UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TESE DE DOUTORADO

PARTIÇÃO DA DIVERSIDADE DE INSETOS AQUÁTICOS EM RIACHOS DO SUL DO BRASIL

LUIZ UBIRATAN HEPP

PORTO ALEGRE, ABRIL DE 2011

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UFRGS

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LUIZ UBIRATAN HEPP

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Orientador: Prof. Dr. Adriano Sanches Melo

Comissão Examinadora

Prof. Dr. Marcos Callisto (UFMG)
Prof. Dr. Sandro Santos (UFSM)
Prof. Dra. Sandra Hartz (UFRGS)

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Resumo

Partição da diversidade de insetos aquáticos em riachos do Sul do Brasil. O presente estudo teve por objetivo principal avaliar a distribuição espacial de insetos aquáticos (Ephemeroptera, Plecoptera e Trichoptera; EPT) em riachos do Sul do Brasil. Para tanto, foram realizados diferentes estudos com objetivos específicos direcionados a (i) avaliar o efeito de fatores ambientais e espaciais sobre a distribuição dos organismos, (ii) verificar as escalas heirárquicas onde ocorreram maior variação da comunidade (diversidade beta), (iii) testar a existência de relação entre a composição de espécies e diferentes distâncias espaciais e (iv) avaliar a importância da inclusão de espécies raras na diversidade beta de insetos aquáticos. No primeiro estudo, realizado em Maquiné-RS, observei que os preditores ambientais possuem maior importância na explicação da diversidade beta das comunidades do que a distância entre os trechos . No segundo estudo, em São José dos Ausentes–RS, particionei a diversidade em múltiplas escalas. A partição aditiva utilizada demonstrou que as escalas maiores (riachos e microbacias) foram as de maior importância para estruturação da comunidade. No último estudo, utilizei um método de decomposição da variância da comunidade em múltiplas escalas espaciais utilizando uma matriz biológica contendo toda a fauna de EPT coletada e outra matriz com exclusão das espécies raras. Neste estudo foi possível observar que a variação existente nas escalas de corredeiras, riachos e microbacias foi baixa. A exclusão das morfo-espécies raras não afetou esta variação, demonstrando que em estudos de distribuição espacial, o esforço pode ser direcionado às espécies comuns. Assim, considerando a importância que pequenos riachos possuem em termos de bacias hidrográficas a manutenção da heterogeneidade destas bacias em múltiplas escalas espaciais poderá contribuir para o incremento da biodiversidade aquática.

Palavras chave: Diversidade beta, partição aditiva, Ephemeroptera, Plecoptera, Trichoptera, ecossistemas lóticos, escala hierárquica.

Abstract

Partitioning diversity of aquatic insects in streams of the Southern Brazil. The present study aimed at assessing the spatial distribution of aquatic insects (Ephemeroptera, Plecoptera and Trichoptera; EPT) in streams of the Southern Brazil. Three studies have been conducted with specific objectives at (i) to evaluate the effect of environmental and spatial factors on organisms distribution, (ii) to verify the hierarchical scales where the highest community variation (beta diversity) was found, (iii) to test the existence of a relationship between species composition and different spatial distances and (iv) to evaluate the importance of including rare species in beta diversity of aquatic insects. In the first study, conducted in Maquiné-RS, I noticed that the environmental predictors are more important in explaining the beta diversity of the communities than the distance between the sites. In the second study in São José dos Ausentes-RS, I partitioned the diversity at multiple scales. The additive partitioning used showed that the larger scales (streams and microbasins) were the most important for community structure. In the last study I used a method of community variance decomposition at multiple spatial scales using a biological full matrix EPT fauna and another array without rare species. In this study I observed that the variation in the riffles, streams and microbasin scales was low. The exclusion of rare morphospecies did not affect this variation, showing that in studies of spatial distribution, the effort can be directed to the common species. Thus, considering the importance that the small streams have in hidrographic basins, in terms of maintaining the heterogeneity of these basins at multiple spatial scales, they may contribute to the increase of aquatic biodiversity.

Key Words: Beta diversity, additive partitioning, Ephemeroptera, Trichoptera, Plecoptera, lotic systems, hierachical scale.

Introdução

Partição da Diversidade

Atualmente, definir *diversidade* pode ser complicado devido ao grande número de significados que a palavra possui (Melo, 2008). Termos como “biodiversidade” ou “diversidade biológica” são utilizados para expressar várias situações ecológicas que dificilmente temos condições claras de definir o significado do termo. Neste trabalho, usarei a palavra *diversidade* para definir *riqueza de espécies*.

Whittaker (1960, 1972) propôs a partição da diversidade em alfa, beta e gama para caracterizar diferentes aspectos ou níveis de diversidade. A diversidade total em uma região (gama, γ) é dividida em dois componentes: a diversidade dentro da comunidade (alfa, α) e a variação entre comunidades (beta, β). MacArthur igualou diversidade dentro do habitat com a diversidade alfa de Whittaker e a diversidade entre habitats com a diversidade beta (Gering et al., 2003). A diversidade alfa é o componente da diversidade regional que pode ser atribuído ao número médio de espécies de uma amostra homogênea. Isso é medido como número de espécies presente no local (riqueza de espécie) ou por outra função (índice) que leve em consideração tanto a riqueza quanto a freqüência relativa das espécies (Legendre et al., 2005). Diversidade beta é o componente da diversidade regional que pode ser atribuído às diferenças na composição das espécies em uma escala espacial ou temporal (Gering e Crist, 2002). Se a variação na composição da comunidade é aleatória e acompanhada de processos bióticos que geram autocorrelação espacial, um gradiente em composição de espécies pode aparecer e a diversidade beta pode ser interpretada como taxa de mudança na composição de espécies ao longo de um gradiente. Se a diferenciação entre pontos é devido a fatores ambientais, a diversidade beta poderia ser analisada com o objetivo de hipotetizar variáveis explanatórias (Legendre et al., 2005). Diversidade gama é quando se tem uma região inteira de estudo. Ou seja, é a diversidade total de um grande número de pontos em uma área. A diversidade gama é medida usando os mesmos índices da diversidade alfa (Legendre et al., 2005).

Embora Whittaker (1960, 1972) e depois Allan (1975) tenham proposto que a diversidade pode ser particionada em diferentes componentes, a idéia foi retomada na década de 1990 por R. Lande, o qual demonstrou analiticamente um método de partição da diversidade dentro e entre comunidades (Veech et al., 2002). O método estabelece que a diversidade total de uma região (gama) pode ser particionada em componentes aditivos representando a diversidade local (alfa) e a diversidade entre comunidades (beta) ($\gamma = \alpha + \beta$; Lande, 1996). A partição aditiva da diversidade decompõe a diversidade gama em componentes alfa e beta que são expressos em mesma unidade e podem ser comparados ao longo de escalas espaciais e temporais, fazendo com que o método seja uma promissora ferramenta de análise de padrões de diversidade para estudos hierárquicos (Crist et al., 2003).

Análises de padrões de diversidade em ecossistemas aquáticos têm ignorado a diversidade beta, principalmente considerando riachos de pequena ordem (Clarke et al., 2008). A diversidade beta pode ser fortemente influenciada pela dinâmica das populações biológicas e da comunidade. Adicionalmente, substrato, fluxo de corrente e aporte de matéria orgânica são fatores chave na distribuição de organismos em pequenas escalas espaciais (Miserendino, 2001; Zilli et al., 2008). Baixa diversidade beta em escalas menores indica uma homogeneidade de habitats, servindo como um bom indicativo para o direcionamento de esforços na conservação da biodiversidade (Windberg et al., 2007).

Várias medidas de diversidade beta têm sido propostas para avaliar diferentes comunidades ao longo de gradientes ambientais. Magurran (2004) cita três categorias para avaliação da diversidade beta: (i) medidas de diferenças entre duas ou mais áreas quanto à diversidade alfa, utilizando medidas de riqueza de espécies, índice de Whittaker ou o método de partição; (ii) medidas de composição de espécies entre áreas utilizando índices de similaridade ou dissimilaridade, e; (iii) medidas que exploram a relação espécie-área.

Nos últimos anos alguns estudos têm discutido aspectos acerca da análise da partição aditiva e interpretação dos resultados fornecidos por esta abordagem. Crist et al. (2003) desenvolveram um método baseado em dois modelos nulos. O primeiro teste observa a partição da diversidade baseada na aleatorização dos indivíduos, onde é assumido que os indivíduos de cada espécie estão distribuídos de maneira aleatória entre as amostras do menor nível hierárquico. O segundo modelo nulo aleatoriza as unidades amostrais, obtendo a partição da diversidade a partir da aleatorização das unidades amostrais do menor nível hierárquico para o imediatamente superior. Isso preserva os padrões de agregação intra-específico dos dados.

Mais recentemente, Legendre et al. (2005) propõem o uso de análises de ordenação canônica para avaliar a partição da diversidade. Os autores sugerem o uso de Análise de Correspondência Canônica parcial (pCCA) para avaliar a variação da composição da comunidade considerando os efeitos do ambiente e do espaço. Este método possibilita avaliar a explicação gerada puramente pelo ambiente, puramente pelo espaço e a explicação compartilhada (ambiente e espaço) sobre a composição da comunidade. No mesmo estudo, Legendre et al. (2005) discutem o uso da pCCA e do teste de Mantel para explicar a partição da diversidade. Os autores concluem que a variância da composição da comunidade é uma medida de diversidade beta, enquanto que a variância de matrizes de dissimilaridades não pode ser considerada uma medida de diversidade beta.

Um ano depois, Tuomisto e Ruokolainen (2006) discutiram os resultados de Legendre et al. (2005), destacando principalmente o fato de as duas abordagens (pCCA e Mantel) poderem ser utilizadas para particionar a diversidade, porém com finalidades diferentes. Os autores citam que quando a abordagem de estudo é para “explicar a diversidade beta”, o método de ordenação canônica é mais indicado, pois avalia a variação na composição da comunidade. Por outro lado, o teste de Mantel, baseado em matrizes de dissimilaridade é mais indicado para “analisar a diversidade beta”, pois avalia a variação na diversidade beta.

Vários estudos têm utilizado estas abordagens de análise para avaliar a partição da diversidade e diversidade beta. Chandy et al. (2006) avaliaram a partição da diversidade da vegetação em uma escala espacial hierárquica. Jankowski et al. (2009) estudaram os efeitos da especialização do habitat sobre a diversidade beta de aves tropicais utilizando teste de Mantel parcial. A partição da diversidade beta da vegetação foi objeto de estudo de Legendre et al. (2009). Jost et al. (2010) propõem o uso da partição para estudos de conservação da diversidade como uma abordagem vantajosa para indicar áreas prioritárias para conservação. Estudos da partição da diversidade de macroinvertebrados aquáticos Stendera e Johnson (2005) estudaram os componentes alfa e beta da diversidade de invertebrados aquáticos na Suécia. Na Hungria por Schmera e Erös (2008), avaliaram a variação da diversidade de Trichoptera em corredeiras e poções. Mais recentemente, Clarke et al. (2010) destacaram a importância do conhecimento da contribuição dos componentes alfa e beta para a conservação da diversidade de macroinvertebrados bentônicos. No Brasil estudos com esta abordagem são incipientes. Costa e Melo (2008) utilizaram a pCCA para avaliar a diversidade beta entre microhabitats e entre riachos. Os autores concluíram que o habitat dentro dos riachos é mais importante para a variação na composição da comunidade (diversidade beta). Ligeiro et al. (2010) realizaram um estudo de partição da diversidade da comunidade bentônica em riachos no sudeste brasileiro. Os autores observaram a importância do substrato e da escala de estudo para a composição da comunidade de macroinvertebrados bentônicos.

Riachos e Insetos Aquáticos

Em uma bacia hidrográfica, os riachos de pequena ordem (1ª e 2ª ordens) são os principais componentes da rede hídrica, pois compreendem cerca de três quartos de toda a área de drenagem. Desta forma, estes ambientes são importantes locais de processamento de matéria orgânica e ciclagem de nutrientes, além de fontes de manutenção da biodiversidade (Clarke et al., 2008).

Rios e riachos são complexos mosaicos de tipos de habitats e gradientes ambientais, caracterizados por uma alta conectividade e complexidade espacial (Allan, 2004). Recentemente, alguns ecólogos têm discutido a distribuição de organismos aquáticos em uma perspectiva de paisagem causando um efeito significativo na distribuição dos organismos (Clarke et al., 2008).

A importância de riachos de pequena ordem em uma escala mais ampla (paisagem) deve-se às características hierárquicas da área de drenagem o que possibilita o estudo da diversidade em caráter sistêmico (bacia hidrográfica) e não pontos particulares (riachos) (Clarke et al. 2008). A interdependência de variáveis ambientais ao longo de múltiplas escalas resulta em uma complexa relação entre a biota e seu ambiente (Feld e Hering, 2007). Em cada escala espacial, ocorrem variações nas condições ambientais e a comunidade de insetos aquáticos reflete esta heterogeneidade (Heino et al., 2004). A variação na distribuição de invertebrados em pequenas escalas tem sido muito estudada, no entanto, são raros os estudos que consideram a variação da comunidade em largas escalas ao longo de microbacias. Heino et al. (2004) citam que riachos são muito heterogêneos e recentes estudos têm mostrado os efeitos desta heterogeneidade na estrutura das comunidades em múltiplas escalas. Efeitos de escala sobre a distribuição de insetos aquáticos podem ocorrer em escalas menores ou mais amplas, dependendo da influencia ambiental (Parsons et al., 2003). Downes et al. (1993) não observaram diferenças significativas na riqueza de bentos em escalas maiores (entre riachos distantes 1,5 km), enquanto que para densidade foi observado diferenças em escalas menores (entre corredeiras).

A heterogeneidade ambiental pode proporcionar grande possibilidade para a ocorrência de espécies raras. De acordo com Allan e Castillo (2007) é muito comum observar em coleções biológicas um pequeno número de espécies dominantes e um grande número de espécies raras. Assim, espécies raras podem contribuir de maneira significativa para a diversidade beta em pequenos riachos e, desta forma, contribuir consistentemente para a diversidade regional (diversidade gama) (Clarke et al., 2008). No entanto, pouco se sabe sobre qual a real contribuição das espécies raras na diversidade beta de uma determinada região considerando gradientes espaciais ou ambientais (Heino e Soininen, 2010).

Parsons et al. (2003) explicam que a composição de macroinvertebrados varia pouco entre trechos de mesmo riacho por que a fauna não responde a diferenças nas características hidráulicas e de substrato de áreas adjacentes. No entanto, Mykrä et al. (2004) citam que os riachos são reconhecidamente ambientes heterogêneos e a fauna responde a esta heterogeneidade. Esta contradição, porém, é reflexo do conhecimento da relevância das escalas é pouco ou quase nada estudado para contribuir com o entendimento da estrutura da comunidade.

A estrutura das comunidades de macroinvertebrados tem sido objeto de muitos estudos em sistemas lóticos. Estes organismos são componentes importantes nas cadeias tróficas aquáticas, ciclagem de matéria orgânica e nutrientes (Vannote et al., 1980; Yoshimura et al., 2006). Além disso, são sensíveis a alterações na química da água, morfologia dos riachos e disponibilidade de alimentos. Isso atribui a estes organismos uma forte característica de bioindicação da qualidade das águas (Beauger et al., 2006).

Os insetos aquáticos constituem cerca de 90% da fauna de macroinvertebrados bentônicos encontrada em riachos. Para as comunidades bentônicas fatores locais são de grande importância na distribuição desses organismos (Crisci-Bispo et al., 2007). Os padrões de distribuição dos organismos aquáticos dependem de interações geomorfológicas, do substrato, da temperatura e de interações biológicas (Baptista et al., 2001; Silveira et al., 2006), além da vegetação ciliar (Bispo et al., 2002), disponibilidade alimentar (Gage et al., 2004), sazonalidade (Bispo et al., 2006), microhabitats (Buss et al., 2002), heterogeneidade de habitats (Crisci-Bispo et al., 2007) e uso e ocupação da terra (Hepp e Santos, 2009).

Dentre a fauna de insetos encontrada em riachos, as ordens Ephemeroptera, Plecoptera e Trichoptera têm sido consideradas ordens muito representativas da fauna aquática de riachos de pequena ordem. Ephemeroptera e Trichoptera geralmente estão distribuídos ao longo da bacia de drenagem, enquanto que Plecoptera tem sua ocorrência concentrada em áreas mais altas da bacia (Bispo et al., 2002; Beauchard et al., 2003; Pond, 2010). Esses organismos são sensíveis a perturbações ambientais que ocorrem nos corpos hídricos e esta característica atribui a eles característica de indicadores de qualidade de água, sendo utilizados em programas de biomonitoramento (Rosenberg e Resh, 1993; Bispo et al., 2006; Haidekker e Hering, 2008).

Vinson e Hawkins (1998) citam que é necessário documentar padrões em diversidade de insetos aquáticos, procurando identificar quais os principais fatores ambientais que controlam os padrões de estruturação das comunidades, bem como definir quais fatores controlam a riqueza de insetos considerando aspectos da dependência da escala. É de conhecimento geral que a heterogeneidade dos substratos acarreta em um incremento da riqueza de insetos aquáticos. No entanto, este efeito é evidente em escalas menores, como por exemplo, indivíduos em pedras (Vinson e Hawkins, 1998).

Notas sobre a Estrutura e Objetivos do Trabalho

Explorar o papel dos componentes da diversidade (alfa, beta e gama) na definição de padrões espaciais para comunidades de invertebrados aquáticos em riachos de pequena ordem é uma promissora área de pesquisa na ecologia de riachos, pois facilitará o entendimento dos padrões de estrutura espacial dessas comunidades em escalas maiores. Além disso, compreender estes padrões em uma perspectiva de múltiplas escalas espaciais torna-se relevante, pois a maioria dos estudos sobre o tema utiliza variáveis ambientais para explicar as variações na comunidade de insetos aquáticos em detrimento do espaço como uma variável explanatória da variação da comunidade de insetos aquáticos. A correlação existente entre espaço e ambiente pode ser um problema para a determinação da real explicação de cada um destes fatores, assim, considerar o espaço e ambiente de maneira conjunta como variáveis explanatórias também pode ser considerada uma lacuna na ecologia de riachos.

O presente estudo possui como objetivo principal avaliar a distribuição espacial de insetos aquáticos das Ordens Ephemeroptera, Plecoptera e Trichoptera (EPT), estudando a partição dos componentes alfa, beta e gama na estruturação das comunidades destes organismos em riachos na região Sul do Brasil. Além disso, alguns objetivos específicos foram propostos para nortear a realização do trabalho. São eles: (i) avaliar os efeitos da heterogeneidade de substrato, velocidade de correnteza e matéria orgânica sobre a abundância e riqueza de insetos aquáticos; (ii) verificar em quais escalas há maior variação da abundância e riqueza de espécies e composição da fauna; (iii) testar se existe relação entre similaridade em composição de espécies e distância geográfica e distância linear (pelo corredor de riachos); (iv) avaliar a contribuição das diversidades alfa e beta para a diversidade regional; (v) avaliar a importância da inclusão de espécies raras na diversidade beta de insetos aquáticos.

Esta tese foi organizada em três capítulos, estruturados em forma de manuscritos, que procuraram discutir os objetivos propostos. As citações no texto e referências ao final do capítulo seguem as normas dos respectivos periódicos para onde serão submetidos. Desta forma, cada um dos três capítulos possui uma formatação diferente quanto a este item. O Capítulo 1 será enviado para a *International Review of Hydrobiology*. Este capítulo discute as diversidades alfa e beta de insetos aquáticos em um estudo experimental realizado no município de Maquiné – RS. Neste trabalho procurei avaliar os efeitos de características ambientais, como tipo de substrato, velocidade de correnteza e matéria orgânica e a distância entre os trechos, seguindo o corredor do riacho sobre a variação na comunidade dos insetos aquáticos. Os resultados demonstraram que os preditores ambientais possuem maior importância na explicação da diversidade beta das comunidades, no entanto, a distância entre os trechos também foi significativa na explicação da variação das comunidades. O Capítulo 2 será submetido para o periódico *Hydrobiologia* e apresenta resultados de um estudo realizado em riachos da região dos Campos de Cima da Serra, em São José dos Ausentes – RS. Neste capítulo procurei discutir a partição da diversidade em múltiplas escalas espaciais considerando os componentes alfa (área de coleta do amostrador Surber), beta (particionado em vários níveis: entre unidades Surber, trechos, riachos e microbacias hidrográficas) e gama (bacia hidrográfica). O método de partição aditiva utilizado demonstrou que as escalas maiores (riachos e microbacias) foram as de maior importância para estruturação da comunidade. O Capítulo 3 será enviado para o periódico *Limnmologica* e apresenta resultados da aplicação de um método de decomposição da variância da comunidade em múltiplas escalas espaciais utilizando uma matriz biológica contendo toda a fauna de EPT coletada e outra matriz com exclusão das morfo-espécies raras (abundância < 0,5%). Neste estudo foi possível observar que a variação existente nas escalas de corredeiras, riachos e microbacias foi baixa, embora, na maior escala tenha sido levemente maior que as demais. A exclusão das morfo-espécies raras não afetou esta variação, sendo que os resultados permaneceram muito semelhantes.

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Capítulo 1

Alpha and beta diversities of stream insects: effects of environmental factors and geographical distance[1]

Abstract

We evaluated the effect of environmental factors on the abundance and genera richness of aquatic insects colonizing artificial substrates. We also assessed the relative effects of environmental factors on assemblage variation (beta diversity), and contrasted its magnitude with the variation associated with the spatial position of reaches in a Neotropical stream. Homogeneous and heterogeneous bricks were installed in seven stream reaches and removed after 60 d. Substrate type and organic matter showed significant effects on abundance. For observed richness, substrate type was the only important variable. For rarefied richness, no explanatory variable was important. A NMDS ordination of bricks revealed only weak effects of spatial position. A pRDA indicated that the environmental matrix explained 12.44% of the total variation, while reach position explained 7.41%. We conclude that local factors were preponderant in determining the composition of the insect assemblage in the stream.

Keywords: Diversity partitioning, Ephmeroptera, heterogeneity substrate, Plecoptera, pRDA, Trichoptera.

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[1] Este manuscrito será submetido à revista International Review of Hydrobiology com co-autoria de Victor Lemes Landeiro e Adriano Sanches Melo. As citações ao longo do texto e as referências no final seguem as normas da referida revista.

Introduction

The diversity of assemblages at local and regional scales is a key issue for better understanding of natural phenomena. Moreover, the different components of diversity can be employed to optimize measures for the conservation and recovery of ecosystems (CRIST et al., 2003; BASELGA and JIMENEZ-VALVERDE, 2007). Assemblages are subjected to variations of the environment, space, and biological interactions that ultimately determine the abundances of species in an area. These result in different assemblages when different habitats and regions are compared (GONZÁLEZ and GRAÇA, 2005; COSTA and MELO, 2008; JIANG *et al.*, 2010). Previous studies recognized the effects of biological interactions and environmental factors in the determination of assemblages, and, for many systems, determined which factors best explained variations in one component of diversity, usually local species richness (or alpha diversity) (MAGURRAN, 2004).

The total diversity in a region can be partitioned into two components: (i) the local component, termed alpha diversity, and (ii) the changes in species composition (turnover) among local assemblages, termed beta diversity (WHITTAKER, 1960; LOREAU, 2000). The alpha component can be estimated as the local average richness or values from a diversity index (MAGURRAN, 2004). The beta diversity component represents the turnover in species composition among sites, and can be estimated by dissimilarity indexes (KOLEFF *et al.*, 2003) or simply as the difference between regional and local diversities (CRIST et al., 2003). According to CLARKE *et al.* (2008), beta diversity is a fundamental aspect for understanding diversity patterns and, at small spatial scale, it is mostly determined by i) environmental dissimilarities, and ii) geographical distance among places. At large spatial scales, evolutionary processes such as speciation are the key factors in the differentiation of biota. Recently, emphasis has been given to i) the quantification of changes in diversity among assemblages (KOLEFF *et al.*, 2003; MAGURRAN 2004), ii) how the total diversity in a region is partitioned among lower spatial scales and habitats (CRIST *et al.*, 2003; LIGEIRO *et al.*, 2010), and iii) the determination of factors that explain variation in beta diversity (LEGENDRE *et al.*, 2005; COSTA and MELO, 2008).

Streams are heterogeneous in terms of physical characteristics, and this is reflected in the high variability of assemblages only a few meters apart from each other (HEINO *et al.*, 2004; COSTA and MELO, 2008). Most of the physical variations within streams are caused by slope, which in turn determines current velocity and, together with the geological constitution of the area, substrate type (HEINO *et al.*, 2004). Current velocity and substrate type are key factors in the determination of the stream biota, and have been studied extensively (HYNES *et al.*, 1976; HART and FINELLI, 1999; GRAÇA *et al.*, 2004; JIANG *et al.*, 2010). In addition to differences in physical characteristics, variability of the stream insect fauna can be caused by restrictions on dispersal that slow the colonization of disturbed areas (DEATH, 1996; WATANABE *et al.*, 2008), or those in which only a few or even no females were able to successfully deposit eggs (BUNN and HUGHES, 1997). Despite the recognition of potential patchiness in stream fauna caused by dispersal restrictions, even among sites less than 30 km apart (WATANABE *et al.*, 2008), few studies have evaluated geographical distance as an explanatory variable (SOININEN, 2004; MUNN *et al.*, 2009). Additionally, few studies have evaluated the relative importance of environmental differences and geographical distance simultaneously in the determination of the spatial variability of stream insect assemblages (COSTA and MELO, 2008, LANDEIRO *et al.*, 2011).

The concept of beta diversity has been used extensively in the study of spatial gradients (HARRISON *et al.*, 1992; MAGURRAN, 2004), although turnover in gradients is the result of environmental dissimilarities and geographical distances. The intrinsic correlation between environmental and spatial components represents a problem for the determination of the exclusive contribution of each component (DINIZ-FILHO *et al.*, 2003; GENNER *et al.*, 2004; LEGENDRE *et al.*, 2005). Studies that evaluate both environmental and spatial factors, usually partitionate total variability in species composition in four fractions: [a] variability explained by exclusively by the environment, [b] variability explained by the environment and space (shared fraction), [c] explained exclusively by space, and [d] unexplained (residual) variance.

We studied the diversity of insects of the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) colonizing clay bricks in several reaches of a single stream. First, we investigated the effect of brick heterogeneity, water flow, and trapped coarse detritus on genera richness (alpha diversity). Previous studies reported higher richness in heterogeneous substrates containing large amounts of coarse detritus. However, substrate heterogeneity and organic matter cause an increase in the density of organisms, and thus it is not clear whether high genera richness in heterogeneous substrates associated with coarse detritus is an indirect effect of high abundance. We therefore evaluated the effect of these three factors, taking into account abundance using rarefaction. Second, we investigated the effects of local factors (brick heterogeneity, current velocity, and amount of coarse detritus) on assemblage variation (beta diversity), and contrasted its magnitude with the variation associated with the spatial position of reaches in the stream.

Materials and Methods

Study area

Our experiment was set up in the Forqueta stream, a tributary of the Maquiné River located in Maquiné county, state of Rio Grande do Sul, Brazil (29°31’57”S, 50°14’55”W; Fig. 1). The region is inserted in the extreme southern portion of the Atlantic Rain Forest. The Forqueta stream has a catchment area of 116.1 km^2 mostly covered by old-growth and secondary forests, base flow discharge of 1.42 m^3 s^{-1}, and annual rainfall of 1400 mm. The water is well oxygenated (dissolved oxygen >7 mg L^{-1}), and has lightly acid pH (6.5), and low electrical conductivity (<50 µS cm^{-1}). The streambed is composed of gravel, stones, and scattered boulders.

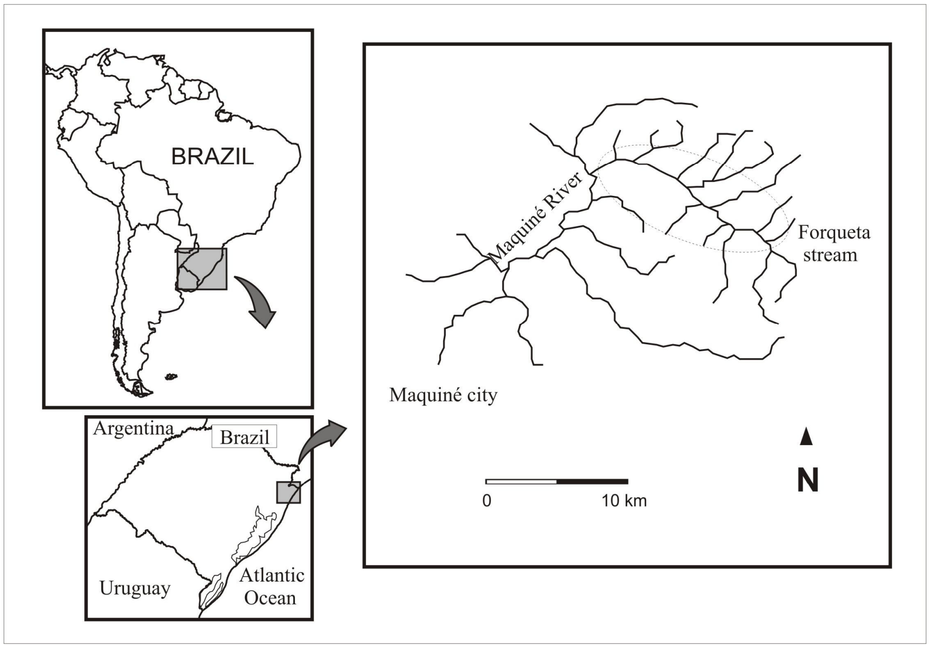

Figure 1. Location of study area in Maquiné city (Brazil) and stretch studied stretch in Forqueta stream.

Field experiment

To evaluate substrate heterogeneity on EPT, we constructed substrates using hollow clay bricks, 25.5 x 12 x 10.5 cm. The bricks were filled with bags of sand to assure substrate stability in the streambed, and were closed by attaching two unglazed clay tiles with silicone glue. Two substrate types, differing in heterogeneity, were constructed (Fig. 2). The heterogeneous substrates were confectioned by carving lines ca. 3 mm deep in the lateral surfaces using an electric concrete saw and by attaching tiles with their grooved sides facing out. In addition, we attached two pieces of tiles (ca. 5 x 5 cm) on each side of the bricks and two plastic strips (ca. 5 x 2 cm) on the top and bottom surfaces (grooved tile surfaces, see Fig. 2). To avoid losing bricks downstream, we attached them to nylon lines anchored to iron bars buried ca. 40 cm deep and located 1 m upstream from the brick. The major axis of the brick was installed parallel to the stream flow and with the tile sides facing up and down.

One set of six bricks (three heterogeneous and three homogeneous bricks) was installed in each of seven consecutive reaches (430 – 920 m apart). Within reaches, bricks were installed in similar riffles. The bricks were installed in the stream in July 2007 and removed after 60 d. We used a U-net to retain invertebrates during brick removal. The bricks were washed and carefully examined for attached insects. The organisms were fixed with 70% ethanol. In the laboratory, insects of the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) were separated from the detritus and identified to genus according to MERRITT and CUMMINS (1996), FERNÁNDEZ and DOMÍNGUEZ (2001), SALLES *et al.* (2004), and COSTA *et al.* (2006). Previous studies have showed the effectiveness of using EPT groups and quantitative data to uncover even subtle patterns in stream ecology studies (MELO, 2005).

The current velocity and organic matter associated with each brick were quantified during its removal. The current velocity was measured before removal of the brick positioning a flowmeter on top of brick. The coarse particulate organic matter adhered to the bricks was removed and incinerated in a muffle oven (550ºC for 5 h). The organic matter was obtained by the difference of the total mass and the remaining mass.

Data Analysis

We employed a multiple linear regression to evaluate the effect of flow velocity, organic matter, and brick heterogeneity on log (abundance + 1) and on the number of genera at each brick. The model included reaches as blocks. We removed unimportant variables ($P > 0.05$) and refit the model until the partial effects of explanatory variables were important. We repeated the analysis using rarefied genera richness, in order to test whether the effect of the three variables on richness was an indirect effect of abundance (MCCABE and GOTELLI, 2000; GOTELLI and COLWELL, 2001). Because the comparisons were done within blocks (reaches), we applied rarefaction to each of the five bricks in a reach to obtain a richness estimate for the subsample size (number of individuals) similar to that observed in the brick harboring the lowest abundance.

We initially explored the relative importance of environmental conditions and space on the resemblance among the faunas colonizing bricks using Non-Metric Multidimensional Scaling (NMDS) ordination on two axes. A single brick harbors a limited number of individuals and genera, and thus may not represent very well the potential fauna available. We therefore opted to run a second NMDS ordination using pooled samples including the three bricks of the same heterogeneity type and reach. This analysis included 14 pooled samples (7 reaches x 2 brick types). The resemblances among objects were obtained using the Bray-Curtis dissimilarity index on log-transformed (log[abundance+1]) data.

The relative importance of the environmental variables (at brick scale) and geographical distance (at reach scale) was analyzed using a partial Redundancy Analysis (pRDA). The analysis is aimed at the second level of abstraction of TUOMISTO and RUOKOLAINEN (2006), the variation in the raw-data table. The environmental data matrix used in pRDA included three variables: i) flow velocity at bricks (continuous), ii) organic matter (continuous), and iii) brick type (categorical, two levels). We employed a single geographical variable, distance from the most upstream reach through the stream corridor, to model the effect of space on assemblage variability. The relative importance of the environmental and spatial matrices was contrasted using adjusted R^2 (PERES-NETO *et al.*, 2006). This approach was used because the environmental matrix contained three variables versus only one variable (distance from the first upstream reach) in the spatial matrix. Analyses were done in the R environment (THE R DEVELOPMENT CORE TEAM, 2009) using the “vegan” package (OKSANEN *et al.*, 2009) for the rarefaction and multivariate analyses.

Figure 2. Bricks used as substrate in the experiment. In detail, complementary plates glued to the brick surface to increase heterogeneity.

Results

Samples from the seven reaches contained 16,299 individuals and 34 genera of EPT. Ephemeroptera was the most abundant order, and included 14,153 individuals (86.8%) and 11 genera (Table 1). Trichoptera included 1931 individuals (11.8%) and 18 genera, and Plecoptera 215 individuals (1.4%) and six genera. *Baetodes* (Ephemeroptera, Baetidae), *Farrodes* (Ephemeroptera, Leptophlebiidae), and *Smicridea* (Trichoptera, Hydropsychidae) were the most abundant genera.

The reduced regression model for abundance data retained organic matter and substrate type. Abundances observed on heterogeneous bricks were higher than on homogeneous bricks (b = 0.93; P < 0.001) and on those harboring large quantities of organic matter (*b* = 0.19; *P* = 0.020). For the observed genera richness, substrate type was the only important variable, and, similarly to abundance, more genera were found on the heterogeneous bricks (*b* = 3.00; *P* = 0.007). No explanatory variable was important to explain the variation in rarefied genera richness, indicating that the positive effect of heterogeneous substrate on the observed richness was a consequence of high abundance.

The NMDS ordination of bricks revealed only weak effects of spatial position (Fig. 3A). For instance, sample units from downstream reaches 1-4 tended to be scored in the upper right-hand corner, while upstream reaches 5-7 tended to be positioned immediately below the center (origin) of the diagram. The stress of the analysis was 22.4%. The NMDS ordination of pooled samples (sum of three bricks) best reflected the substrate type and spatial position (Fig. 3B). The first axis separated samples according to spatial position, and scored downstream reaches 1-4 in the left-hand portion of the ordination diagram. The second axis separated samples according to substrate type, with heterogeneous bricks scored in the upper part of the diagram (Fig. 3B).

The pRDA indicated that the environmental matrix explained 12.44% of the total faunal variation on bricks (adjusted R^2) ($P < 0.001$), while distance from the first upstream reach explained 7.41% ($P < 0.001$). The shared explained variation by the two groups of variables was near zero (negative adjusted R^2), indicating that the environmental and spatial effects were independent from each other. Most of the variation in species composition and relative abundances remained unexplained (80.8%).

Table 1. Total individuals, observed and rarefied richness, flow, and ash-free dry mass (AFDM) in homogeneous and heterogeneous substrates in Forqueta stream, Maquiné, Brazil.

Variables	Substrate type	
	Homogeneous	Heterogeneous
Total organisms	4665	11,634
Mean of organisms per brick	222.1(±195.3)	554 (±735.2)
Observed richness	13.1 (±2.5)	16.8 (±3.8)
Rarefied richness	9.9 (±2.9)	9 (±3)
Current velocity (cm s^{-1})	23.6 (±20.8)	20.8 (±8.8)
Organic matter (g)	0.94 (±1.11)	1.69 (±1.8)

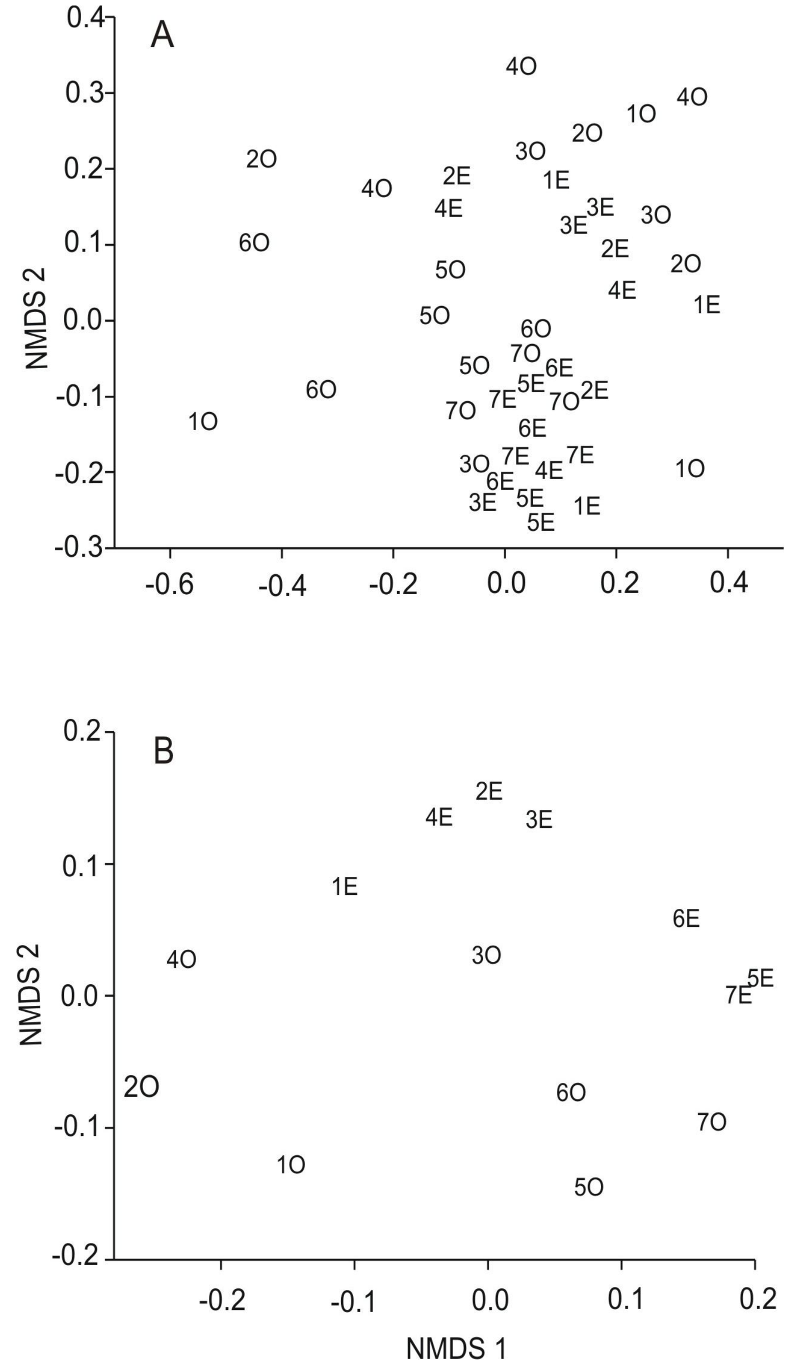

Figure 3. Non-Metric Multidimensional Scaling ordination of (A) 42 sample units (stress = 22.4%) and (B) of 14 pooled samples (stress = 12.7%) in seven reaches of the Forqueta stream. Codes 1 to 7 indicate the stream reach. The reaches are numbered consecutively from downstream to upstream. O = homogeneous substrate. E = heterogeneous substrate.

Discussion

We found that substrate heterogeneity increased the observed abundance of individuals and genera richness. Also, higher abundances were found in bricks with larger amounts of organic matter. These findings corroborates previous studies of other stream types and regions evaluating substrate heterogeneity and availability of coarse organic matter on abundance (JOHNSON *et al.,* 2003; HEINO *et al.,* 2004; GRAÇA *et al.,* 2004; GONZÁLEZ and GRAÇA, 2005). Substrates with high heterogeneity contribute to organic-matter retention, reduce negative interactions (predation and competition), create flow refuges (MUNN *et al.,* 2009), and protect from disturbance events (BROWN, 2007). We observed a positive effect of brick heterogeneity on observed richness; however, this effect was not observed for rarefied richness (i.e., removing the effect of abundance). Previous studies evaluating the effect of substrate heterogeneity in streams have reported a positive relationship between richness and heterogeneity (BEISEL *et al.,* 2000; BOYERO, 2003). However, these studies did not remove the effect of abundance on richness, and therefore the effect they observed may in fact be caused by an indirect effect of larger sample size (i.e. higher abundance) (GRAÇA *et al.*, 2004; GONZÁLEZ and GRAÇA, 2005). MCCABE and GOTELLI (2000) studied the effect of small-scale disturbance in streams, and found that its effects on observed richness were actually an indirect effect of abundance. They showed that the use of rarefied richness resulted not only in different conclusions, but also in a straightforward interpretation of results. An unimportant effect of high heterogeneity on rarefied richness indicates that each taxon is affected similarly by the increase in abundance. However, this is not inevitable. It would be plausible to expect that high heterogeneity allows not only an abundance increase, but also colonization by species that are not able to persist in homogeneous substrates. Accordingly, the excess of taxa on heterogeneous substrates would be composed by two sets of species. The first set would be composed by those rare species that have a higher probability of being sampled because of the increased sample effort (number of individuals). The second set would be comprised by taxa that are not commonly found on a homogeneous substrate. Although we did not observe such a true taxa increase at the scale of the bricks, it would be plausible to expect such a possibility at higher spatial scales.

The effect of the substrate heterogeneity on abundance and genera richness observed in the multiple regressions was corroborated by the NMDS ordination. The NMDS ordination of pooled samples best reflected the effect of spatial position (dimension 1) and brick heterogeneity (dimension 2) on the assemblage. Some studies report that the substrate and the accumulated organic matter are key factors in the distribution of organisms at small spatial scales (GONZÁLEZ and GRAÇA, 2005; FELD and HERING, 2007; ZILLI *et al.*, 2008; JIANG *et al.*, 2010). Therefore, the coarse organic matter accumulated in the substrate increases the substrate heterogeneity and results in the increase of abundance and richness of organisms.

The pRDA analysis showed that both environmental variables and reach position had important effects on assemblage structure. Environmental variables explained 12.4% of the total variation. In Central European streams, FELD and HERING (2007) observed that environmental variables explained 22% of the variance of benthic assemblage structure at reach scale. At micro-scale (25 x 25 cm), the variance explained by environmental variables decreased to 15.8%, a percentage of explanation similar to that found in our study. The importance of environmental factors should likely increase as different habitats are included. For example, COSTA and MELO (2008) showed that environmental factors, expressed as categories of microhabitats, explained 42% of the total variation in the structure macroinvertebrate assemblages present in riffles, pools, moss attached to rocks, and submerged roots of terrestrial plants, while space (stream sites in the same catchment, also coded as a categorical variable) explained 22% of the total variation. The high percentage of unexplained variation is common in ecological studies. The high amount of unexplained variance are due, at least in part, to important variables that are missing in the analysis (GENNER *et al.*, 2004).

In conclusion, the abundance of organisms is higher in heterogeneous substrates, but the richness of taxa appeared not to differ with substrate heterogeneity. The observed taxa richness was related to substrate heterogeneity, but this relationship was spurious, as observed in the analysis of rarefied richness. The heterogeneity of substrate and the amount of organic matter had a direct positive effect on insect abundances, causing an increase in the observed EPT genera richness. The variation in the structure of the assemblages was partially explained by environmental variables at the brick scale, and by the spatial position of reaches (scale of km).

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Capítulo 2

Dissimilarity of stream insect assemblages: effects of multiple scales and spatial distances[2]

Abstract

In addition to the effects of environmental conditions, assemblages may exhibit spatial structure depending on the scale of study. We tested whether the dissimilarity of stream insect assemblages is related to two types of spatial distances (stream corridor and overland distance), and evaluated the relative importance of diversity components at multiple spatial scales. Field data included the assemblages of Ephemeroptera, Plecoptera and Trichoptera found in 16 streams in four microbasins. We evaluated the relationship of the dissimilarity of assemblages with the distance types, using Mantel tests. Additionally, we evaluated the relationships among the diversity components at multiple spatial scales, using additive partitioning analysis. The biological dissimilarities were correlated only with the geographical distances. Additive partitioning showed that the values of richness observed in the $\beta 1$ (among Surber), $\beta 2$ (among riffles), $\beta 3$ (among streams), and $\beta 4$ (among microbasins) were significantly higher than those expected. The highest absolute variation of the richness was found in $\beta 3$ (30.6%). We conclude that streams that are geographically close to one another have similar faunas, although streams that is close to

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[2] Este manuscrito será submetido para Hydrobiologia com co-autoria de Adriano Sanches Melo. As citações ao longo do texto e as referências no final do mesmo seguem as normas da referida revista.

one another along the aquatic present lower similarity. Our results show that stream faunas are structured spatially according to the hierarchical nature of stream networks.

Keywords: Additive partitioning, alpha diversity, beta diversity, dispersal, Neotropical streams.

Introduction

Ecosystems have been studied as hierarchical systems, in which their constituting scales differ in dynamics, size, form and successional stage (Wu & Loucks, 1995). These characteristics give ecosystems a high environmental heterogeneity in their multiple spatial scales, which in turn should be reflected in their biological diversity.

Streams are part of a complex hydric network (Clarke et al., 2008) and show a variety of habitats and environmental gradients, characterized by high spatial complexity (Allan, 2004). In a catchment basin, a hierarchical organization can be established from patches, to habitats, to stream segments, to microbasins and to larger basins. The importance of environmental factors and regional processes for the structure of aquatic assemblages varies according to the scale (Collier & Clements, 2011). As a consequence, some approaches in the study of multiple scales favor the understanding of ecological attributes that explain the composition of biological assemblages at specific spatial and temporal scales (Parsons et al., 2004).

Understanding how assemblages of aquatic invertebrates at multiple spatial scales are structured has been the focus of some recent studies (Li et al., 2001; Boyero, 2003; Parsons et al., 2003; Stendera & Johnson, 2005). Several studies have shown that most of the assemblage variation at small scales (habitats) is influenced by substrate types (Stendera & Johnson, 2005; Costa & Melo, 2008; Ligeiro et al., 2010). However, the large-scale distribution of aquatic insects is determined not only by habitat conditions, but also by dispersal and reproductive success (Bunn & Hughes, 1997; Malmqvist, 2002).

Aquatic insect dispersal may occur in water or by the movement of adults between segments of a single stream (stream corridor) or between unconnected streams through the terrestrial matrix (Petersen et al., 2004). Accordingly, insect dispersal is important for the maintenance of assemblages, while barriers to dispersal maintain variation among assemblages (Clarke et al., 2008). Ephemeropterans, plecopterans and trichopterans have a limited dispersal capacity. These insects usually disperse over only a few dozen meters, and their dispersal may be affected by land use (Petersen et al., 2004; Winterbourn et al., 2007). In addition, the limited dispersal of aquatic insects between streams may explain the organization of their assemblages over multiple scales (Myrkä et al., 2004). Thus, the low connectivity among streams, compared to terrestrial landscapes, and differences in dispersal abilities among species are key factors determining the alpha and beta diversity components of assemblages (Clarke et al., 2008; Clarke et al., 2010).

The distribution of species total diversity and its components within and among communities provides a structure in which diversity can be measured at different levels of organization (Heino et al., 2004). Whittaker (1960) defined alpha, beta and gamma diversity and associated them with diversity on different hierarchical scales, within sites, among sites and on the landscape level, respectively (Candy et al., 2006). Beta diversity is the component of regional diversity that can be attributed to the differences in the composition of species at a lower spatial or temporal scale (Gering & Crist, 2002). Thus, beta diversity is essentially a measurement of how sites differ in relation to species composition. Several beta-diversity components can be identified in a hierarchy, each representing variation among levels of a scale in the hierarchy. Ecologists have recently employed additive partitioning of species diversity to assess the relative importance of scales and whether alpha and beta components along the hierarchy differ from expectations of null models (Crist et al., 2003).

In additive partitioning, gamma diversity is separated into local alpha and beta components for each spatial scale. The latter components are obtained by subtracting the alpha diversities of two adjacent scales. Stendera & Johnson (2005) suggested in their study of macroinvertebrate diversity at different spatial scales that additive partitioning enables understanding of the relationships of diversity patterns and the processes that generate these patterns. Recently, Ligeiro et al. (2010) additively partitioned the diversity of aquatic insect families on microhabitat scales (Surber sampling units), riffles, segments and streams. They observed that local richness and beta diversity at smaller scales were lower than those expected according to a null model. The opposite was found for larger scales, where they observed higher beta diversity than that expected by the null model.

Determining the effects of environmental variables and space is important to understand beta diversity. However, the correlation between these two makes it difficult to perform a more specific analysis to determine the real importance of each of these components. In this study, we obtained samples from similar riffle habitats on a hierarchy of spatial scales, to best assess pure spatial effects. We (1) tested whether the dissimilarity of Ephemeroptera, Plecoptera and Trichoptera assemblages was related to two types of spatial distances, through the stream corridor and through the terrestrial (overland) environment (geographical distance); and (2) evaluated the relative importance of alpha- and beta-diversity components at multiple spatial scales. We hypothesized that limited dispersal across the terrestrial landscape leads to a low similarity among headwater streams that are geographically close but located in different microbasins. Accordingly, the distance through the stream corridor should be a better predictor of assemblage similarity than the geographical distance. We also hypothesized that beta diversity is unevenly distributed along the scales studied. Accordingly, we expected an important contribution of beta diversity to gamma diversity, at larger scales, as the sampling sites were environmentally homogeneous.

Material and Methods

Study area and sampling design

The study was carried out in São José dos Ausentes in northeastern Rio Grande do Sul state, Brazil (28º36’ S, 49º56’ W). The mean altitude is 1200 m, and the topography consists of plateaus and incised valleys. The annual mean temperature is 14.4ºC and the annual mean precipitation 1468 mm (Lemos, 1973). The predominant vegetation is highland grassland fields, with patches of forests including the Paraná pine Araucaria angustifolia (Buckup et al., 2007).

We selected four streams in each of four microbasins (Marcos, Lajeadinho, Santa Rosa and Divisa rivers) (Figure 1). The streams are second order, with natural vegetation along their margins, minimal human impact, streambeds composed mostly by stones, and similar frequency and length of riffles. In each of the 16 streams studied, we defined three riffles with stony bottoms. These riffles were ca. 150 m distant from each other. In each of the 48 riffles we obtained two sample units, 2 m apart. This gave a total of 96 sampling units (4 microbasins x 4 streams in each microbasin x 3 riffles in each stream x 2 Surber samples in each riffle = 96 sampling units).

Sampling, aquatic insect identification and environmental variables

We obtained Surber samples (area = 0.09 m2; mesh = 250 µm) in the stony substrate of riffle zones. The organisms were preserved with 80% ethanol. In the laboratory, we sorted individuals of Ephemeroptera, Plecoptera and Trichoptera (EPT), and identified them to family or genus using the identification keys of Merritt & Cummins (1996) and Fernández & Domínguez (2001). Individuals within genera or families were further separated into morphospecies. Previous studies have demonstrated the effectiveness of using EPT morphospecies and quantitative data to uncover even subtle patterns in stream ecology (Melo, 2005).

The main goal of this study was to evaluate the effect of spatial distances and multiple spatial scales on the aquatic insect composition. Therefore, we reduced the influence of environmental factors by selecting similar sampling sites. For each stream riffle, we measured the mean width, mean depth, current velocity, water temperature, turbidity, electrical conductivity, pH and dissolved oxygen (Table 1).

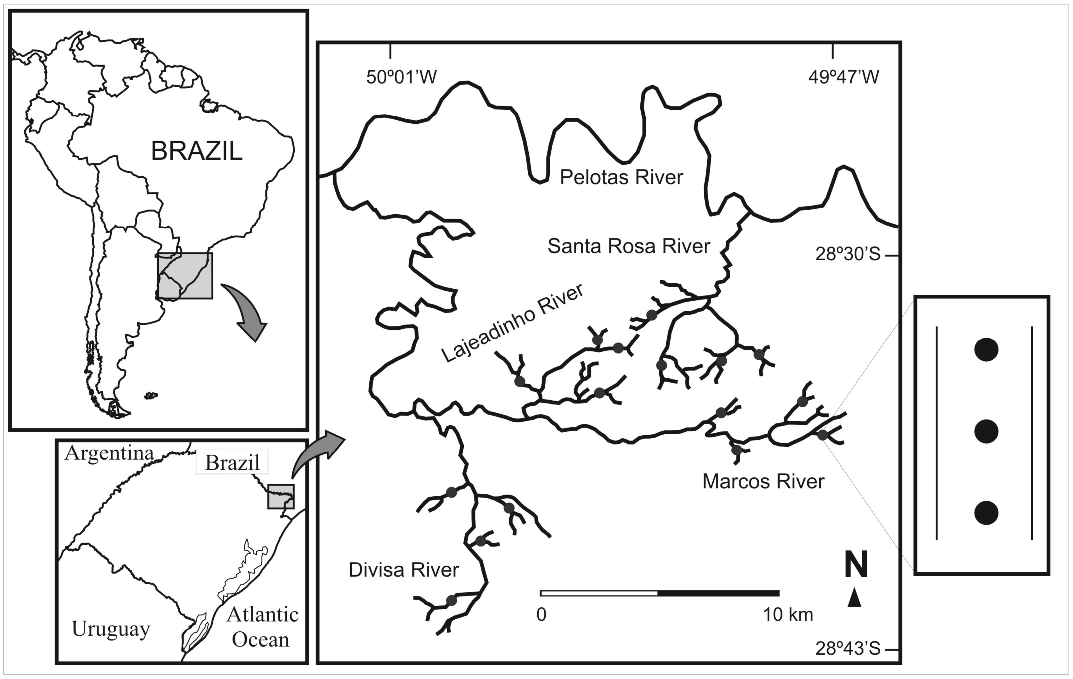

Figure 1. Location of study sites in São José dos Ausentes, Brazil, showing the four river microbasins and the four streams in each microbasin. Three riffles were sampled in each stream (detail).

Table 1. Environmental variables (mean±standard deviation) of the streams studied in the four basins in São José dos Ausentes (Brazil).

	Basins			
	Santa Rosa	Lajeadinho	Marcos	Divisa
Altitude (m)	1165.9±27.5	1235.1±35.9	1218.9±27.6	1200±30.5
Width (m)	1.10±0.23	1.12±0.17	1.04±0.13	1.01±0.2
Water Temperature (ºC)	18.25±3.34	18.35±2.77	18.81±1.33	19.63±2.20
Conductivity (μS cm^{-1})	25.54±5.13	24.60±5.34	23.69±5.76	20.34±1.43
Total Dissolved Solids (mg L^{-1})	10.58±1.83	10.00±2.17	9.33±2.35	8.42±0.67
pH	7.37±0.34	7.00±0.45	7.34±0.34	7.55±0.41
Dissolved Oxigen (mg L^{-1})	9.41±1.11	9.45±1.17	7.95±0.98	7.48±0.41

Data analyses

As an exploratory analysis, we employed a cluster analysis to assess the main patterns of similarity among the assemblages. The samples from each stream riffle (combination of two sample units) contained on average 134 individuals, which may be unrepresentative and inadequate to reflect the spatial hierarchy in the cluster analysis. Therefore, we based the analysis on the stream sites (pooling of three riffles). The cluster analyses were done using the UPGMA linkage method and Bray-Curtis dissimilarity matrix, obtained from a matrix of abundances previously transformed by log2 (x+1).

We evaluated the association of the dissimilarities among assemblages in stream riffles with the two types of distances, using the Mantel test. A spurious positive association, however, may occur due to spatially structured environmental autocorrelation.

We attempted to avoid this problem by sampling in similar environmental conditions. However, in order to assure that environmental conditions did not affect our results, we used the Mantel test to assess the potential relationship between biological and environmental dissimilarities. The environmental dissimilarity matrix was obtained by Euclidian distance on variables (Table 1) standardized in the range 0-1. The standardization was done for each variable separately. Subtract the minimum value of each variable. Then, divide each value by the maximum value found previously. No correlation was observed ($r = -0.05$; $P = 0.79$), allowing us to assess the sole effect of space on assemblage dissimilarities. We used two spatial distance matrices. The first was the geographical distances (geographical coordinates) among the streams, and the second was the linear distance among the streams along the watercourse. The analyses were performed in the R statistical environment (The R Development Core Team, 2009) using functions of the vegan package (Oksanen et al., 2010).

We evaluated the relationships among components of diversity at multiple spatial scales, using additive partitioning analysis. We organized our data according to the following hierarchical scheme: Surber unit (α), among Surber units ($\beta1$), among riffles of the same streams ($\beta2$), among streams ($\beta3$) and among microbasins ($\beta4$). Thus, the diversity model evaluated in our study was: γ (regional diversity) = $\alpha + \beta1 + \beta2 + \beta3 + \beta4$. We employed a null model to evaluate whether beta-diversity components of scales 2-4 of our model differed from the richness that would be expected if sampling units are distributed randomly among spatial scales. The sample-based null model does not allow a test of the first scale (the finest scale; Crist et al., 2003) and thus we tested it using a null model in which individuals are randomized among sampling units (Ribeiro et al., 2008). The significance was obtained by contrasting our observed values against those obtained in

1000 randomizations (Crist et al., 2003). The test assessed whether the observed values were higher or lower than those expected by chance. This was done by computing the proportion of randomizations in which the statistic (diversity components) was similar to or higher than the observed values (Propexp>obs). High proportions (e. g. > 0.975) indicate that observed values are lower than those expected by chance. On the other hand, low proportions (e. g. < 0.025) indicate that the observed values are higher than expected. We carried out the analyses using the function s.based routine in R language (The R Development Core Team, 2009) written by Ribeiro et al. (2008).

Results

A total of 6433 organisms were collected, distributed in 74 morphospecies of Ephemeroptera, Plecoptera and Trichoptera. Ephemeroptera was the most abundant order with 3451 individuals (53.7%), followed by Trichoptera with 2564 (39.8%) and Plecoptera with 418 (6.5%). However, Trichoptera showed the highest morphospecies richness (32), followed by Ephemeroptera (29) and Plecoptera (13). Of the total morphospecies, 14.9% of them occurred with only one or two individuals, and 67% showed a relative abundance lower than 1%. The most abundant morphospecies were Baetis sp.1 (15.9%) (Ephemeroptera), Smicridea sp.1 (9.2%), Hydroptilidae sp.1 (4.6%) and Helicopsychidae sp.1 (4.5%) (all Trichoptera).

The cluster analysis of stream riffles did not reflect the hierarchical scheme of our study (Figure 2). There was a tendency, albeit slight, for stream riffles from the Divisa River microbasin to be classified in basal positions in the dendrogram, indicating greater dissimilarity between them and the other riffles.

The Mantel test indicated that the biological matrix was correlated with the geographical distances ($r = 0.35$, $P < 0.001$). However, no relationship with distances through the stream corridors was observed ($r = 0.11$, $P = 0.21$).

The additive partitioning showed that the richness observed at the smallest scale (α = Surber-unit scale) represented 13.6% of the total richness, and was lower than that expected according to the null model in which individuals are randomized among sampling units (Propexp>obs = 0.999; Table 2). On the other hand, the observed beta-diversity component of the first scale (among Surber sampling units) accounted for 7.9% of the total richness, and was larger than expected under the null model in which individuals are randomized among sampling units (β1, Propexp>obs = 0.001). Similarly, all remaining observed beta-diversity components were higher than those expected under the null model of randomizations of sampling units. The beta diversity among riffles was 18.2% (β2, Propexp>obs = 0.009), among streams was 30.6% (β3, Propexp>obs = 0.001) and among microbasins was 29.7% (β4, Propexp>obs = 0.002; Table 2).

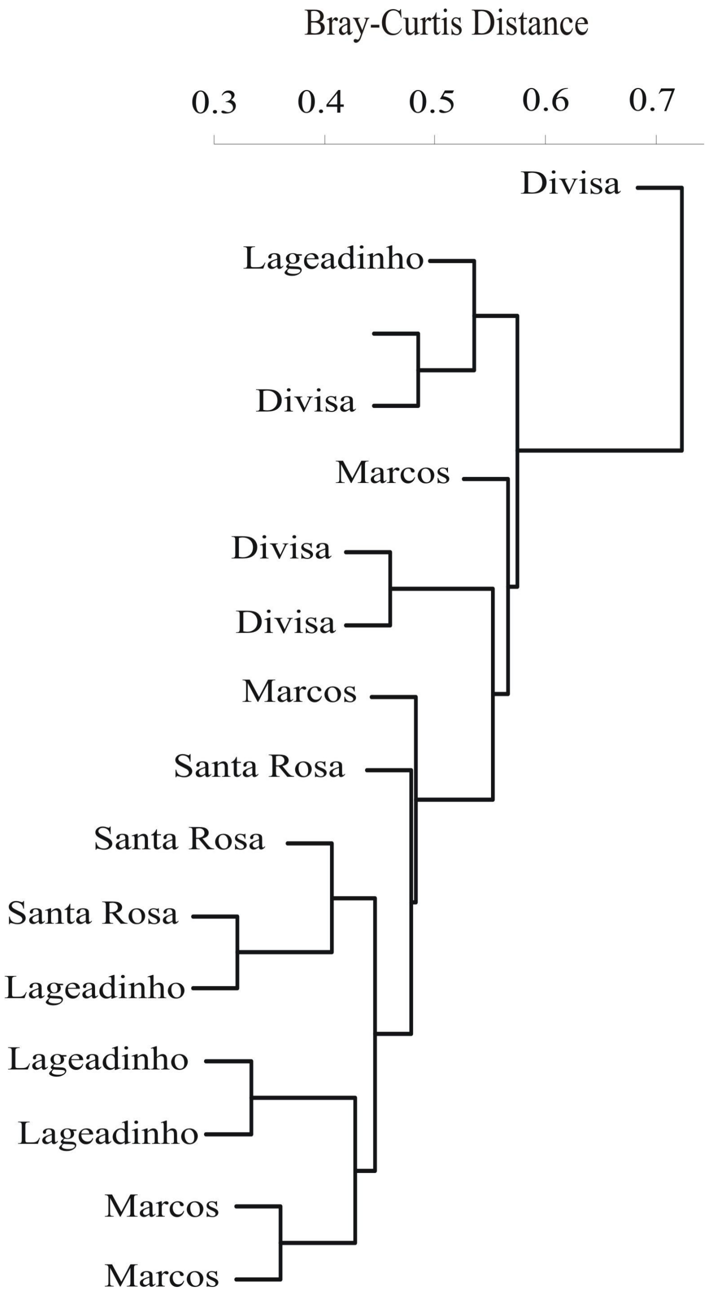

Figure 2. Dendrogram obtained using UPGMA as linkage method and Bray-Curtis dissimilarities of aquatic insects in streams (combination of three riffles) in São José dos Ausentes, Brazil.

Table 2. Observed and expected total diversity partitioned into α (Surber sampling unit), β1 (among Surber sampling units), β2 (among riffles), β3 (among streams), and β4 (among microbasins) in four river microbasins in southern Brazil.

Diversity Component		Observed	Expected	$\text{Prop}_{\text{Exp>Obs}}$
Surber sampling unit	α	10.09	12.39	0.999
Among Surber sampling units	β1	5.84	3.54	< 0.001
Among riffles	β2	13.43	12.99	0.009
Among streams	β3	22.63	20.20	< 0.001
Among microbasins	β4	22.00	19.24	0.002
Total	γ	74		

Discussion

Streams are highly heterogeneous habitats, and this is reflected in the variations in the composition of their faunal assemblages. This environmental variation may confound the estimation of the part of the assemblage variation that is caused by space. In this study, we avoided this problem by selecting similar sampling sites. The absence of correlation between the environmental and biological dissimilarity matrices ratifies the homogeneity of the stream riffles sampled.

The cluster analysis showed that the assemblages sampled were not strongly structured according to the spatial hierarchy studied. This is partially at odds with our expectations, since the stream riffles were mostly similar in terms of environmental conditions, and therefore a spatial structure would be expected. A plausible explanation would be the small spatial extent of the study, particularly among fine spatial scales (riffles, streams), which would allow frequent dispersal by insects. There was a relatively low (r = 0.35) but significant correlation between biological dissimilarity and geographical distance among the streams. This result is in accordance with the findings of Munn et al. (2009) who also identified important effects of space on biological assemblages.

The low correlation between the biological dissimilarity and the geographical distance, and the lack of correlation between biological dissimilarity and distance along the stream corridors can be explained by the dispersal capacity of the insects studied and the small spatial extent of the study (maximum geographical distance = 19.8 km). Aquatic insects have limited dispersal capabilities (Collier & Smith, 1998), but the small extent of the study should have been enough to allow homogenization of nearby sites. Ephemeroptera, Plecoptera and Trichoptera adults have limited flight capacity and, at least for forested catchment basins, many of them have a tendency to fly along the stream channel, particularly upstream (Müller, 1982).

The species richness partitioning showed that richness on the smallest scale (α, Surber sampling units) was lower than that expected by chance. This demonstrates that species are distributed in an aggregated way at this scale. A similar result was found by Ligeiro et al. (2010), studying families of macroinvertebrates in streams of the Brazilian Cerrado (savanna vegetation). This may have occurred by the macroinvertebrates selecting for preferential or specific habitats (Robson & Chester, 1999; Downes et al., 2000; Costa & Melo, 2008), or more likely, since our study was done in similar riffle habitats, concentrated deposition of eggs (Encalada & Peckarsky, 2006) and low dispersal by immatures (Bunn & Hugues, 1997). All beta-diversity components were larger than expected, indicating limited dispersal on all spatial scales studied. The magnitude of the beta-diversity components increased with coarser scales, indicating that dispersal tended to be reduced among streams and among microbasins. Although Ligeiro et al. (2010) did not study the diversity among microbasins, they also found that diversity among streams was higher than that expected by chance, and was usually the highest among the beta-diversity components studied. Studying streams in Finland, Mykrä et al. (2004) obtained similar results to the present study, where the variability in the assemblages of aquatic invertebrates was highest at the drainage scale. These results indicate that the faunas are differentiated on these spatial scales, highlighting the spatial effect on the assemblage organization. The contribution of species richness at the smallest scale (α) was 13.6%, while at the largest scale (β4) this contribution was 29.7%. This reflects the effect of space on the community. Both scales (small and large) are important in the diversity variation (beta diversity). In concordance with our results, Stendera and Johnson (2005) also found a wide variation in assemblages at large scales, among streams in Sweden.

We conclude that over the short distance studied (ca. 20 km), mutually distant streams have dissimilar faunas, although this did not hold for streams that are distant from one another along the aquatic corridor. Although present, the spatial effect was relatively small, since it was not able to reflect the hierarchical spatial structure of the sampling design. The partitioning of the total diversity indicates that this spatial effect is more pronounced at the upper levels of the hierarchy, that is, among streams and microbasins.

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Capítulo 3

Multi-scale decomposition of variance in stream insect assemblages[3]

Abstract

The hierarchical structure of lotic systems may affect aquatic insects communities differently on distinct scale and thus produce complex patterns of spatial distribution. We evaluated the variation of assemblage composition and structure of aquatic insects of the orders Ephemeroptera, Plecoptera and Trichoptera along a hierarchical lotic system. The study was carried out in southern Brazil in three hydrographic basins and included three spatial scales: riffles, streams, and microbasin. We employed hierarchical Analysis of Variance to decompose the variance of total abundance and species richness and partial Canonical Correspondence Analysis to decompose the variance of assemblage composition. The analyses were conducted using full biological matrices and a matrices without rare species (<0.5% of total abundance). The most important spatial scale for total abundance was riffle for both datasets. For richness the most important scales was riffle and stream for both datasets. The matrix of environmental variables explained 23% and the spatial variables 8.2% of the variation in assemblage composition. Using the matrix without rare species did not cause important differences (environment explained 24% and space 8.4%).The variation of assemblage composition explained by the three scales studied was 16.8%. The use of common species only increased explained variation slightly (19.5%). In conclusion, the variation among scales for abundance and richness was only in

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microbasin scale. For the range of scales studied, variation in assemblage composition was most associated to environmental conditions. However, the space showed important effect on assemblage composition mainly when analyzed the different hierarchical levels.

Keywords: beta diversity, hierarchical design, lotic systems, partial CCA, spatial scale.

Introduction

River systems have a hierarchical structure composed of drainage area, channel reach and habitats (riffles and pools) (Allan, 2004). The richness and abundance of organisms may vary in different scales. At fine scales, variation should be caused mostly by the environment, while space should tend to be relatively more important in coarse scales due to restriction of dispersion (Parsons et al., 2003). In general, assemblages are affected by environmental and/or spatial factors which are prevalent in specific scales in a hierarchical system. Previous work have suggested that for aquatic organisms the proportion of variance explained by environmental factors increases when the scale decreases, while the spatial effects become more important when the scale increase (Mykra et al., 2007; Heino et al., 2010). Evidence for this claim can be observed in studies reporting beta diversity (turnover) reduction when reducing the scale of a study in a single habitat (Clarke et al., 2010). On the other hand, variation in environmental conditions is considerable at small scales and the biological communities usually reflect environmental dissimilarities (Heino et al., 2004; Costa and Melo, 2008).

It is important to consider the spatial scale of the study because distinct patterns and process are present in different levels of the hierarchy (Heino, 2009). Thus, regional processes and local environmental factors are important for the assemblage composition that may vary with the scale of study (Mÿkra et al., 2007). In addition to space and environment, assemblage composition may vary due to biological interactions, mainly in small scales (Downes et al., 1993). However, the pattern of variability that occurs in multiple scales suggests that variation must be considered in each level of study (Li et al., 2001). Thus, the dependence on environmental variables along the spatial scales results in a complex relation between the biota and its environment (Feld and Hering, 2007). While the selection of suitable scales to measure diversity is fundamental to interpret and understand lotic systems, explicit recognition of this issue and proper sampling designs are not common in ecological studies (Parsons et al., 2004).

The hierarchical structure of lotic systems and the dependence of factors that affect aquatic insects on scale result in complex patterns of distribution of assemblages in space (Grand and Mello, 2004). Accordingly, attention should be devoted to approaches that assess the magnitude of variation associated to different scales. The variance decomposition approach proposed by Cushmann and McGarigal (2002) may help the identification of important factors that may otherwise be misinterpreted in traditional analyses. The technique makes possible to examine the effects of environmental and spatial factors on assemblage structure in each level or scale of study (Grand and Mello, 2004). According to Cushmann and McGarigal (2002), the methodology presents the great advantage of allowing the evaluation of the relationships among the factors studied in each scale. Additionally, it allows assessment of exclusive and shared effects of factors in the study. In this approach, the first tier of decomposition uses the total biological dataset to assess the relative importance (exclusive variance explained) and redundancy (shared variance explained) of each data set of explanatory factors (e.g. environmental and spatial factors). In a second tier of decomposition, the independent and shared effects are quantified for each scale separately.

The knowledge about species richness, assemblage composition and how they are spatially structured is a fundamental measure to guide strategies of conservation and to improve regional diversity (Zamora et al., 2007). Generally, conservation plans considers the species distribution along the landscape, selecting priority areas to set biological reserves. However, this approach demands a good understanding on species distribution. Accordingly, approaches of study that consider the assemblage composition at multiple spatial scales are very advantageous in obtaining consistent results (Clarke et al., 2010). They can, for instance, best identify the scales where substantial portions of the rare species are located. The concept of rare species depends on the scale of the investigation and on the manner in which the assemblage has been studied (Magurran, 2004). Rare species have restricted spatial distribution besides being species with low density (Fontana et al., 2008). According, rare species significantly increase assemblage richness and are important for beta diversity in a particular region (Clarke et al., 2008; Reichert et al., 2010). However, the occurrence of rare species can be affected by environmental heterogeneity (Clarke et al., 2008), dispersion limitation (Malmqvist, 2002), and environmental fragmentation (Fagan et al., 2002).

We evaluated the variation of assemblage composition and structure of aquatic insects of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) along a hierarchical system composed by riffles, streams and microbasins in the Neotropical region. Specifically, we (i) assessed the magnitude of variation associated to each scale studied in terms of species richness, assemblage composition and structure using a multiple-scale approach that decomposes the total variation in fractions explained by environmental and spatial factors and (ii) evaluated the effect of rare species on the partition of variation among scales. Our expectation was that the relative importance of space, in terms of proportion of variance explained, tend to increase at coarse scales. Additionally, most of this explained variation at coarse scales should be caused by patch distribution of rare species. Abundant species should be occur at high frequency all over the study area and thus space should be a weak predictor for them.

Materials and methods

Study area

The study was carried out in São José dos Ausentes, in the northeast of Rio Grande do Sul state, Brazil (28º54’44’’S, 50º03’57”W). The average altitude is 1200 m and the topography present plateaus and incised valleys. The annual mean temperature is 14.4°C and annual mean precipitation of 1468 mm (Lemos, 1973). The predominant vegetation is highland grassland fields with patches of forests with *Araucaria angustifolia* pine trees (Buckup et al., 2007).

Sampling of stream insects

We selected four streams in each of three microbasins (Marcos river, Lajeadinho river, and Divisa river). Streams were second order, with natural vegetation in their margins, absence of anthropogenic activities, substrate composed mostly by stones and similar frequency and extension of riffles. In each of the 12 streams studied we defined three riffles with substrate composed by stones. These riffles were 150 m distant to each other and in each one we obtained two Surber sampling units. The study was composed of 72 sampling units (3 microbasins x 4 streams x 3 riffles x 2 Surber sampling units).

We obtained Surber sampling units (area = 0.09 m^2; mesh = 250 μm) in stone substrate of riffle zones. The organisms were preserved with 80% ethanol. In laboratory, we selected individuals of Ephemeroptera, Plecoptera and Trichoptera and identified them until family or genus using Merritt and Cummins (1996) and Fernandez and Domingues (2001) identification keys. Individuals within genera or families were further separated in morphospecies (hereafter termed species for simplicity). We measured at each stream riffle current velocity, water temperature, turbidity, electrical conductivity, pH and dissolved oxygen using a multiparameter analyser.

Data Analysis

We decomposed the variance of total abundance (transformed in log[x+1]) and species richness with hierarchical analysis of variance, where microbasin, streams and riffles were considered nested factors. Surber sampling units formed the error component of our hierarchical analysis of variance (Downes et al., 1993). We used four models with different dependent variables: (1) total abundance, (2) total species richness, (3) abundance excluding rare species (abundance < 0.5%), and (4) species richness excluding rare species (abundance < 0.5%).

We used partial Canonical Correspondence Analysis (pCCA) to identify the effects of hierarchically structured explanatory datasets on aquatic insect distribution (Cushmann and McGarigal, 2002). We conducted a series of CCA and pCCA analyses to partition the variance in the community in fractions explained by each explanatory dataset. We used the biological matrices based in the insect total abundance and insect excluding rare species, both transformed by log (x+1). The riffle scale was composed by union of two Surber sample units. We conducted two sets of pCCA. First, we used two quantitative explanatory matrices of environmental variables and geographic coordinates. The second set of pCCAs employed a categorical matrix to reflect the hierarchical organizations of streams. We used this last approach to determinate the variance explained in each scale studied. For this second set of analyses, we used three datasets of categorical variables, each one representing a scale of study (riffle, stream and microbasin). The second approach of decomposition provided information about the relative importance of each scale (exclusive variance explained) and their redundancies (shared variance) in the hierarchical design (riffle, stream and microbasin). In CCA and pCCA analyses of community data, we recorded the sum of canonical eigenvalues and divided it by the total inertia (total variation in the biological data) to estimate the proportion of the total variation explained by each set of variables. In the second set of decomposition of variance, the percentage of total species variation explained by riffle, stream, and microbasin scale together are obtained by difference between the components (different scales) variance divided by total inertia.

The statistical significance the CCA and pCCA analyses were obtained by a Monte Carlo unrestricted permutation test with 199 permutations of all canonical axes combined. The same method was used to decompose the variance of the biological data excluding rare species. The analyses were accomplished in the statistical environment R (R Development Core Team, 2010) using functions from the *vegan* package (Oksanen et al., 2010).

Results

A total of 4911 individuals of Ephemeroptera, Plecoptera and Trichoptera were collected, distributed in 74 species. Exclusion of rare species reduced total abundance to 4644 individuals (5.4% reduction) distributed in 34 species (54% reduction).

The most important scale for species richness was riffle (29.4%, $F_{24,36} = 2.61$, P = 0.004) and stream scale (25.4%, $F_{9,36} = 2.60$, P = 0.030). Exclusion of rare species, however, decreased the importance of the riffle scale (20.6%, $F_{24,36} = 2.15$, P = 0.018) and increased the variance of the stream scale (33.7%, $F_{9,36} = 3.62$, P = 0.006). The total abundance presented variation only in the riffle scale (38.9%, $F_{24,36} = 3.67$, P = 0.001). Exclusion of rare species caused a slight decrease in the variance accounted by riffle scale for abundance data (34.8%, $F_{24,36} = 3.42$, P = 0.001) (Table 1).

The matrix of environmental variables explained 23% of the variation in assemblage composition (P = 0.015) and the spatial variables 8.2% (P = 0.005). The variation shared by environment and space was 1.48% (Figure 1A). Explained variances did not change considerably when using the matrix without rare species. The environmental matrix explained 24% (P = 0.020), the spatial matrix explained 8.4% (P = 0.010) and the variation shared by both matrices was 2.17% (Table 2; Figure 1B).

The second set of pCCA decomposed variation using categorical explanatory variables to represent the hierarchical scales where the study was conducted (riffles, streams and microbasin). In these analyses the matrices used for each scale were analyzed individually, and included the spatial matrix (geographical coordinates) as covariable. The variation of total assemblage composition explained by the three scales studied was 16.8% (Figure 2A). The variance explained exclusively by the riffle scale was 4.3% (P = 0.010), by the stream scale 4.4% ($P = 0.005$) and by the microbasin scale 5% ($P = 0.010$) (Figure 2A). Considering the biological matrix without rare species, the explanation of variance was only slightly higher than those of the full matrix. The variance explained by the three scales was 19.5%. The riffle scale explained exclusively 4.7% ($P = 0.032$) of data variance, the streams scale 4.9% ($P = 0.025$) and the microbasin scale 5.8% ($P = 0.005$) (Table 2; Figure 2B). The variance shared by the three scales for both matrices (total and exclusion of rare species) was very low (1.85% and 2.11%, respectively; Figure 2A and B).

Table 1. Hierarchical Analysis of Variance of species richness and abundance of individuals using the full dataset and after exclusion of rare species (<0.5% total abundance). df = degrees of freedom, SS=sum of squares, MS=mean of squares.

Source	df	SS	MS	F-ratio	*P*-value	% Variance
Richness						
Microbasin	2	218.58	109.29	1.83	0.215	8.60
Streams	9	537.08	59.67	2.60	0.030	25.47
Riffles	24	550.33	22.93	2.61	0.001	29.43
Surber (Residuals)	36	316.00	8.77			36.50
Abundance						
Microbasin	2	3.08	1.53	3.08	0.096	17.05
Streams	9	4.49	0.49	1.83	0.113	14.93
Riffles	24	6.52	0.27	3.67	0.001	38.94
Surber (Residuals)	36	2.66	0.07			29.07
Richness (without rare species)						
Microbasin	2	191.36	95.68	1.83	0.215	9.72
Streams	9	469.79	52.19	3.62	0.006	33.79
Riffles	24	345.33	14.38	2.15	0.018	20.67
Surber (Residuals)	36	240.5	6.68			35.82
Abundance (without rare species)						
Microbasin	2	3.65	1.82	3.19	0.089	18.72
Streams	9	5.14	0.57	2.07	0.074	17.63
Riffles	24	6.61	0.27	3.42	0.001	34.88
Surber (Residuals)	36	2.89	0.08			28.78

Table 2. Results of first and second tier partial Canonical Correspondence Analyses used to partition the total variance in the distribution of aquatic insects by explanatory variables (environmental, geographic coordinates, and hierarchical scales represented as categorical variables).

Matrices	Sum of Canonical Eigenvalues	% Variance explained	*P*-value
Biological Matrix: insect abundance. Total inertia = 3.0002			
Environment + Space			
Environmental variables	0.6938	23.12	0.015
Space (geographic coordinates)	0.2483	8.27	0.005
Shared component	0.0447	1.48	
Hierarchical scale (Space with covariable)			
Variance Explained by Riffles scale	0.1292	4.31	0.010
Variance Explained by Stream scale	0.1328	4.43	0.005
Variance Explained by Microbasin scale	0.1508	5.03	0.010
Shared Riffles + Stream scales	0.0000	0.00	
Shared Riffles + Microbasin scales	0.0272	0.91	
Shared Stream + Microbasin scales	0.0095	0.32	
Shared Riffles + Stream + Microbasin	0.0557	1.85	
Biological Matrix: insect abundance excluding rare species. Total inertia = 1.8817			
Environment + Space			
Environmental variables	0.4577	24.32	0.020
Space (geographic coordinates)	0.1588	8.44	0.010
Shared component	0.0410	2.17	
Hierarchical scale (Space with covariable)			
Variance Explained by Riffles scale	0.0898	4.77	0.032
Variance Explained by Stream scale	0.0926	4.92	0.025
Variance Explained by Microbasin scale	0.1097	5.83	0.005
Shared Riffles + Stream scales	0.0000	0.00	
Shared Riffles + Microbasin scales	0.0105	0.56	
Shared Stream + Microbasin scales	0.0164	0.87	
Shared Riffles + Stream + Microbasin	0.0397	2.11	

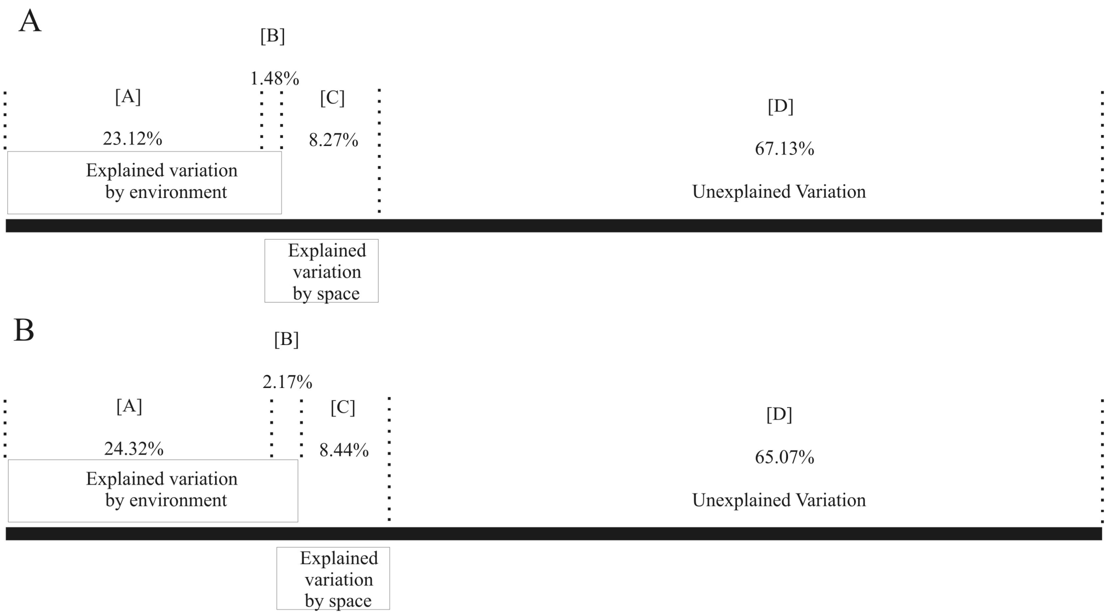

Figure 1. Partition of total variance in the (A) full dataset of aquatic insect abundance and (B) reduced dataset (without rare species <0.5% abundance) of aquatic insect abundance in components explained by environmental and spatial variables, shared (environmental and space), and unexplained variation.

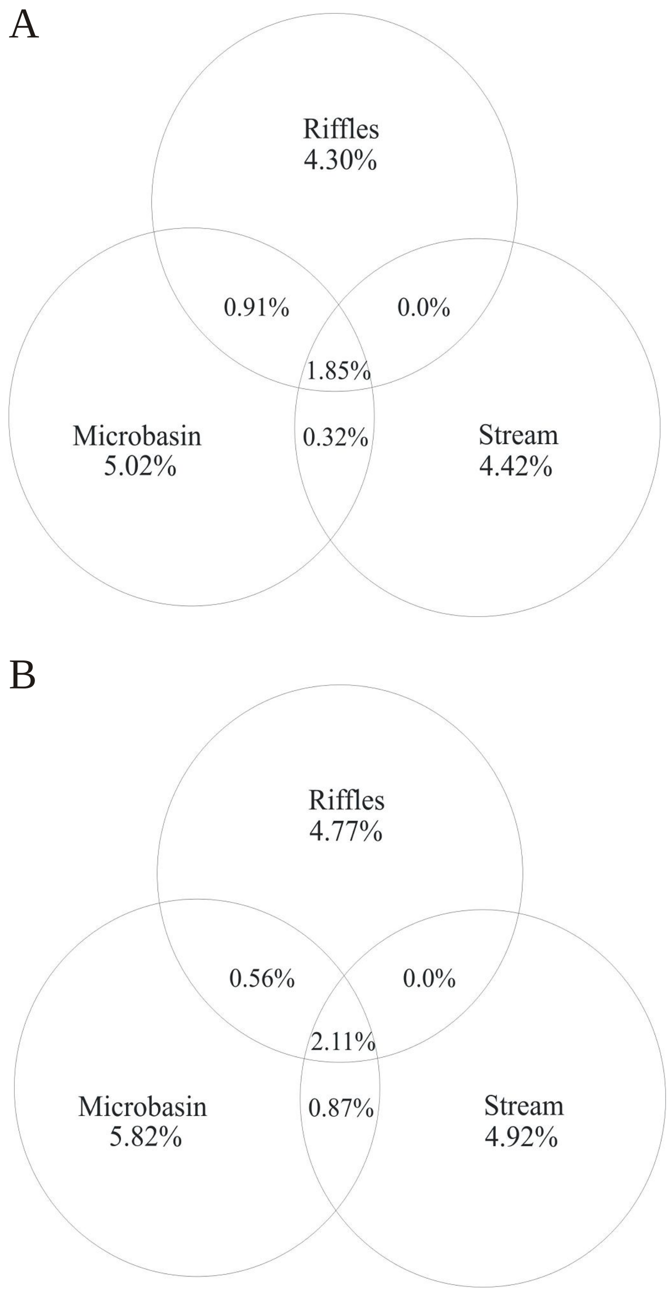

Figure 2. Percent of total variance in the (A) aquatic insect abundance data and (B) aquatic insect abundance data excluding rare (<0.5% abundance) explained by riffles, streams and microbasin scales, as well as variance explained by each combination of factors. Figure is not drawn to scale.

Discussion

The exclusion of rare species caused a severe reduction of the EPT richness sampled in the study area. However, as it was expected, the organism abundance reduction was very low. These reductions did not strongly reflected in the hierarchical partition of variance of abundance and richness for the two datsets employed (total and without rare species). We observed that the small scale (stream and riffle) was the most important variation componen for richness and for the two datsets. While the riffle scale was important for abundance in both dataset. The exclusion of rare species did not showed significant influence in assemblage composition variation. The low magnitude of the variance components may reflect the physical similarity between the studied riffles, streams and microbasin The fact that most of the richness variation was accounted by the residual component indicate that species richness varies greatly from patch to patch (Surber). On the other hand, for abundance, the variance occurs from riffle to riffle.

We expected that inclusion of rare species would increase the importance of variance components at different scales. This would be evidence that they present restricted distribution in space. However, despite the important reduction of total species richness after exclusion of rare species, variance components were similar to those calculated using all species. Accordingly, most of the variations of rare species occur at fine scale (Surber to Surber).

Previous studies have reported considerable variation of total abundance in small scales of streams (Downes et al., 1993). This is at agreement with results of the present study, where the main scale accounting for variation in abundance was stream and riffle scales. We deliberately obtained sample units in areas of the same order, and a similar substrate mesohabitat (2nd order, rocks in riffles, respectively). Thus, the homogeneity of sampling sites may be one reason for lower variation in fine scales. However, we can show with our results, the existence of an effect on the spatial variation of abundance and richness of insects.

Previous works have suggested that environmental variables should be most important to assemblage structure at fine spatial scales (Mykra et al., 2007). On the other hand, space should be most important for organism distribution at coarse scale. We did not assessed the relative importance of environmental factors and space at each spatial scale. However, for the three scales studied taken together, environment factors accounted roughly by three times the variation explained by space. This is despite our deliberate sampling design aimed to sample similar environments (cobbled riffles of headwater streams). The low percentage of variation shared among the environmental and spatial components shows that the effects were mostly independent. Some studies have presented results similar to the ones in this work, where the environmental variables explained most of the data variation (Mykra et al., 2007; Costa and Melo, 2008). The exclusion of rare species did not alter the variation explained by the environmental and spatial components, although caused a slightly increase of explained variation. This demonstrates that the rare species have a relatively small importance in this study for the beta diversity. Similar results were obtained by Heino and Soininen (2010) which concluded that the spatial variation in aquatic communities can be adequately described using common species. Although rare species are important for aquatic diversity, the use of species common in studies of spatial variation seems to be enough. This can be accepted by the fact that, as there are many rare species, is possibly irrelevant to evaluate these species and effort can be channeled into common species.

Regarding scales specifically, we expected to observe large variation at coarse scales. We observed an increase in the percentage of explained variation in coarse hierarchical scales, but of too low magnitude (~1%). The low variation shared by the different scales shows that the effects of changing scales on the assemblage variation occur in an independent way. In other words, there is not influence of the two or more scales on assemblage composition. The similarity between the aquatic insect assemblage composition among the scales was evident with the results of the variance decomposition analyses. The scales studied (riffle, stream and microbasin) present a physical uniformity that does not contribute for the aggregation of new species, possibly because of the substrate (stones) and hydraulic conditions (riffles) (Parsons et al., 2003). Adult dispersal of EPT should homogenize faunas, mostly at low spatial scales (Li et al., 2001; Mÿkra et al., 2007; Ligeiro et al., 2010), as most EPT species have a limited capacity of dispersion and restrict their flight to the stream corridor. Our results show that although limited, dispersal rate is large enough to cause homogeneous fauna over the coarsest scale studied.

The low variance in the assemblage composition observed in this study, where the sample units were obtained in physically very similar conditions, shows a real and weak effect of space on the assemblages. The increase in the variation of the assemblage composition with the increase on scale showed a small improvement from the local diversity to the regional diversity. According to Clarke et al. (2010) high alpha diversity and low beta diversity occur in small scales. When beta diversity is low in the smallest scales it is an indication of physical similarity among locals (Winberg et al., 2007). This is a strong indicator for conservation programs. The streams in the region studied are very similar regarding the physical structure (e.g. substrate and current speed). With our results it is visible the importance of maintaining the environmental heterogeneous conditions in all scales of a hierarchical system such as a hydrographic basin, contributing for the increase in the diversity of species. Another application for our study is the biomonitoring. It is important to consider the scale of study in a hydrographic basin to evaluate the environmental integrity, since a simple sampling in few streams will be sufficient to represent the entire fauna of basin.

In this study, most of the variation of abundance and species richness occurred at the finest scale (Surber, riffle, and stream) and moderately at the coarsest scale (microbasin). In assemblage composition the variation was more explained by environmental variables. However, the space showed important effect on assemblage composition mainly when analyzed the different hierarchical levels. Although more than half of the total species were rare (<0.5% abundance), their exclusion did not affected considerably the relative importance of variance components in terms of abundance, species richness and assemblage composition.

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Conclusões Gerais

Os fatores ambientais foram importantes na explicação da variação das assembléias de Ephemeroptera, Plecoptera e Trichoptera (EPT) nos riachos estudados (Maquiné e São José dos Ausentes). No entanto, em todos os estudos aqui apresentados, o espaço, mesmo tendo uma porcentagem de explicação menor que o ambiente, apresentou significativa importância na variação das assembléias dos insetos aquáticos estudados.

Inúmeros estudos relatam uma relação positiva entre riqueza de espécies e heterogeneidade do substrato. Porém, a heterogeneidade pode causar uma agregação de matéria orgânica no substrato e resultar em um aumento da abundância de organismos. Isso causaria um aumento natural da riqueza, não expressando de maneira clara os efeitos da heterogeneidade sobre a riqueza. Dentre as variáveis ambientais avaliadas no Capítulo 1, o tipo de substrato e o conteúdo de matéria orgânica aderido aos substratos artificiais foram as variáveis mais relevantes para a riqueza e abundância dos insetos. Entretanto, o efeito da heterogeneidade do substrato sobre a riqueza de organismos deixou de existir quando o efeito da abundância de insetos foi excluído por meio de uma análise de rarefação. Assim, concluí que a heterogeneidade do substrato apresenta um efeito indireto sobre a riqueza, visto que contribui para o acúmulo de matéria orgânica e, conseqüentemente, para o acúmulo de organismos. Considerando os efeitos do ambiente e distância entre trechos sobre a variação na composição da assembléia (diversidade beta), as variáveis ambientais explicaram cerca de 12% da variação enquanto que a posição dos trechos explicou cerca de 7%. Por fim, a ordenação das unidades amostrais apresentou relação entre posição (NMDS 1) e tipo de substrato (NMDS 2). A porcentagem de explicação não explicada pelas variáveis estudadas pode ser atribuída à pequena escala de estudo (aproximadamente 5 km entre primeiro e último trecho).

Quando avaliei a dissimilaridade das assembléias de EPT em múltiplas escalas espaciais (Capítulo 2) concluí que há maior variabilidade nas escalas maiores (riachos e microbacias). Neste estudo, como houve similaridade ambiental entre os locais estudados, mesmos nas diferentes escalas, foi possível observar a real contribuição do espaço na variabilidade das comunidades. A distância geográfica foi mais importante que a distância pelo corredor dos riachos para a diversidade beta. Isso pode ter ocorrido pela capacidade limitada de dispersão das espécies adultas de EPT. Estes organismos voam apenas a poucos metros lateralmente em relação aos riachos, sendo que o padrão de vôo é principalmente ao longo do riacho em direção às nascentes. Isso faz com que haja menor variabilidade das comunidades entre os trechos de corredeiras e maior entre riachos e microbacias. A não existência de um padrão hierárquico entre os riachos estudados, ocorreu, possivelmente, pela proximidade entre os locais de estudo, mesmo pertencentes a microbacias diferentes.

No último estudo desenvolvido neste trabalho (Capítulo 3) observei maior variação da composição das comunidades nas escalas mais amplas (microbacia). Porém, para abundância e riqueza de espécies, observei maior variabilidade nas escalas mais finas (corredeiras e riachos). Neste estudo, a exemplo do Capítulo 1, as variáveis ambientais apresentaram maior porcentagem de explicação para a variação da comunidade. No entanto, quando eliminei o efeito ambiental e considerei apenas os efeitos espaciais (diferentes escalas), observei que a contribuição geral do espaço foi de aproximadamente 19% (para matriz completa e com exclusão das espécies raras). A exclusão das espécies raras na análise dos efeitos das escalas sobre a variação da comunidade foi levemente superior. Isso indica que para estudos em diferentes escalas o uso apenas das espécies dominantes é suficiente.

Em linhas gerais, este trabalho mostrou os efeitos das escalas espaciais na diversidade alfa e beta e, conseqüentemente, sua importância para a diversidade regional (gama). Além disso, ficou evidente a importância da heterogeneidade ambiental como fator de incremento da diversidade em diferentes escalas. Quando avaliei diferentes tipos de substratos (homogêneos e heterogêneos, Capítulo 1), estes se mostraram importantes para a diversidade alfa e beta. Da mesma forma, quando avaliei tipos de substrato semelhantes (pedras em corredeiras, Capítulos 2 e 3) estes foram relevantes no aumento de variação conforme aumentava a escala de estudo. Considerando a importância que pequenos riachos possuem para bacias hidrográficas, a manutenção da heterogeneidade das bacias hidrográficas em múltiplas escalas espaciais poderá contribuir para o incremento da biodiversidade aquática.

Diante do exposto, saliento que o assunto não está esgotado e futuras investigações devem ser realizadas acerca da temática deste trabalho. A realização de estudos com desenhos experimentais semelhantes, mas com escalas mais amplas (> 100 km) podem apresentar resultados interessantes quanto à dissimilaridade das assembléias nas diferentes escalas hierárquicas. Avaliar a dispersão de adultos de EPT ao longo do corredor dos riachos ou lateralmente, em relação aos riachos, pode reforçar os efeitos do espaço sobre a diversidade beta dessas assembléias. Além disso, o uso de outras variáveis ambientais, como características da paisagem (e.g. uso da terra) podem auxiliar na identificação de padrões de distribuição dos organismos aqui estudados.

Anexos

Tabela 1. Gêneros de Ephemeroptera, Plecoptera e Trichoptera encontrados nos sete trechos do riacho Forqueta em Maquiné (RS, Brasil). NI = gênero não identificado.

	Trechos						
	01	02	03	04	05	06	07
Ephemeroptera							
Baetidae							
Baetis		x	x	x	x	x	x
Baetodes	x	x	x	x	x	x	x
Camelobaetis	x	x	x	x	x	x	x
Cloeodes	x	x	x	x	x	x	x
Moribaetis	x	x	x	x	x	x	x
Rivudiva				x			
Leptohyphidae							
Leptoyphes	x	x	x	x	x	x	x
Leptophlebiidae							
Hagenolopsis	x						
Farrodes	x	x	x	x	x	x	x
Thraulodes	x	x	x	x	x	x	x
Plecoptera							
Grypopterigydae							
Gripopteryx	x	x	x	x	x	x	
Paragripopteryx	x		x	x	x		x
Tupiperla		x	x	x			
Perlidae							
Anacroneuria	x	x	x	x	x	x	x
Kempnyia	x	x	x	x			
Trichoptera							
Hydropsychidae							
Smicridea	x	x	x	x	x	x	x
Leptonema	x	x	x	x	x	x	x

Continua.

Tabela 1. Continuação.

	Trechos						
	01	02	03	04	05	06	07
Trichoptera							
Hydrobiosidae							
Atopsyche	x	x	x	x	x	x	x
Hydrobiosidae NI	x	x	x				
Glossosomatidae							
Itaura	x	x	x	x	x	x	x
Protoptila	x	x	x	x	x	x	x
Helicopsychidae							
Helicopsyche		x	x		x	x	x
Hydroptilidae							
Anchitrichia	x						
Metrichia	x	x	x	x			x
Neotrichia	x	x	x		x	x	x
Alisotrichia	x	x	x	x	x	x	x
Zumatrichia	x	x	x	x		x	x
Hydroptila	x	x	x	x			
Leptoceridae							
Leptoceridae NI		x	x	x	x	x	x
Philopotamidae							
Wormaldia	x	x	x	x	x	x	x
Sericostomatidae							
Grumicha	x	x	x	x	x	x	x
Gênero NI-1		x			x	x	x
Gênero NI-2	x	x		x		x	
Gênero NI-3	x	x	x	x	x	x	x

Tabela 2. Gêneros e morfo-espécies de Ephemeroptera, Plecoptera e Trichoptera encontrados nos riachos das quatro bacias hidrográficas estudadas em São José dos Ausentes (RS, Brasil).

	Bacias Hidrográficas			
	Santa Rosa	Lageadinho	Marcos	Divisa
Ephemeroptera				
Baetidae				
Aturbina			x	
Baetis	x	x	x	x
Baetodes sp1	x	x	x	x
Baetodes sp2	x	x	x	x
Baetodes sp3	x	x	x	x
Baetodes sp4	x	x		
Baetodes sp5	x			
Cloeodes sp1	x	x	x	x
Cloeodes sp2			x	
Camelobaetis sp1	x	x	x	x
Camelobaetis sp2	x	x	x	x
Camelobaetis sp3	x			
Moribaetis sp1	x	x		x
Moribaetis sp2	x	x	x	x
Caenidae				
Caenis	x	x	x	x
Leptophlebiidae				
Askola	x	x	x	x
Farrodes sp1	x	x	x	x
Farrodes sp2	x			x
Farrodes sp3	x		x	
Thraulodes sp1	x	x	x	x
Thraulodes sp2	x	x	x	x

Continua.

Tabela 2. Continuação.

	Bacias Hidrográficas			
	Santa Rosa	Lageadinho	Marcos	Divisa
Ephemeroptera				
Leptohyphidae				
Leptoyphes sp1	x	x	x	x
Leptoyphes sp2	x		x	x
Leptoyphes sp3	x	x	x	x
Trichorytodes sp1	x	x	x	x
Trichorytodes sp2	x		x	
Trichorytodes sp3	x	x		
Trichorytodes sp4	x		x	
Ephemereliidae				
Hexagenia		x		
Plecoptera				
Grypopterigydae				
Gripopteryx sp1	x	x	x	x
Gripopteryx sp2	x	x		x
Paragripopteryx sp1		x		
Paragripopteryx sp2	x	x	x	x
Paragripopteryx sp3		x		
Tupiperla sp1	x	x	x	x
Perlidae				
Anacroneuria sp1	x	x	x	x
Anacroneuria sp2	x	x		x
Anacroneuria sp3	x	x	x	x
Anacroneuria sp4	x			
Anacroneuria sp5	x	x		x
Kempnyia sp1		x		
Kempnyia sp2		x		x

Continua.

Tabela 2. Continuação.

	Bacias Hidrográficas			
	Santa Rosa	Lageadinho	Marcos	Divisa
Trichoptera				
Philopotamidae				
Chimarra	x			x
Hydropsychidae				
Smicridea sp1	x	x	x	x
Smicridea sp2		x	x	x
Smicridea sp3	x	x	x	x
Smicridea sp4	x	x	x	x
Polycentropodidae				
Polyplectropus		x	x	x
Hydrobiosidae				
Atopsyche sp1	x	x	x	x
Atopsyche sp2		x		
Atopsiche sp3		x		x
Atopsiche sp4			x	
Atopsiche sp5			x	x
Atopsiche sp6				x
Atopsiche sp7		x		
Glossosomatidae				
Itaura sp1	x	x	x	x
Itaura sp2		x		
Protoptila	x	x	x	x
Hydroptilidae				
Metrichia	x	x		x
Hydriptilidae sp1	x	x	x	x
Hydroptilidae sp2		x	x	

Continua.

Tabela 2. Continuação.

	Bacias Hidrográficas			
	Santa Rosa	Lageadinho	Marcos	Divisa
Trichoptera				
Hydroptilidae				
Neotrichia		x	x	x
Oxytrichia sp1		x	x	x
Oxytrichia sp2	x	x		
Helicopsychidae				
Helicopsyche sp1	x	x	x	x
Helicopsyche sp2	x	x	x	
Leptoceridae				
Nectopsyche	x	x	x	x
Leptoceridae sp1	x			x
Leptoceridae sp2		x	x	x
Leptoceridae sp2	x		x	
Odontoceridae				
Marilia	x	x	x	x
Calamoceratidae				
Phylloicus sp1		x		
Phylloicus sp2	x	x	x	x
Phylloicus sp3				x