c	Δ_i	w_i
7	Local + Landscape + Spatial	0.426	108.18	0	0.494
5	Local + Spatial	0.351	109.43	1.251	0.264
6	Landscape + Spatial	0.356	110.95	2.770	0.124
2	Landscape	0.195	112.80	4.623	0.049
3	Spatial	0.266	113.30	5.125	0.038
4	Local + Landscape	0.214	114.26	6.086	0.024
1	Local	0.122	116.74	8.563	0.007

Discussion

Ecological filters and chironomid associations

Even though it has been highly recognized that stream communities are structured by processes operating at several spatial scales (Vinson & Hawkins, 1998; Clarke *et al*., 2008), disagreements prevail about which scales and factors are the most influential. The best model in our study was the global model, which included local and landscape variables, and spatial information (i.e., the model with the highest number of parameters). In other words, models including variables from any single scale performed worse in fitting the data. Thus, our results add more evidence for the importance of different scales and spatial structure on community organization (Richards, Johnson & Host, 1996; Johnson *et al*., 2007).

The fact that the two models selected by AIC were a combination of local, landscape and spatial components indicates that variables at different scales can interact directly and indirectly in structuring chironomid taxon association. In general, the abundance of the associated genera tended to be lower in streams characterized by a low proportion of mud in the stream bed (local PC1) and on streams located in forested areas (landscape PC1), particularly those located in the well-preserved areas of the Atlantic coastal region. Geomorphology influences stream ecosystems and their communities through differences in water velocity, input of sediments, nutrient loading, material retention, decomposition rates and food availability (Frissel *et al.*, 1986). The low abundance of associated chironomids in the Atlantic Forest region seems to be related to the geomorphology of the area, which is characterized by high level of declivity and by a rock matrix. These may result in streams with poor retention of detritus and low nutrient concentrations (Richards *et al.*, 1997), features that are directly related to the predictor variables local PC1 and landscape PC1. The low abundance of chironomids in the coastal streams may also be related to the high abundance of predators like shrimps, ephemeropterans, plecopterans and trichopterans, when compared to streams inland (see Souza & Moulton, 2005; Roque & Trinho-Strixino, 2007 for fine-scale experimental evidence).

We found that some physicochemical factors also contributed to explaining the abundance of associated taxa. A low abundance of chironomids was found in streams with high pH and conductivity values (local PC2), located in the karstic region of the São Paulo state. The responses of chironomids to pH and conductivity are variable with different patterns being observed in temperate and tropical regions (Cranston *et al.*, 1997). In our case, the low abundance of chironomids could be attributable to the high conductivity, due to high $CaCO_3$ concentration, high pH and nutrient-poor waters, which may negatively filter populations of some associated genera with acidophilic tropical species (e.g., *Polypedilum* and *Tanytarsus*). Larvae of these genera are usually numerous in naturally acidic and nutrient-enriched and/or polluted streams (see Cranston *et al.*, 1997). Model average coefficients also indicate that landscape PC2 and PC3 were the predictors that contributed the least (smallest partial coefficients) to explaining CTA. The abundance of associated genera tended to be higher in streams surrounded by forested watersheds (as indicated by EVI) and in streams not subjected to the direct influence of urban areas (landscape PC2). This last result was unexpected, particularly with regard to the genus *Polypedilum*, because these taxa are usually abundant in urban streams with high concentrations of nutrients and low dissolved oxygen (Cranston *et al*., 1997; Helson *et al*., 2006). However, it should be noted that, although some of our streams were located near urban areas, none receive organic effluents. Finally, streams located in *Eucalyptus* plantations (landscape PC3) also supported a lower number of chironomid larvae. This agrees with previous studies that have shown low abundance of macroinvertebrates in *Eucalyptus* streams, which may be a consequence of the changed hydrology of the system and/or of the low quality of detritus as food (Abelho & Graça, 1996). Note that streams surrounded by *Eucalyptus* forests were also characterized by a high proportion of muddy substratum and, according to our analysis, such streams should have supported a high abundance of chironomid larvae. Thus, the interplay between local and landscape filters can be visualized in this example. Specifically, although the abundance of chironomids is predicted to increase in muddy streams, the occurrence of *Eucalyptus* may alter this pattern.

The inclusion of spatial information among the best supported model indicates that other factors affected assemblage structures, such as colonization processes, unmeasured spatially autocorrelated local environmental variables, and dispersal pathways among habitat patches (Caley & Schluter, 1997). Furthermore, anthropogenic impacts are not randomly distributed in Southeastern Brazil. Most degraded areas are in the sedimentary basin, where intensive land conversion to agriculture (e.g., sugar cane and coffee) and pasture has occurred. These factors probably reflected some environmental variables that were spatially structured and that were captured by the spatial variables given by the eigenfunction analysis. Last but not least, models that included solely local or landscape variables were among the worst in explaining CTA, but when the spatial information was accounted for, and combined with environmental variables at both scales, they explained CTA in an appreciable manner. So, we urge future studies on stream insects' distribution to incorporate spatial information into data analysis.

Overall, our main result adds to the increasing number of studies that have pointed out the importance of considering both local and regional variables for explaining aquatic insect community patterns in streams. Moreover, chironomid taxon association seems to respond in a predictable way to land use gradients. This opens a promising new avenue for the exploration of patterns of chironomid distribution in tropical streams.

Implication for biomonitoring and environmental assessment in Neotropical streams

Most studies on surrogacy of aquatic biodiversity have focused on examining the effects of taxonomic resolution on assemblage patterns and the utility of higher taxa in bioassessment (Heino & Soininen, 2007). We have found a low number of associated genera (14% of the total number of taxa), which means that most taxa responded individualistically to the environmental gradients. In this context, although few data are available about the evolution of traits among chironomids, it should be remembered that some genera seem to have high phylogenetic inertia in some traits (e.g., all species of *Rheotanytarsus* are rheophilous) while others do not (e.g., different species of *Polypedilum* live in different habitats). In other words, the use of genera as bioindicators may be adequate for detecting general patterns only when within-genus variability, in terms of responses to environmental gradients, is low (see Poff *et al*., 2006). In relation to the utility of higher taxa as surrogate of groups of taxa, our findings indicate that the responses of chironomid associations to environmental gradients do not follow any high-level taxonomic classification (i.e., associated taxa belong to different tribes and subfamilies). This indicates that previous suggestions that subfamilies or tribes might be useful in biomonitoring of Neotropical streams are not well founded (Roque, Corbi & Trivinho-Strixino, 2000).

Although associated taxa represented a small proportion of the total generic richness, they accounted for 63.95% of total numerical abundance. This result indicates that we were dealing with the most common genera and that groups of these taxa respond similarly to environmental gradients. However, despite the fact that chironomid taxon association responded predictably to environmental and anthropogenic factors at distinct scales, the important question remains of whether monitoring just one of the associated genera as a surrogate for the whole group of concordant taxa would be sufficient for assessing impacts in streams? Unfortunately, the situation is not so simple. First, our study included a marked environmental gradient, ranging from extensive monocultures of sugar-cane to well-preserved areas, so the pattern detected may be valid only for strong gradients arising from human activities. In these cases other well-established bioindicators are also expected to perform well (see Bonada *et al*., 2006). Second, the concordant taxa *Tanytarsus*/*Caladomyia* complex, *Polypedilum*, and *Pentaneura* are among the most diverse, frequent and abundant genera in Neotropical streams (Coffman *et al*., 1992; Roque & Trivinho-Strixino, 2007; Roque *et al*., 2007). Together with the *Corynoneura* group they account for more than 40% of chironomid diversity in Southeastern Brazil’s Atlantic Forest streams (Roque *et al*., 2007). These taxa are characterized by different species that inhabit distinct types of environments. In this context, taxonomic resolution and taxon associations have practical consequences for freshwater biomonitoring. Identification to genus or the analysis of associations of genera should be used with caution for some monitoring purposes, because a number of genera contain species with different tolerances to a particular impact (see Cranston, 2000, Raunio, Paavola & Muotka, 2007). For example, some species of *Chironomus* can colonize extremely acid or hot habitats (Armitage, Cranston & Pinder, 1995; Cranston *et al*., 1997) whereas others are found only in pristine streams (Correia & Trivinho-Strixino, 2007). Thus, using generic level identification could in some cases result in misinterpretations of stream conditions.

Another fundamental issue is whether GIS metrics can explain patterns in community structure and make predictions in biomonitoring programmes? The use of landscape metrics to explain patterns in the biodiversity of stream macroinvertebrates is controversial. Some authors have reported strong relationships between catchment-derived variables and macroinvertebrate community organization (e.g., Townsend *et al*., 1997; Feld & Hering, 2007), whereas other studies have revealed a stronger explanatory power of habitat characteristics measured at the reach scale (e.g., Death & Joy, 2004; Heino, Mykra & Kotanen, 2008). In general, our results suggest that single-scale variables should not be taken into account alone, which adds more evidence that GIS metrics are valuable for predicting biological patterns in streams only when linked with local environmental features (Pyne *et al*., 2007).

In conclusion, chironomid associations in Southeastern Brazilian streams appear to be influenced by local and landscape filters. Moreover, the influence of some unmeasured and spatially structured environmental factors, as suggested by the importance of the spatial variables, cannot be discarded. This finding, although requiring caution, opens new possibilities for the use of a reduced number of taxa in the assessment of anthropogenic impacts on tropical streams.

Acknowledgments

We are grateful to the BIOTA/FAPESP team for helping us during the development of our project. The São Paulo state Research Foundation sponsored the study within the BIOTA/FAPESP – The Biodiversity Virtual Institute Program (www.biota.org.br). T. Siqueira received a scholarship from CNPq, L.M. Bini and S. Trivinho-Strixino are researchers of CNPq and acknowledge this agency for research grants. We would like to thank Professor Alan

Hildrew and two anonymous reviewers for their comments and suggestions that largely contributed to the improvement of this manuscript.

References

Abelho M. & Graca M.A.S. (1996) Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia*, **324**, 195-204.

Akaike H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716-723.

Allan J.D. (1995) *Stream Ecology: Structure and Function of Running Waters*. Chapman & Hall, London.

Armitage P.D., Cranston P.S. & Pinder L.C.V. (1995) *The Chironomidae: The Biology and Ecology of Non-Biting Midges*. Chapman Hall, New York.

Bagan H., Wang Q., Watanabe M., Yang Y. & Ma J. (2005) Land cover classification from MODIS EVI times-series data using SOM neural network. *International Journal of Remote Sensing*, **26**, 4999-5012.

Bengtsson J., Engelhardt K., Giller P., Hobbie S., Lawrence D., Levine J., Vilà M. & Wolters V. (2002) Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. In: *Biodiversity and Ecosystem functioning - Synthesis and perspectives* (Eds. M. Loreau, S. Naeem, P. Inchausti), pp. 209-220. Oxford University Press Inc, New York.

Bonada N., Prat N., Resh V.H. & Statzner B. (2006) Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual Review of Entomology*, **51**, 495-523.

Borcard D. & Legendre P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. *Ecological Modeling*, **153**, 51-68.

Borcard D., Legendre P., Avois-Jacquet C. & Tuomisto H. (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology,* **85**, 1826-1832.

Burnham K.P. & Anderson D.R. (2002) *Model selection and multimodel inference. A practical information-theoretical approach*. Springer, New York.

Caley M.J. & Schluter D. (1997) The relationship between local and regional diversity. *Ecology*, **78**, 70-80.

Clarke A., Nally R.M., Bond N. & Lake P.S. (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, **53**, 1707-1721.

Coffman W.P., De La Rosa C., Cummins K.W. & Wilzbach M.A. (1992) Species richness in some Neotropical (Costa Rica) and Afrotropical (West Africa) lotic communities of Chironomidae (Diptera). *Netherlands Journal of Aquatic Ecology*, **26**, 229-237.

Correia L.C.S. & Trivinho-Strixino S. (2007) New species of *Chironomus* Meigen (Diptera: Chironomidae: Chironominae) from Brazil. *Zootaxa*, **1504**, 53-68.

Cranston P.S. (2000) Monsoonal tropical *Tanytarsus* van der wulp (Diptera: Chironomidae) reviewed: new species, life histories and significance as aquatic environmental indicators. *Australian Journal of Entomology*, **39**, 138-159.

Cranston P.S., Cooper P.D., Hardwick R.A., Humphrey C.L. & Dostine P.L. (1997) Tropical acid streams - the chironomid (Diptera) response in northern Australia. *Freshwater Biology*, **37**, 473-483.

Death R.G. & Joy M.K. (2004) Invertebrate community structure in streams of the Manawatu-Wanganui region, New Zealand: the roles of catchment versus reach scale influences. *Freshwater Biology*, **49**, 982-997.

Delettre Y.R. & Morvan N. (2000) Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology*, **44**, 399-411.

Diniz-Filho J.A.F., Bini L.M. & Hawkins B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53-64.

Diniz-Filho J.A.F. & Bini L.M. (2005) Modelling geographical patterns in species richness using eigenvector based spatial filters. *Global Ecology and Biogeography*, **14**, 177-185.

Diniz-Filho J.A.F., Rangel T.F.L.V.B. & Bini L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479-488.

Feld C.K. & Hering D. (2007) Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, **52**, 1380-1399.

Fittkau E.J. (2001) Amazonian Chironomidae (Diptera, Chironomidae): A contribution to chironomid research in the neotropics. *Amazoniana-Limnologia et Oecologia Regionalis Systemae Fluminis Amazonas*, **16**, 313-323.

Frissel C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in the watershed concept. *Environmental Management*, **10**, 199-214.

Ferrington Jr L.C. (2008) Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater. *Hydrobiologia*, **595**, 447-455.

Griffith D.A. & Peres-Neto P.R. (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**, 2603-2613.

Hawkins C.P. & Norris R.H. (2000) Effects of taxonomic resolution and use of the subsets of the fauna on the performance of RIVPACS-type models. In: *Assessing the Biological Quality of Fresh Waters. RIVPACS and Other Techniques* (Eds. J.F. Wright, D.W. Sutcliffe & M.T. Furse), pp. 217-228. Freshwater Biological Association.

Heino J., Muotka T., Mykrä H., Paavola R., Hämäläinen H. & Koskenniemi E.S.A. (2003) Defining macroinvertebrate assemblage types of headwater streams: Implications for bioassessment and conservation. *Ecological applications*, **13**, 842-852.

Heino J., Mykra H. & Kotanen J. (2008) Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. *Landscape Ecology*, **23**, 417-426.

Helson J.E., Williams D.D. & Turner D. (2006) Larval chironomid community organization in four tropical rivers: human impacts and longitudinal zonation. *Hydrobiologia*, **559**, 413-431.

Hynes H.B.N. (1970) *The ecology of running waters*. University of Toronto Press, Toronto.

Johnson J.B. & Omland K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101-108.

Johnson R.K. (2007) Environmental Assessment meets Landscape Ecology meets Land use Planning. *Freshwater Biology*, **52**, 907-907.

Johnson R.K., Furse M.T., Hering D. & Sandin L. (2007) Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. *Freshwater Biology*, **52**, 939-958.

Kronka F.J.N. (2005) Inventário florestal da vegetação do Estado de São Paulo. Ed. Imprensa Oficial, Secretaria do Meio Ambiente / Instituto Florestal, São Paulo 200p.

King J.R. & Jackson D.A. (1999) Variable selection in large environmental data sets using principal components analysis. *Environmetrics*, **10**, 67-77.

Legendre P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659-1673.

Legendre P. (2005) Species Associations: The Kendall Coefficient of Concordance Revisited. *Journal of Agricultural Biological and Environmental Statistics*, **10**, 226-245.

Legendre P. & Gallagher E.D. (2001) Ecologically Meaningful Transformations for Ordination of Species Data. *Oecologia*, **129**, 271-280.

Levin S.A. (1992) The Problem of Pattern and Scale in Ecology. *Ecology*, **73**, 1943-1967.

McGarigal K., Cushman S.A., Neel M.C. & Ene E. (2002) Fragstats: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html

Metzger J.P. (2008) Landscape ecology: perspectives based on the 2007 IALE world congress. *Landscape Ecology*, **23**, 501-504.

Metzger J.P., Ribeiro M.C., Ciocheti G. & Tambosi L.R. (2008) Uso de índices de paisagem para a definição de ações de conservação e restauração da biodiversidade do Estado de São Paulo. In: *Diretrizes para Conservação e Restauração da Biodiversidade no Estado de São Paulo* (Eds. R.R. Rodrigues, C.A. Joly, M.C.W. Brito, A. Paese, J.P. Metzger, L. Casatti, M.A. Nalon, N. Menezes, N.M. Ivanauskas, V. Bolzani, V.L.R. Bononi), pp. 120-127. Secretaria do Meio Ambiente & FAPESP, São Paulo.

Nijboer R.C., Verdonschot P.F.M. & Van Der Werf D.C. (2005) The use of indicator taxa as representatives of communities in bioassessment. *Freshwater Biology*, **50**, 1427-1440.

Oden N.L. (1984) Assessing the significance of a spatial correlogram. *Geographical Analysis*, **16**, 1-16.

Odum E.P (1971) *Fundamentals of Ecology.* 3rd Edition. W.B. Saunders Company, Philadelphia.

Peres-Neto P.R., Jackson D.A. & Somers K.M. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. *Ecology*, **84**, 2347-2363.

Peres-Neto P.R., Jackson D.A. & Somers K.M. (2005). How many principal components? stopping rules for determining the number of non-trivial axes revisited. *Computational Statistics & Data Analysis*, **49**, 974-997.

Petersen Jr R.C. (1992) The RCE: a Riparian, Channel, and Environmental Inventory for small streams in the agricultural landscape *Freshwater Biology*, **27**, 295-306.

Pinder L.C.V. (1986) Biology of freshwater Chironomidae. *Annual Review of Entomology*, **31**, 1-23.

Poff N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391-409.

Poff N.L., Olden J.D., Vieira N.K.M., Finn D.S., Simmons M.P. & Kondratieff B.C. (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, **25**, 730-755.

Pyne M.I., Rader R.B. & Christensen W.F. (2007) Predicting local biological characteristics in streams: a comparison of landscape classifications. *Freshwater Biology*, **52**, 1302-1321.

Rabeni C.F.& Wang N. (2001) Bioassessment of streams using macroinvertebrates: are the Chironomidae necessary? *Environmental Monitoring and Assessment*, **71**, 177-185.

Rangel T.F.L.V.B., Diniz-Filho J.A.F. & Bini L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321-327.

Raunio J., Paavola R. & Muotka T. (2007) Effects of emergence phenology, taxa tolerances and taxonomic resolution on the use of the Chironomid Pupal Exuvial Technique in river biomonitoring. *Freshwater Biology*, **52**, 165-176.

Ribeiro M.C., Metzger J.P., Ponzoni F.J., Martensen A.C. & Hirota, M.M. (2009). Brazilian Atlantic forest: how much is left and how the remaining forest is distributed? Implications for conservation. *Biological Conservation*, **142**, 1141-1153.

Richards C., Johnson L.B. & Host G.E. (1996) Landscape scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 295-311.

Roque F.O., Corbi J.J. & Trivinho-Strixino S. (2000) Considerações sobre a utilização de larvas de Chironomidae (Diptera) na avaliação da qualidade da água de córregos do Estado de São Paulo. In: *Ecotoxicologia: perspectivas para o século XXI*. (Eds. E.L.G. Espíndola, C.M.R.B. Paschoal, O. Rocha, M.B.C. Bohrer, A.L.O. Neto), pp. 115-126. São Carlos: Rima Artes e Textos, São Paulo.

Roque F.O. & Trivinho-Strixino S. (2007) Spatial distribution of chironomid larvae in low-order streams in southeastern Brazilian Atlantic Forest, a multiple scale approach. In: *Contributions to the Systematics and Ecology of Aquatic Diptera - A Tribute to Ole A. Sæther* (Ed T. Andersen), pp. 255-264. The Caddis Press, Columbus, Ohio.

Roque F.O., Trivinho-Strixino S., Milan L. & Leite J.G. (2007) Chironomid species richness in low-order streams in the Brazilian Atlantic Forest: a first approximation through a Bayesian approach. *Journal of the North American Benthological Society*, **26**, 221-231.

Rosenberg D.M. (1992) Freshwater biomonitoring and Chironomidae. *Aquatic Ecology*, **26**, 101-122.

Silver P., Wooster D. & Palmer M.A. (2004) Chironomid responses to spatially structured, dynamic, streambed landscapes. *Journal of the North American Benthological Society*, **23**, 69-77.

Sokal R.R. & Oden N.L. (1978a) Spatial autocorrelation in biology. 1. Methodology. *Biological Journal of the Linnean Society*, **10**, 199-228.

Sokal R.R. & Oden N.L. (1978b). Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society*, **10**, 229-249.

Souza M.L. De & Moulton T.P. (2005) The effects of shrimps on benthic material in a Brazilian island stream. *Freshwater Biology*, **50**, 539-550.

Statzner B., Hildrew A.G. & Resh V.H. (2001) Species traits and environmental constraints: entomological research and the history of ecological theory. *Annual Review of Entomology*, **46**, 291-316.

Stephens P.A., Buskirk S.W. & del Rio C.M. (2007) Inference in ecology and evolution. *Trends in Ecology & Evolution*, **22**, 192-197.

Thienemann A. (1954) Ein drittes biozonotisches Grundprinzip. *Archiv fur Hydrobiologie*, **49**, 421-422.

Thioulouse J., Chessel D. & Champely S. (1995) Multivariate analysis of spatial patterns: a unified approach to local and global structures. *Environmental and Ecological Statistics*, **2**, 1-14.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265-275.

Townsend C.R., Arbuckle C.J., Crowl T.A. & Scarsbrook M.R. (1997) The relationship between land use and physiochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. *Freshwater Biology,* **37**, 177-192.

Townsend C.R., Dolédec S., Norris R.H., Peacock K.A. & Arbuckle C.A. (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology*, **48**, 768-785.

Umetsu F., Metzger J.P. & Pardini R. (2008) Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. *Ecography*, **31**, 359-370.

UNFCCC (1992) *United Nations Framework Convention on Climate Change*. United Nations, New York

Vinson M.R. & Hawkins C.P. (1998) Biodiversity of stream insects: variation at local, basin, and regional spatial scales. *Annual Review of Entomology*, **43**, 271-293.

Wagner H.H. & Fortin M.J. (2005) Spatial Analysis of Landscape: concepts and statistics. *Ecology*, **86**, 1975-1987.

Wiens J.A. (2002) Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, **47**, 501-515.

Williams P.H., Margules C.R. & Hilbert D.W. (2002) Data requirements and data sources for biodiversity priority area selection. *Journal of Biosciences*, **27**, 327-338.

8. Considerações finais

O entendimento dos processos que influenciam a diversidade biológica é fundamental para o avanço teórico da ecologia e para o sucesso da conservação das comunidades e ecossistemas. Atualmente, reconhece-se que a diferença no nicho das espécies pode não ser a principal explicação para os padrões que observamos na natureza. A maioria dos ecólogos de comunidade incluí variáveis espaciais como importantes variáveis ecológicas. Nesta tese, eu tive como objetivo central identificar os principais processos que influenciam a distribuição eabundância de espécies de ambientes aquáticos em escala regional. No primeiro capítulo, eu encontrei forte evidência de uma relação positiva entre abundância local e distribuição regional. Assim, gêneros que são abundantes localmente, tendem e ser amplamente distribuídos na paisagem. Essa relação positiva já foi encontrada para diversos grupos de animais e plantas em ambientes terrestres, porém ainda são escassos os exemplos em ambientes aquáticos continentais, principalmente na região neotropical. Além disso, eu mostrei que essa relação positiva também para gêneros. Diferentemente da maioria dos estudos prévios, no entanto, o nicho dos táxons explicou pouco ou não explicou a relação. Eu especulo que a relação abundância-distribuição não deve ser gerada unicamente por diferenças nos nichos dos táxons. Processos regionais relacionados à dispersão de espécimes entre habitats podem exercer um papel importante.

No capítulo dois, eu usei dez bases de dados sobre comunidades aquáticas em diferentes regiões e tipos de ambientes aquáticos do Brasil – e.g., pequenos riachos, lagos interconectados, ambientes higropétricos em topos de montanhas – para testar se espécies comuns e raras são influenciadas por processos ambientais e espaciais de diferentes maneiras. A teoria de metacomunidades prediz que as estruturas de comunidades formadas por espécies raras (ou especialistas) seriam mais bem explicadas por variáveis ambientais locais, enquanto que aquelas de espécies mais abundantes (ou generalistas) seriam explicadas por processos espaciais regionais. Eu usei uma série de análises estatísticas multivariadas que envolvem partição da variância para testar estas predições. Processos ambientais foram os que mais influenciaram na distribuição e estrutura de conjuntos de espécies comuns e raras. Porém, processos espaciais também explicaram uma parte (menor) da variação nos conjuntos de dados. Surpreendentemente, no entanto, esses conjuntos de espécies responderam e maneira muito similar a ambas as forças estruturantes – ambientais e espaciais. Eu postulo que espéciescomuns e raras podem ser funcionalmente equivalentes em termos de suas respostas ao gradiente ambiental.

No terceiro e último capítulo, eu busquei identificar associações de táxons, entre os Chironomidae que ocorrem em riachos do Estado de São Paulo sob diferentes níveis de preservação, que respondessem de maneira similar a gradientes ambientais. Além disso, eu construí alguns modelos contendo informação sobre processos ambientais e espaciais em diferentes escalas para predizer essas associações. A base de dados usada inclui dados de abundância e distribuição de larvas de Chironomidae (Diptera) em 61 riachos no Estado de São Paulo, 47 deles em áreas preservadas e 14 em áreas sob diferentes tipos de práticas agropecuárias, e variáveis ambientais locais e de paisagem. Além dessas variáveis ambientais, também gerei variáveis espaciais a fim de representar processos de dispersão. Eu encontrei um grupo de táxons associados, composto por sete gêneros. Os modelos foram avaliados através de um procedimento de seleção de modelos baseado no critério de Akaike(AIC). O modelo com menor valor de AIC (melhor modelo) foi o modelo completo,com todas as variáveis. Assim, a abundância da associação de táxons é mais bem explicada por um modelo que contém informações sobre variáveis ambientais, locais e de paisagem, e variáveis espaciais. Isso foi surpreendente por que no cálculo do valor de AIC há uma penalização para modelos com muitas variáveis. Essa é, então, uma forte evidência de que as comunidades aquáticas estão sob influência de diferentes tipos de processos, em diferentes escalas espaciais. Portanto, não é recomendável que estudos sobre comunidades aquáticas e monitoramento sejam baseados em dados de uma única escala espacial. Isso poderá gerar interpretações equivocadas, principalmente se o objetivo do estudo for predição. Por exemplo, eu encontrei que a abundância de táxons associados tende a ser menor em riachos com leito predominantemente arenoso – que é característica da maioria dos riachos da encosta do Estado de São Paulo, que correm para o mar. Se eu usasse somente essa variável local para predição, concluiria que riachos, cujo leito é caracterizado por matéria orgânica fina, suportam uma abundância maior de táxons associados. Porém, eu também encontrei que riachos localizados em uma paisagem dominada por eucaliptos (variável em escala de paisagem) tem baixa abundância. Ou seja, apesar de apresentar a condição local para suportar maior abundância – leito com matéria orgânica fina, a matriz circundante dominada por eucaliptos faz com que a abundância dos táxons associados seja baixa. Esse é um bom exemplo da interação entre duas escalas espaciais na estruturação de comunidades aquáticas.

De maneira geral, considerando os três estudos aqui apresentados, é possível concluir que: i) Chironomidae de riachos da Mata Atlântica que possuem alta abundância local tendem a ser amplamente distribuídos regionalmente; ii) essa relação abundância-distribuição não pode ser explicada pelas diferenças nas características do nicho das espécies; iii) existe um conjunto de táxons de Chironomidae que responde de maneira similar a gradientes ambientais presentes em riachos do estado de São Paulo; iv) a abundância desse grupo concordante é melhor explicada usando informações sobre as condições locais dos riachos, a paisagem na qual estão inseridos e as relações espaciais entre os riachos; v) para compreendermos como comunidades aquáticas são estruturadas, é preciso incluir não somente as variáveis ambientais usuais em ecologia de ambientes aquáticos, e.g., pH, oxigênio dissolvido, temperatura da água, mas também variáveis ambientais em outras escalas como métricas de paisagem e variáveis que representem processos espaciais como dispersão; vi) espécies raras e comuns, em um contexto regional, são influenciadas pelos mesmos tipos de processos e de maneira similar. Em geral, esses resultados indicam que diferentes conjuntos de espécies (delimitados com base na abundância) respondem de maneira similar aos processos estruturantes. Essas espécies parecem não diferir marcadamente em seus nichos realizados. Ou seja, elas são capazes de ocupar partes do gradiente ambiental de maneira muito similar sem a necessidade de exclusão. Isso abre um caminho promissor para programas de monitoramento e conservação da biodiversidade. Podemos mudar o foco para processos ao invés de considerar as espécies (e.g., espécies bandeira, espécies raras). Podemos também, usar um número reduzido de táxons para monitorar grande parte das comunidades. Em minha opinião, agora devemos nos aprofundar para conseguir desenvolver métodos para medir de maneira mais precisa processos espaciais como dispersão e colonização. Isso trará um refinamento maior aos modelos teóricos sobre dinâmica de metacomunidades e às explicações dos padrões observados.

8. Anexos

ANEXO I. Lista das publicações resultantes de parcerias e projetos paralelos que fiz parte durante o doutorado.

1. PADIAL, A. A. ; NABOUT, J. C. ; SIQUEIRA, T. ; BINI, L. M. ; DINIZ-FILHO, J. A. F. . Weak evidence for determinants of citation frequency in ecological articles. Scientometrics (Print), 2010.

2. SIQUEIRA, T. ; PADIAL, A. A. ; BINI, L. M. . Mudanças climáticas e seus efeitos sobre a biodiversidade: um panorama sobre as atividades de pesquisa. Megadiversidade (Belo Horizonte), 2010 (no prelo).

3. ROQUE, F.O.; SIQUEIRA, T.; ESCARPINATI, S. Do fallen fruit-dwelling chironomids in streams respond to riparian degradation? Pan-American Journal of Aquatic Sciences, v. 4, p. 357-362, 2009.

4. NABOUT, J.C.; SIQUEIRA, T.; BINI, L.M.; NOGUEIRA, I.S. No evidence for environmental and spatial processes in structuring phytoplankton communities. Acta Oecologica (Montrouge), v. 35, p. 720-726, 2009.

5. PEPINELLI, M.; SIQUEIRA, T.; SALLES, F.F.; SHIMBORI, E.M. First report of Simuliidae and Chironomidae (Diptera) living on nymphs of Lachlania Hagen (Ephemeroptera: Oligoneuriidae) in South America. Biota Neotropica (Online. Edição em Inglês), v. 9, p. 245-247, 2009.

6. ROQUE, F.O.; LECCI, L.S.; SIQUEIRA, T.; FROEHLICH, C.G. Using environmental and spatial filters to explain stonefly occurrences in Southeastern Brazilian streams: implications for biomonitoring. Acta Limnologica Brasiliensia, v. 20, p. 117-130, 2008.