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# Relações espaciais e ambientais da biodiversidade em florestas tropicais

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Tese defendida em 21 de Novembro de 2011

Manaus, Amazonas

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# Relações espaciais e ambientais da biodiversidade em florestas tropicais

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Co-Orientador: Dr. Luis Mauricio Bini (UFG)

Tese apresentada ao Programa de Pós-Graduação em Ecologia do Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Biologia (Ecologia).

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**Sinopse:**

Este trabalho faz uma revisão sobre as principais análises espaciais usadas em ecologia e discute em quais situações algumas delas devem ser utilizadas. Estudou-se a distribuição de diversos grupos taxonômicos em florestas da Amazônia considerando fatores ambientais e espaciais na geração desses padrões. Adicionalmente, avaliou-se a possibilidade de usar grupos substitutos para facilitar estudos de monitoramento biológico em florestas da Amazônia

**Palavras-chave:** Substitutos, fatores ambientais, fatores espaciais, ecologia espacial

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## Resumo

Este trabalho teve como objetivo avaliar questões referentes à ecologia espacial e como as análises espaciais podem ajudar os ecólogos a entender os padrões de distribuição de espécies. Inicialmente fizemos uma revisão da literatura mais atual sobre ecologia espacial e tentamos explicar alguns conceitos básicos através de simulação de dados para ilustrar diversas possibilidades com que os ecólogos podem se deparar. Em uma segunda etapa nós avaliamos a importância de definir bem as variáveis espaciais para serem incluídas em modelos ecológicos, avaliando a diferença entre análises usando uma matriz de distância que define rotas de dispersão pelo curso d'água e rotas de dispersão em linha reta, sobre a terra. Uma das técnicas mais recentes e utilizadas da ecologia espacial, os autovetores espaciais, podem ser tão flexíveis na geração de padrões espaciais que não importa qual matriz de distâncias é utilizada que os mesmos padrões serão gerados. Usando dados de peixes, de insetos aquáticos (Trichoptera) e dados simulados nós mostramos que a técnica de autovetores não é tão flexível como esperado. Portanto, a definição correta da matriz de distâncias é muito importante para que uma análise adequada seja feita. Em um próximo passo nós avaliamos duas abordagens para analisar dados ecológicos. Uma delas, usando dados brutos e a outra usando matrizes de distância. Uma discussão recente sobre o uso dessas duas abordagens se instalou na ecologia, porém ainda não há um consenso sobre quando usar cada uma delas. Assim, nós usamos e comparamos as duas abordagens para analisar dados de distribuição de Trichoptera em 89 riachos da Amazônia central, distribuídos em 3 regiões distintas (Reserva Ducke, áreas do PDBFF e no município de Presidente Figueiredo). Nós avaliamos o efeito da extensão espacial e da heterogeneidade ambiental nas análises da distribuição das espécies de Trichoptera. Os fatores ambientais foram os mais relacionados com a distribuição de Trichoptera em todas as escalas analisadas. Analisamos a distribuição de anuros em 72 parcelas amostrais da Reserva Ducke e observamos que o padrão de distribuição das espécies é muito relacionado ao tipo de reprodução das espécies. Espécies de anuros com reprodução aquática são mais bem explicadas por padrões ambientais enquanto as espécies com reprodução terrestre são mais explicadas por padrões espaciais. Desta forma, anuros com reprodução aquática são mais indicados para estudos de monitoramento biológico e avaliação de efeitos de alterações ambientais do que o uso de anuros com reprodução terrestre ou que o uso de ambos. Por fim, nós avaliamos a concordância nos padrões de distribuição de 22 grupos taxonômicos (15 de plantas e 7 de animais) amostrados da Reserva Ducke. Avaliamos também se é possível reduzir a resolução taxonômica de espécies para gêneros e a resolução numérica, de abundância para dados de presença e ausência sem a perda de informações importantes. Observamos que o uso de dados de presença e ausência e que identificações em nível de gênero são suficientes para analisar o padrão de distribuição dos grupos analisados. Houve grande concordância no padrão de distribuição das espécies de plantas, enquanto os grupos de animais foram pouco concordantes. Os fatores ambientais foram os mais relacionados à alta concordância entre os grupos, mostrando que o ambiente é o principal responsável pela distribuição das plantas na Reserva Ducke. Embora alguns grupos tenham apresentado forte padrão espacial não houve relação entre a concordância entre os grupos e os fatores espaciais. Os grupos mais concordantes, e possíveis candidatos a grupos substitutos, foram lianas da família Bignoniaceae, ervas, samambaias e árvores das famílias Lecythidaceae e Fabaceae.

## Spatial and environmental relationships of biodiversity in tropical forests

### Abstract:

This study aimed to evaluate issues related to spatial ecology and how spatial analysis can help ecologists to understand patterns of species distribution. Initially, we reviewed the current literature on spatial ecology and illustrated basic concepts with simulated data represented various situations that ecologists frequently face. In a second step we evaluated the importance of clearly defining the spatial variables to be included in ecological models, assessing the differences between analyses using a matrix that defines dispersal routes through stream distance and routes of dispersal in a straight line overland. One of most frequently used techniques spatial ecology, spatial eigenvector functions, is generally considered to be so flexible in generating spatial patterns that it should generate the same patterns no matter what distance matrix is used. Using data from fish, aquatic insects (Trichoptera) and simulated data, we show that the technique of eigenvectors is not as flexible as expected. Therefore, the correct definition of the matrix of distances is important for an effective analysis. In the next step, we evaluated two approaches to analyze ecological data. One of them uses raw data and the other using distance matrices. A recent discussion on the use of these two approaches has been polemical and we try to clarify what types of questions each of these approaches is better able to analyze. To do this we used data on the distribution of Trichoptera in 92 streams of central Amazonia, sampled in three distinct regions (Ducke Reserve, at PDBFF areas, and at the municipality of Presidente Figueiredo). We also evaluated the effect of spatial extent and environmental heterogeneity to on the distribution of Trichoptera species. We found that environmental factors were more related to the distribution of Trichoptera than undefined factors that caused spatial clumping at all scales examined. We analyzed the distribution of anuran species at 72 sample plots in Ducke Reserve and observed that the species distribution pattern is much related to the type of reproduction of the species. The distribution of species with aquatic reproduction is better explained by environmental patterns, while species with terrestrial reproduction are better explained by spatial patterns. We conclude that anurans with aquatic reproduction are better indicated for biomonitoring and for studies evaluating the consequences of environmental disturbances than the use of species with terrestrial reproduction or than the use of both. Finally, we evaluated the congruence in the distribution patterns of 22 taxa (15 plants and 7 animal groups) sampled at Ducke reserve. We also evaluated if it is possible to reduce the taxonomic resolution of species to genera and the numeric resolution from abundance data to presence-absence data with little loss of information. Presence-absence data and genus-level identification was sufficient to capture most of the spatial patterns of most groups. There was strong congruence in the distribution pattern of plant groups, while animal groups were less concordant. Measured environmental factors were closely related to the high congruence among the groups, indicating that environment is primarily responsible for the distribution of plants in the Ducke Reserve. Although some groups showed strong spatial patterns, there was no relationship between the congruence among groups and spatial factors. The groups that were more concordant with other groups, and possible candidates as surrogates, were the lianas of the family Bignoniaceae, herbs, ferns, and trees of the families Fabaceae and Lecythidaceae.

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## Introdução geral

Geralmente, espécies diferentes requerem condições ambientais diferentes para persistir. Estas diferenças podem ter surgido em escalas evolucionárias em que os indivíduos de cada espécie se especializaram em explorar otimamente certas condições de habitats e recursos. O estudo da distribuição de espécies e as relações espécie-ambiente é um tema central da ecologia. Estes estudos formam a base para a conservação e planos de manejo de espécies ameaçadas, para prever impactos das mudanças globais e impactos do uso da terra, bem como de outros estudos de impacto ambiental.

O estudo dos efeitos ambientais na distribuição de espécies, geralmente chamados de efeitos do nicho, surgiram há bastante tempo e formam os pilares da ecologia. Diversos conceitos de nicho já foram propostos (e.g. Krebs, 2008) e em geral os ecólogos tentam explicar a distribuição das espécies com base nas variáveis ambientais medidas em cada local. Desta forma, dados de comunidades são relacionados aos dados ambientais utilizando diversos tipos de análises, onde, em geral, tenta-se avaliar quanto da distribuição das espécies é explicado pelas variáveis ambientais. Quando um conjunto de dados de algum grupo biológico é explicado por um conjunto de dados ambientais presume-se que àquele grupo biológico é controlado por fatores referentes ao nicho das espécies.

Na tentativa de explicar a distribuição das espécies de outra forma, pensando mais nos fatores espaciais, Hubbell (2001) unificou duas grandes teorias da ecologia, a teoria neutra e a teoria de biogeografia de ilhas. Na teoria de Hubbell (2001), todos os indivíduos de todas as espécies são equivalentes ecologicamente, mas limitações na capacidade de dispersão, iguais para todas as espécies, geram os padrão de distribuição de espécies que observamos na natureza. Neste modelo, as distribuições e abundâncias podem variar entre espécies, mas estas diferenças são somente devido à fatores aleatórios e pouco afetadas por fatores ambientais (limitações do nicho). A partir dessa teoria, muitos pesquisadores passaram a avaliar se as comunidades estudadas eram mais afetadas por fatores ecológicos relacionados aos nichos das espécies, ou se o padrão se deve mais aos fatores neutros, relacionados à dispersão limitada das espécies (e.g. Gilbert e Lechowicz, 2004; Adler *et al.*, 2007; Smith e Lundholm, 2010; Diniz-Filho *et al.*, 2011).

Um dos principais objetivos da ecologia é entender a distribuição das espécies, identificando as escalas em que os processos ecológicos que controlam a distribuição. Os problemas associados à presença de autocorrelação espacial em conjuntos de dados foram apontados há muito tempo (Cliff e Ord, 1973; Sokal e Oden, 1978a,b). A autocorrelação espacial descreve a tendência de variáveis assumirem valores, em pares de locais a certa distância, mais similares (autocorrelação positiva) ou menos similares (autocorrelação negativa) do que esperado ao acaso (Legendre, 1993; Legendre e Legendre, 1998). Diversas discussões sobre a possibilidade de possíveis erros na interpretação de dados e conclusões erroneamente tiradas de análises que não consideram a autocorrelação espacial

surgiram na literatura ecológica (Legendre, 1993; Lennon, 2000; Diniz-Filho *et al.*, 2003; Hawkins *et al.*, 2007; Dormann *et al.*, 2007).

Porém, até pouco tempo grande parte das pesquisas ecológicas não levava em consideração os componentes espaciais, considerando apenas o efeito de fatores ambientais. Uma nova oportunidade e direção surgiram na ecologia com o início das discussões sobre os efeitos da autocorrelação quando Legendre (1993) trouxe o assunto novamente à tona em um dos artigos mais citados da literatura ecológica recente (1219 citações no ISI em 28 de Julho 2011). A grande contribuição desse artigo foi mostrar que a autocorrelação não deveria ser vista como um problema e sim como uma oportunidade de desenvolvimento de novas perguntas ecológicas. Uma nova forma de se estudar ecologia. A partir dali, diversos métodos têm sido propostos para incluir o espaço como um preditor na ecologia, levando em consideração os efeitos da autocorrelação espacial (Dormann *et al.*, 2007).

A autocorrelação em variáveis biológicas resulta de causas (físicas ou biológicas) que agem simultaneamente e aditivamente (Legendre e Legendre, 1998). Dois tipos de causas de autocorrelação espacial podem ser observados, dependendo de se os processos que geram a estrutura espacial na distribuição de espécies são endógenos ou exógenos (Kissling e Carl, 2008). Os processos endógenos são propriedades inerentes à própria variável, no qual o valor da variável resposta em um local depende dos valores de locais próximos. Os processos bióticos relacionados à distância, como a dispersão e reprodução são processos endógenos (Legendre *et al.*, 2002 nomearam apenas os processos endógenos como "autocorrelação espacial"). Já os processos exógenos geram autocorrelação espacial por causas independentes das variáveis de interesse, na qual a variável resposta é estruturada espacialmente em função de variáveis explanatórias que são estruturadas espacialmente, como o vento e condições climáticas (Legendre *et al.* 2002 trataram os processos exógenos como processos com dependência espacial). A terminologia da literatura espacial é controversa, e comumente autores apresentam glossários de termos para evitar confusão (e.g. Peres-Neto e Legendre, 2010).

O problema da autocorrelação espacial não se limita a distâncias lineares. As ligações entre pontos de amostragem podem ser complexas, como ao longo do sistema de drenagem em bacias hidrográficas (Ganio *et al.*, 2005; Peterson *et al.*, 2007), onde a distância pelo curso d'água pode descrever melhor as relações espaciais do que a distância em linha reta. Diferentes grupos taxonômicos podem se comportar de diferentes formas em relação a distâncias aquáticas. Para peixes, a distância pelo curso d'água pode ser mais importante, pois eles precisam percorrer esta distância para dispersar de um ponto a outro. Para lagartos, cobras, plantas e insetos aquáticos, a distância linear pode ser mais importante, já que estes organismos não necessariamente migram percorrendo a distância pelo curso d'água. Há também casos em que os organismos são dispersos pela água (e.g. anfíbios, peixes, insetos) ou possuem dispersores associados à água (e.g. algumas plantas). Nestes casos, ambas as distâncias, linear e pela água, podem ser relacionadas com as distribuições destas espécies.

É importante ter em mente que nenhum ecólogo deixa de reconhecer o nicho como um fator importante na estruturação de comunidades (e.g. Rosindell *et al.*, 2011). Os defensores dos modelos espaciais e da teoria neutra apenas querem buscar uma forma de facilitar o entendimento de outros processos que controlam a distribuição de espécies, bem como geram modelos preditivos da distribuição de espécies. Em alguns casos, os modelos que contemplam a autocorrelação espacial podem possuir maior poder preditivo que os modelos não-espaciais (Currie, 2007). Os modelos não-espaciais da dinâmica de comunidades dão apenas uma visão simplificada do mundo real e podem ajudar a entender grandes problemas de interações entre espécies. Porém, para muitas espécies em muitas comunidades a localização dos indivíduos no espaço importa e, portanto, é desejável entender as consequências disso na dinâmica de comunidades (Law e Amarasekare, 2005).

Modelos espaciais partem de modelos simples, não espaciais. Uma linha de pensamento sobre a dinâmica de comunidades preconiza a existência de manchas com condições favoráveis a certas espécies inseridas em uma matriz de ambientes não adequados, onde a dispersão é frequente entre manchas. Os modelos de dinâmica de manchas são similares, mas a dispersão entre manchas é tida como sendo rara e a dinâmica dentro das manchas é mais importante. Outra linha preconiza que todos ambientes são adequados, contudo, algumas manchas são mais favoráveis a algumas espécies, que dominam essas manchas. Contrário a estes, a teoria neutra de Hubbell (2001) é baseada na equivalência ecológica entre todas as espécies, e a variação na abundância deve-se a fatores estocásticos como deriva genética e dispersão aleatória (Holyoak *et al.*, 2005). Teorias a parte, a ideia central é entender como os fatores que controlam a dinâmica de comunidades muda com a mudança de uma escala mais restrita (indivíduos e comunidades locais) para escalas mais amplas (metacomunidades) e aplicar este conhecimento em ações práticas como delimitar reservas e criar planos de manejo adequados a cada caso.

Atualmente existe uma grande quantidade de modelos e análises para lidar com o problema da autocorrelação espacial (Dormann *et al.*, 2007). Conforme discutido por alguns autores (Guisan e Thuiller, 2005; Dormann *et al.*, 2007), não existe um modelo exatamente certo para todos os casos. Com isso, é necessário avaliar qual modelo melhor satisfaz os objetivos propostos. Dormann *et al.* (2007) sugerem o uso de diferentes métodos, pois não existem informações mecanísticas suficientes que suportem a escolha *a priori* de algum método, embora a escolha sempre esteja ligada às questões e escalas de interesse (Diniz-Filho *et al.*, 2007).

Duas correntes principais surgiram na análise de dados de comunidades que tentam fazer inferências sobre a distribuição de espécies em relação aos fatores neutros e aos fatores relacionados ao nicho das espécies. Uma dessas correntes analisa os dados em forma de matrizes de distância (Tuomisto e Ruokolainen, 2006) que definem a dissimilaridade ou a distância entre pares de locais amostrados. As dissimilaridades podem ser calculadas em relação à composição de espécies (mede quão diferentes dois locais são em relação às espécies presentes), ou em relação aos fatores ambientais que caracterizam cada local amostrado (mede a diferença ambiental entre dois locais). Nestes casos a

distância ou dissimilaridade na composição de espécies é analisada em relação à distância ambiental (representando o nicho) e/ou em relação à matriz de distâncias geográficas (representando o espaço, ou a dispersão limitada). As análises mais comuns da abordagem utilizando matrizes de distância são o Mantel e o Mantel parcial (Mantel, 1967) e a regressão de matrizes (Tuomisto e Ruokolainen, 2006).

A outra abordagem visa a utilização dos dados brutos, ao invés de utilizar as matrizes de distância calculadas a partir dos dados brutos (Legendre *et al.*, 2005). Nessa abordagem, a tabela de dados das espécies é analisada em relação à tabela de dados ambientais e em relação à tabela de dados geográficos (espaciais). A forma de gerar os dados espaciais é bastante variável, mas em geral usa-se os dados de latitude, longitude e seus polinômios (Legendre e Fortin, 1989; Borcard *et al.*, 1992; Legendre e Legendre, 1998) ou autovetores que são gerados a partir da matriz de distâncias geográficas (Borcard e Legendre, 2002; Dray *et al.*, 2006; Griffith e Peres-Neto, 2006; Blanchet *et al.*, 2008b). Os autovetores são considerados melhores, pois, além de serem ortogonais, os autovetores podem representar uma gama maior de padrões espaciais que os padrões representados pelos polinômios.

Muita confusão existe entre essas duas abordagens, principalmente em relação à quais questões elas podem ser usadas para responder (Legendre *et al.*, 2005, 2008; Tuomisto e Ruokolainen, 2006, 2008; Laliberté, 2008; Péliissier *et al.*, 2008). De fato, o debate sobre qual dessas análises deve ser utilizada ainda não terminou. Muito debate também tem sido criado em torno da partição de variâncias em estudos de ecologia (Smith e Lundholm, 2010; Gilbert e Bennett, 2010; Landeiro e Magnusson, 2011). Embora não haja um consenso sobre quais técnicas utilizar, a partição de variâncias tanto para a abordagem de dados brutos quanto para matrizes de distâncias continua a ser bastante utilizada.

Em geral, discute-se cerca de três hipóteses gerais sobre as forças que controlam a distribuição de espécies em florestas tropicais. A primeira diz que a diversidade alfa é alta, mas a diversidade beta é baixa, o que faz com que a distribuição de espécies seja uniforme ao longo de grandes áreas. A segunda entra no escopo da teoria neutra de Hubbell (2001), na qual as espécies seriam distribuídas aleatoriamente, porém espacialmente autocorrelacionadas devido à dispersão limitada das espécies. A terceira e mais difundida é a que sugere o controle ambiental na distribuição de espécies, segundo a qual existiriam manchas com condições ambientais homogêneas e adequadas a certas espécies (Tuomisto *et al.*, 2000; Tuomisto *et al.*, 2003; Hopkins, 2007; Schulman *et al.*, 2007).

A hipótese de uniformidade é a que possui menos suporte empírico até o momento, enquanto as hipóteses de controle ambiental e de controle neutro são frequentemente apontadas como responsáveis por partes relativamente iguais de explicação, mas dependendo dos autores uma pode ser levemente maior que a outra (Condit *et al.*, 2002; Tuomisto *et al.*, 2003). Por exemplo, Tuomisto *et al.* (2003) observaram que em florestas de terra firme as diferenças florísticas são mais bem explicadas por fatores ambientais (diferenças de nicho), principalmente as características edáficas. No entanto, estas abordagens só perguntam o quanto das diferenças podem ser explicadas e ignoram o quanto das

distribuições originais não é relacionado com os fatores ambientais. Isto é, só compartilham a variância e não podem explicar a grande similaridade entre todas as áreas em vários parâmetros da comunidade. Apesar de ser óbvio que fatores ambientais afetam a distribuição de espécies, eles não são suficientes para explicar o grande número de espécies sintópicas na floresta tropical (Rosindell *et al.*, 2011).

Em geral, a estrutura uniforme das florestas tropicais e a grande diversidade dificultam a capacidade visual em distinguir "tipos de comunidades" (Vormisto *et al.*, 2000). A Amazônia é caracterizada por uma condição climática e topográfica que possui características relativamente distintas de outros locais onde se estudam os efeitos da autocorrelação espacial em modelos de distribuição de espécies. A Amazônia possui pouca variação topográfica e climática, mesmo em grandes escalas, o que talvez faça com que fatores em pequena escala sejam mais importantes (características do solo, substrato).

### *Conteúdo do Capítulo 1*

No primeiro capítulo fizemos uma revisão dos principais artigos científicos que tratam do assunto "autocorrelação espacial". Discutimos quais os principais problemas relacionados a dados autocorrelacionados e possíveis formas para resolver esses problemas e ainda utilizamos alguns dos métodos mais utilizados em ecologia espacial para exemplificar alguns conceitos. Para exemplificar os diversos casos possíveis nós usamos rotinas de simulação de dados para criar dados com distribuições e padrões conhecidos de antemão, que posteriormente foram analisados usando diferentes métodos de análise. Os dois tipos de problemas comumente associados à presença de autocorrelação espacial são relacionados à probabilidade de erro tipo 1 e às estimativas dos coeficientes em modelos de regressão. Os problemas relacionados às probabilidades e testes de hipóteses são mais antigos e mais reconhecidos pela comunidade científica (Legendre, 1993; Dormann *et al.*, 2007). Já os problemas relacionados às estimativas de coeficientes de regressão são mais recentes e tem gerado mais polemias (Lennon, 2000; Diniz-Filho *et al.*, 2003; Hawkins *et al.*, 2007; Beale *et al.*, 2007).

Em geral, observamos que existem métodos que possuem grande precisão, porém baixa acurácia, assim como métodos com grande acurácia e baixa precisão. Nenhum método sozinho foi considerado melhor que os outros, mas, dependendo dos objetivos, alguns desses métodos podem ser mais indicados (Landeiro e Magnusson, 2011). Embora ainda não seja possível tomar uma decisão fácil e objetiva, é importante saber que algo precisa ser feito em relação à autocorrelação espacial (Dormann *et al.*, 2007), principalmente em estudos que testam hipóteses e avaliam níveis de significância.



## *Conteúdo do Capítulo 2*

No segundo capítulo nós avaliamos duas questões relativamente recentes na ecologia. Uma mais metodológica e uma mais biológica. A questão metodológica consistiu em analisar uma característica comumente atribuída às análises baseadas em autovetores espaciais, sua grande flexibilidade em gerar padrões espaciais (Borcard e Legendre, 2002; Dray *et al.*, 2006; Griffith e Peres-Neto, 2006). Os autovetores espaciais são variáveis espaciais criadas a partir de uma matriz de distâncias geográficas que representam padrões espaciais em diversas escalas, desde as escalas locais até as escalas mais amplas, global/regional. A questão biológica constituiu na avaliação de rotas de dispersão de organismos aquáticos (seguindo o curso d'água, ou em linha reta por terra). Para isso utilizamos dados de peixes, que se dispersam principalmente pelo curso d'água, e dados de insetos aquáticos da ordem Trichoptera, que dispersam a longas distâncias principalmente através do voo dos adultos. Para avaliar o efeito das rotas de dispersão nós utilizamos duas matrizes de distância entre os pontos amostrados, uma quantificando a distância pelo curso d'água de um ponto ao outro e a outra quantificando a distância em linha reta (distância pela terra ou Euclideana).

O objetivo foi analisar qual dessas duas distâncias melhor descreve a variação na composição de espécies, esperando que os tricópteros fossem mais bem explicados pelas distâncias em linha reta enquanto os peixes pela distância pelo curso d'água. Em relação à questão metodológica, nós esperávamos que, devido à grande flexibilidade atribuída aos autovetores espaciais, a distância utilizada não faria diferença na hora de analisar os dados. Ou seja, os autovetores criados a partir da distância Euclideana gerariam padrões similares aos criados usando a distância pelo curso d'água, fornecendo resultados similares. Testamos isso usando os dados de peixes, de tricópteros e dados simulados (geramos dados de comunidades artificiais que se dispersam essencialmente pelo curso d'água).

Em geral, observamos que as variáveis espaciais criadas com cada tipo de distância representavam padrões espaciais diferentes. Desta forma, a distância pelo curso d'água é muito mais adequada para ser utilizada com grupos que dispersam principalmente pelo curso d'água, como observamos para os dados de peixes e para os dados simulados. Ao contrário, a distância Euclideana é mais adequada para os casos em que se espera que a principal rota de dispersão seja feita em todas as direções. Outras formas de gerar matrizes de distâncias representando rotas de dispersão também podem ser geradas (e.g. Blanchet *et al.*, 2008b), e provavelmente farão diferença ao serem utilizadas para gerar variáveis espaciais.

### *Conteúdo do Capítulo 3*

No terceiro capítulo nós usamos dados de uma ordem de insetos aquáticos bastante diversa na Amazônia central. A ordem Trichoptera está entre as mais bem conhecidas ordens de insetos aquáticos da Amazônia (Pes *et al.*, 2005; Pes, 2005) e suas espécies são bastante utilizadas como indicadoras da qualidade de água (Stuijzand *et al.*, 1999; Couceiro *et al.*, 2006; Couceiro *et al.*, 2007). Como visto no segundo capítulo, os tricópteros são capazes de migrar em todas as direções, portanto a distância Euclideana é um bom descritor espacial desse grupo. Nós avaliamos neste capítulo os fatores ambientais e espaciais que controlam a distribuição de tricópteros em 92 riachos distribuídos em três regiões da Amazônia central. Os dados utilizados foram retirados da tese de Doutorado de Ana Maria Oliveira Pes (Pes, 2005), que permitiu o uso destes dados para a produção do terceiro capítulo. A maioria dos riachos foi amostrada na reserva Ducke (39 riachos), em uma extensão espacial de aproximadamente 10 km. Nas áreas do PDBFF (Projeto Dinâmica Biológica de Fragmentos Florestais) foram amostrados 21 riachos em uma extensão de aproximadamente 60 km. A outra região amostrada foi a de Presidente Figueiredo, onde 32 riachos foram amostrados em uma extensão de aproximadamente 110 km.

Dada as diferentes extensões espaciais amostradas nós esperávamos que a área com maior extensão, Presidente Figueiredo, apresentasse a maior heterogeneidade ambiental, bem como a maior diversidade beta. Portanto, esperávamos que em Presidente Figueiredo as variáveis ambientais e a diferenciação ambiental explicassem bem as diferenças na composição de espécies e a diversidade beta na região, respectivamente. Além disso, esperávamos que, devido à maior extensão espacial, as variáveis espaciais, bem como a distância geográfica, fossem bons preditores da comunidade e da diversidade beta, respectivamente.

Neste capítulo nós também discutimos as diferenças no uso das análises com abordagem em dados brutos e as análises com abordagem em matrizes de distância (Legendre *et al.*, 2005; Tuomisto e Ruokolainen, 2006; Legendre *et al.*, 2008; Tuomisto e Ruokolainen, 2008). Em geral, observamos que o ambiente foi o melhor preditor da composição de espécies de tricópteros analisando os dados de cada região separadamente, bem como analisando os dados de todas as regiões em apenas uma análise. Não observamos nenhum padrão espacial ao analisarmos cada área separadamente, indicando que o ambiente é o mais importante nas três escalas espaciais analisadas, confirmando a qualidade do tricópteros como bons indicadores ambientais. Quando analisamos os dados de todas as regiões em conjunto nós observamos um forte efeito espacial, porém esse efeito praticamente desaparece ao removermos os efeitos ambientais, indicando a grande diferença ambiental e na composição de espécies entre as áreas. As análises feitas com as abordagens em dados brutos e em matrizes de distância forneceram respostas bastante similares, embora seja extremamente importante notar que elas avaliam e respondem questões diferentes (Legendre *et al.*, 2008; Tuomisto e Ruokolainen, 2008).

### *Conteúdo do Capítulo 4*

No quarto capítulo nós avaliamos o padrão de distribuição de espécies de anuros em 72 parcelas amostrais da Reserva Ducke. Neste estudo foram realizadas oito amostragens, cinco no período noturno e três no período diurno. Foram encontradas 29 espécies, das quais 20 possuem reprodução aquática e 9 possuem reprodução terrestre. Sete espécies com reprodução aquática foram encontradas apenas esporadicamente e por isso foram retiradas das análises. Mais detalhes sobre a coleta podem ser encontrados em Menin *et al.*, (2007). Nós avaliamos o padrão de distribuição das espécies em relação aos principais fatores ambientais conhecidos por afetar a distribuição de anuros e em relação às variáveis espaciais que descrevem padrões espaciais em diferentes escalas. Os dados das assembleias de anuros foram divididos em três, um contendo todas as espécies, um contendo apenas as espécies com reprodução aquática e um contendo apenas as espécies com reprodução terrestre.

Devido ao fato de que os anuros são compostos por espécies muito sensíveis ao ambiente, nossa hipótese foi de que o controle ambiental é mais forte do que o controle espacial. Em relação ao tipo de reprodução, nossa hipótese foi de que os dois grupos diferem quanto às principais forças ambientais e espaciais que controlam a distribuição de suas espécies. Nossa previsão foi de que as espécies com reprodução terrestre são mais afetadas por fatores espaciais, pois sua distribuição é mais restrita por limitações de dispersão do que por dependência em disponibilidade de água. Por outro lado, nossa previsão foi que os anuros com reprodução aquática são mais controladas por fatores relacionados ao nicho das espécies, principalmente àqueles relacionados com a disponibilidade de água. Caso estas previsões estejam corretas, as espécies com reprodução aquática podem ser mais adequadas para usos em estudos de monitoramento biológico e avaliação dos efeitos de alterações ambientais do que as espécies com reprodução terrestre, ou do que o uso dos dois tipos em conjunto.

Observamos que nossos modelos explicaram cerca de 35% da variação na distribuição das assembleias de anuros. Quando analisamos todas as espécies, independente do tipo de reprodução, o padrão espacial foi mais representativo do que o padrão ambiental. Contudo, observamos que o tipo de padrão observado depende do tipo de reprodução das espécies. As espécies com reprodução aquática possuem um padrão ambiental forte (i.e. controladas por fatores relacionados ao nicho das espécies). Por outro lado, as espécies com reprodução terrestre possuem um padrão espacial ainda mais forte, indicando que a distribuição dessas espécies é controlada por fatores relacionados à dispersão limitada ou que os fatores ambientais que realmente são importantes para as espécies com reprodução terrestre não foram medidos neste estudo. Estes resultados podem ser bastante úteis durante o planejamento de estratégias de conservação e de estudos de monitoramento biológico e avaliação dos efeitos causados por alterações ambientais, pois as espécies com reprodução aquática podem responder muito mais às alterações ambientais do que as espécies com reprodução terrestre.

## Conteúdo do Capítulo 5

Nesse capítulo nós analisamos dados de 22 grupos biológicos amostrados na reserva Ducke. Destes 22 grupos, 15 são de plantas e 7 de animais. A ideia geral do capítulo foi de medir a congruência no padrão de distribuição dos diversos grupos, avaliando se é possível usar apenas um grupo, ou apenas alguns grupos, em estudos de biomonitoramento (uso de grupos substitutos). Nós também avaliamos se resoluções numéricas (abundância ou presença e ausência) e taxonômicas (nível de identificação) mais finas são necessárias. Ou seja, avaliamos se é necessário coletar dados de abundância ou se dados de presença e ausência, e se é necessário identificar em nível de espécie ou se a identificação em nível de gênero é suficiente para encontrar o mesmo padrão de distribuição ao analisar os dados. Os dados utilizados são de amostragens realizadas em um máximo de 72 parcelas e um mínimo de 30, onde as parcelas amostradas são sempre as mesmas.

Nós também utilizamos dados ambientais e espaciais para avaliar se a congruência observada entre os diversos grupos é mais bem explicada pelo ambiente ou por variáveis espaciais. Os dados biológicos são referentes à abundância relativa dos organismos em cada parcela. Os detalhes amostrais e os conjuntos de dados (biológicos, ambientais e geográficos) estão disponíveis na página de dados e metadados do PPBio (<http://ppbio.inpa.gov.br>).

Em geral, as variáveis ambientais foram bons preditores das comunidades de plantas analisadas, explicando em torno de 20 a 30 %. Em alguns casos, o padrão espacial foi mais forte que o ambiental, como para os sapos noturnos, ervas e para os arbustos do gênero *Psychotria* (Rubiaceae). As comunidades de animais, exceto sapos, não foram bem explicadas nem pelo ambiente nem pelas variáveis espaciais. As comunidades de sapos diurnos foram bem explicadas pelas variáveis ambientais, enquanto os sapos noturnos foram mais bem explicados pelas variáveis espaciais.

Nós observamos que os grupos de plantas são os grupos onde existe maior concordância no padrão de distribuição. Em geral, os grupos mais concordantes foram aqueles que apresentaram padrões espaciais e/ou ambientais fortes, indicando que a distribuição desses grupos está associada aos mesmos fatores ambientais e/ou espaciais. A congruência entre os grupos de animais foi sempre baixa, exceto para sapos, indicando que estes grupos possuem uma distribuição similar a uma distribuição aleatória na escala espacial da reserva Ducke. Observamos também que a resolução numérica e a resolução taxonômica podem ser reduzidas sem grandes problemas para dados de presença e ausência e identificações em nível de gênero. Em especial, as lianas (da família Bignoniaceae), palmeiras, árvores da família Lecythidaceae e Fabaceae e as samambaias e ervas foram os grupos mais congruentes. Lianas foi o grupo com maior concordância, sendo um ótimo candidato a grupo substituto. Embora as lianas sejam difíceis de identificar e de contar no campo, a possibilidade de trabalhar com dados de presença e ausência e identificações em nível de gênero diminui a dificuldade de se trabalhar com lianas. Entretanto, palmeiras, ervas e samambaias são grupos relativamente mais fáceis de se trabalhar e que também possuem um alto nível de congruência com os outros grupos.

## Objetivos

Os principais objetivos deste trabalho foram os seguintes:

- i) Criar um texto de revisão sobre autocorrelação espacial com diversos exemplos ilustrando os principais conceitos relacionados e as principais formas de análise disponíveis (Capítulo 1);
- ii) Discutir o uso de análises espaciais e a definição correta da matriz de distâncias que irá compor a análise, usando exemplos de organismos aquáticos onde a matriz de distâncias pode ser definida através do curso d'água ou através da distância em linha reta, pela terra (Capítulo 2);
- iii) Discutir as possíveis diferenças entre análises baseadas em dados brutos e em matrizes de distância bem como o efeito da escala espacial e a heterogeneidade ambiental das áreas amostradas (Capítulo 3);
- iv) Avaliar o padrão de distribuição de espécies de anuros em relação a fatores ambientais e a fatores espaciais. Avaliar se os padrões ambientais e espaciais observados nas assembleias de anuros dependem do tipo de reprodução das espécies (Capítulo 4).
- v) Avaliar se existe concordância no padrão de distribuição de espécies de diversos grupos taxonômicos indicando um possível grupo substituto para ser utilizado em estudos de monitoramento biológico. Avaliar se a concordância observada é causada por fatores ambientais (nichos) ou fatores não definidos (espaciais), que podem ser neutros ou de nicho. Avaliar se é possível reduzir a resolução taxonômica (de espécie para gênero) e resolução numérica (de abundância para presença e ausência) sem perder informações importantes sobre o padrão de distribuição das espécies (Capítulo 5).

Landeiro, V. L. & W. E. Magnusson, 2011. The geometry of spatial analyses: implications for conservation biologists, *Natureza & Conservação* 9: 7-20.

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## The geometry of spatial analyses: implications for conservation biologists

*Essays & Perspectives*

Title: The geometry of spatial analyses: implications for conservation biologists

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21 **ABSTRACT**

22

23           Most conservation biology is about the management of space and therefore requires spatial  
24 analyses. However, recent debates in the literature have focused on a limited range of issues related to  
25 spatial analyses that are not always of primary interest to conservation biologists, especially  
26 autocorrelation and spatial confounding. Explanations of how these analyses work, and what they do,  
27 are permeated with mathematical formulas and statistical concepts that are outside the experience of  
28 most working conservationists. Here, we describe the concepts behind these analyses using simple  
29 simulations to exemplify their main goals, functions and assumptions, and graphically illustrate how  
30 processes combine to generate common spatial patterns. Understanding these concepts will allow  
31 conservation biologists to make better decisions about the analyses most appropriate for their  
32 problems.

33



## 34 INTRODUCTION

35

36 Spatial ecology has increasingly attracted the attention of ecologists and conservationists, and  
37 spatial analyses are frequently used in biodiversity conservation planning (Diniz-Filho and Telles  
38 2002; Nams et al. 2006; Moilanen et al. 2008). For example, approximately 25% of the articles citing  
39 SAM software, a specialized spatial analysis software (Rangel et al. 2006), were concerned with  
40 biodiversity conservation (Rangel et al. 2010). Beale et al. (2010) listed 4 questions of interest to  
41 conservation biologists that potentially involve spatial analyses: (1) How does the spatial scale of  
42 human activity impact biodiversity or biological interactions? (2) How does the spatial structure of  
43 species' distribution patterns affect ecosystem services? (3) Can spatially explicit conservation plans  
44 be developed? (4) Are biodiversity patterns driven by climate? The third question is probably of most  
45 immediate concern to conservation biologists, and has spurred the development of complex algorithms  
46 to help land-use decision-making processes, such as Marxan with Zones (Watts et al. 2009). The  
47 mathematics associated with this type of question are usually normative (Colyvan et al. 2009), and  
48 designed to optimize the chances of obtaining a consensus decision.

49 Spatial ecology has opened many promising avenues of research for conservation. It has been  
50 used to extrapolate and predict species occurrence (Austin 2002; Betts et al. 2006; De Marco et al.  
51 2008), and may be used to predict the effects of global warming on biodiversity. However, one of the  
52 main strengths of spatial analysis in conservation is its capacity to describe the patterns of diversity at  
53 different spatial scales. Knowing what factors generate beta diversity, and at what spatial scales they  
54 act, can be of great importance to conservation planning (Legendre et al. 2005; Tuomisto and  
55 Ruokolainen 2006). Spatial analysis can be also used to identify patterns of genetic variability at  
56 different spatial scales and define operational units for conservation planning (Diniz-Filho and Telles  
57 2002).

58 The rapid development and sophistication of spatial methods and their applications have  
59 enabled researchers to make predictions of species distributions and plan conservation efforts. For  
60 example, Bini et al., (2006) used simulation procedures to predict anuran species that could be  
61 discovered in the Cerrado biome by 2050, and showed that the predicted distributions lead to different  
62 priorities for placement of reserves than those based on currently known distributions of species. Some  
63 researchers have suggested that spatial interpolation to predict species distributions may be more  
64 effective than models based on environmental variables (Bahn and McGill 2007).

65 Arguably, all conservation related questions should be embedded in a landscape context  
66 (Metzger 2006). Chesson (2003) commented "Would it not be more useful to focus on how physical  
67 environmental variation is translated into patterns exhibited by organisms?" However, recent  
68 discussion of spatial analyses in the scientific literature has focused on descriptive models that produce  
69 the parameters that can be used as inputs to more applied models. Beale et al. (2010) asserted that  
70 "many ecologists ... often believe that spatial analysis is best left to specialists. This is not necessarily

71 true and may reflect a lack of baseline knowledge about the relative performance of the methods  
72 available.” We suggest that, rather than being a problem of not understanding the relative performance  
73 of the methods, most conservationists focus on particular problems that can be approached with  
74 normative mathematics, and not on the problems in obtaining generally robust descriptive statistics  
75 that were derived from simulations using unrealistic ecological assumptions.

76 Most recent comparative evaluations of spatial methods used computer simulations to evaluate  
77 the relative utility of different methods (Dormann et al. 2007; Beale et al. 2010). These simulations are  
78 often difficult for biologists to appreciate because they are couched in terms of distance space and  
79 matrix algebra. In this paper, we use simple geometric models to illustrate the concepts behind  
80 regression analysis of distance data, and discuss what the results imply in terms of ecological  
81 processes that may be of interest to conservationists.

82 The leaders in spatial ecology usually explain ecology with the associated mathematics and  
83 statistics. However, ecologists and conservationists often find the explanations complex, due to the  
84 difference between space and most ecological variables. Ecological variables are generally treated as  
85 linearly additive by appropriate transformations or sampling procedures. That is, each variable  
86 represents a single dimension. However, space is usually measured in two or more dimensions in a  
87 coordinate system. The coordinates themselves do not necessarily represent the conceptual distance  
88 between two objects, which is usually the Euclidean distance. Some believe that space cannot be  
89 represented by linear additive combinations, and that joint analysis of spatial and ecological variables  
90 can only be undertaken by transforming the ecological variables to distances (Tuomisto and  
91 Ruokolainen 2006). Others claim that this procedure produces statistics that are difficult to interpret,  
92 and that space should be converted to linear additive components for inclusion in analyses (Legendre  
93 et al. 2005; Legendre et al. 2008). Although we are inclined towards the latter, we wish to avoid these  
94 difficult conceptual problems because most of the concepts in spatial analysis can be understood in  
95 terms of simple one-dimensional spatial models (e.g. distances along a transect), and it is easier for an  
96 ecologist to appreciate the conceptual problems if they are first presented in models in which space is  
97 described in only one dimension.

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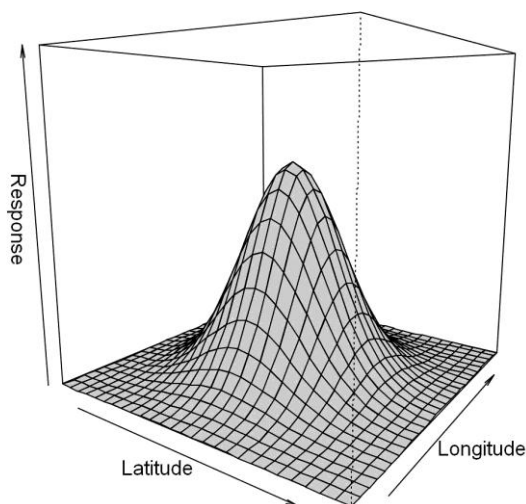
### 99 *Autocorrelation*

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101 Autocorrelation, as the name implies, is the correlation of a variable with itself. This  
102 correlation could be in time or space. For example, values of a variable are temporally autocorrelated  
103 if the values of that variable at short time intervals are more or are less similar than expected for  
104 randomly associated pairs (Legendre and Legendre 1998). The same is true for spatial autocorrelation,  
105 in which values nearby are more similar than values from points separated by greater distances. There  
106 are several causes of spatial autocorrelation and this is the greatest source of confusion, because  
107 different definitions for spatial autocorrelation are used in relation to the process that generates it. For

108 example, according to Peres-Neto & Legendre (2010), autocorrelation results from “spatial structure  
 109 due to the dynamics of the species (or their communities) themselves (e.g., via dispersal)”. Under this  
 110 definition, spatial autocorrelation is not used for predictor variables but rather is used only for  
 111 response variables that are autocorrelated by endogenous causes. The many definitions used in spatial  
 112 ecology generate confusion, such that some authors have published their own glossary (Peres-Neto  
 113 and Legendre 2010). The difference between the definition of Legendre & Legendre (1998), who  
 114 defined autocorrelation in relation to pattern, and that of Peres Neto & Legendre (2010), who defined  
 115 autocorrelation in terms of process, is important, and reflects on another important concept,  
 116 “stationarity.”

117 Stationarity is a requirement of many methods of analysis that specify that the mean, variance,  
 118 and other statistical properties of the distribution be constant over the space or time. Fortin & Dale  
 119 (2005) defined stationarity as “a process, or the model of a process, is stationary (or homogeneous) if  
 120 its properties are independent of the absolute location and direction in space... the parameters of the  
 121 process, such as the mean and variance, should be the same in all parts of the study area and in all  
 122 directions ”. However, whether this refers to the underlying process or the resulting pattern is unclear.  
 123 Consider an organism that colonizes a point in a previously empty space, and then reproduces.  
 124 Assuming that the organism and its descendants have limited dispersal, after a few generations the  
 125 density of the species can be represented by a single peak in the previously empty space (Fig. 1). The  
 126 process that generated that peak was endogenous autocorrelation (we did not need information on  
 127 anything but the density in neighboring sites in the previous generation to produce the peak), and the  
 128 process was stationary (i.e. knowing the process, we only needed information on the densities in  
 129 neighboring sites, independent on where we were in space).



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131 **Figure 1.** A peak of abundance representing the distribution of a species. Some factor  
 132 associated with intrinsic biology of the species, such as reproduction or limited dispersion could create  
 133 such pattern.

134           A problem arises when we only have the pattern and are unsure of the process. Imagine no  
135 endogenous autocorrelation, but that the peak in population density corresponds to a physical peak in  
136 the landscape, which might happen if the density of the organism were related to temperature or some  
137 other correlate of altitude. The pattern is identical, but the density of the organism is a function of  
138 temperature and not a function of the density in neighboring sites. In this case, a combination of  
139 endogenous autocorrelation and an external driving variable can generate exactly the same pattern.  
140 The literature can be confusing because the interpretation of autocorrelation and stationarity depends  
141 on the researcher's assumptions about the underlying processes, and we generally only have  
142 information on the pattern.

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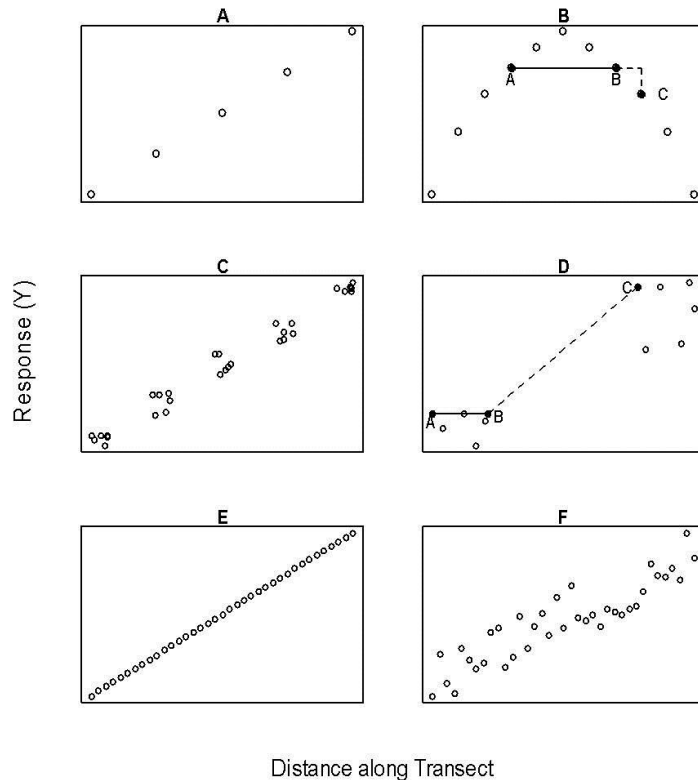
#### 144 *Stationarity in one or two dimensions*

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146           Consider a response variable (Y) that varies with distance along a transect (T), as shown in  
147 Fig. 2A. An assumption of most spatial analyses is that the relationship between Y and space is  
148 stationary. That is, the variation of Y across T is the same independent of the observer's position along  
149 the transect, and in any direction (i.e the relationship is independent of the position in T). That  
150 condition can be seen to hold for the data in Fig. 2A. Starting from any point, an increase in the  
151 distance along T of one unit, will increase the value of Y by a constant amount. This relationship  
152 applies independently of direction. Conversely, if we decrease T by one unit, we decrease the value of  
153 Y by the same constant amount.

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155           It is important to note that the only way for the observed relationship between Y and distance  
156 to be stationary is for the relationship between Y and T to be linear. Any nonlinear relationship will  
157 result in the effect of distance being dependent on spatial location (i.e. the value of T at which we start  
158 to measure the distance). This is illustrated in Fig. 2B, where the relationship between Y and T is  
159 nonlinear. If we start at point B and move 1 unit forward along the T axis to C, Y is reduced by  
160 ~0.287. If we start at A and move four units forward along T, Y remains constant. In one dimension,  
161 the only way that the relationship between Y and distance can be stationary is for Y to have a linear  
162 relationship with distance. In two dimensions, the only way that the relationship between Y and  
163 distance can be stationary is if the value of Y can be represented in space by a flat plane with no  
164 curvature. Note that a small-scale stationary process, such as that described in Figure 1 can generate an  
apparently nonstationary pattern at a larger scale.



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Distance along Transect

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**Figure 2.** The difference between a stationary process and a stationary pattern. A) a stationary pattern, where the effect of distance along a transect is independent of location or direction. B) a non-stationary pattern that could result from a stationary process acting over a limited time period. C) a pattern that could arise from a small-scale stationary process acting over a stationary pattern, such as reproduction with limited dispersal of the organisms illustrated in part A. D) magnification of A), a stationary process may create a non-stationary pattern. E) a stationary pattern similar to that in A), but the organisms are closer together. A small-scale stationary process, such as that illustrated in part C, does not produce a recognizably non-stationary pattern in this case, as seen in part F.

If the relationship between the value of a variable and space is linear in one dimension (i.e. the pattern is unambiguously stationary), it does not matter whether we use a conventional analysis or an analysis based on distances. For instance, we could calculate the differences between the values of  $Y$  ( $\delta Y$ ) for each pair of points and regress this against the distances between the points. A Mantel test uses the absolute value of the distance, but as we are only considering one dimension, we could use a positive or negative sign to indicate direction. The value of the slope of the regression (the amount that the dependent variable increases for a 1 unit increase in the independent variable) is logically the same whether the dependent variable is  $Y$  and the independent variable  $T$ , or whether the dependent variable is  $\delta Y$  and the independent variable  $\delta T$ . However, the values may only be the same if we use geometric mean regression for the second analysis, because we have artificially inflated the variance in  $T$  by using  $\delta T$ , and this biases the estimate of the slope downwards for least-squares regression (Zar 1996). The slope of the relationship is only representative of the “effect of distance” if the relationship with

187 the resultant variable is stationary. As with any simple regression, if the underlying relationship is not  
188 linear (i.e. the effect of space is a variable and not a constant), estimating a single slope parameter is  
189 meaningless.

190 What this means for the construction of most conservation-related models is that useful  
191 parameters are only obtained if that parameter is a constant, unless we are willing to move to  
192 likelihood methods or Bayesian statistics and try to generate a probability distribution for the values of  
193 the parameter. We will use simple one-dimensional models to illustrate the recent discussion in the  
194 literature, and evaluate the relevance of those discussions to ecologists undertaking conservation  
195 research.

196

### 197 *Stationarity of pattern and stationarity of process*

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199 Note that a stationary process does not necessarily generate a stationary pattern (Fortin and  
200 Dale 2005). Let us imagine a secondary process that has a nonlinear relationship with space. For  
201 instance, each point on Fig. 2A could represent a value for a single individual. If that individual  
202 reproduces, and dispersal is limited, we may see a pattern like that on Fig. 2C, with similar values of Y  
203 (similar because of genetic similarity or maternal provisioning) at close by points in space. Although  
204 the process (reproduction with limited dispersal) is the same at each point (i.e. stationary), the  
205 resulting pattern is not stationary. This can be seen by amplifying the area around what were originally  
206 two individuals (Fig. 2D). Although individuals vary in Y, the mean value of Y does not increase  
207 between points A and B. However, the effect of the same difference in Y between B and C is much  
208 greater. This point is important. A stationary process at one scale does not necessarily generate a  
209 stationary pattern at larger scales, and many analyses assume a stationary pattern.

210 We gave an example of a stationary process generating a nonstationary pattern in Fig 2A.  
211 Interpretation of a pattern generated by a nonlinear stationary process can be difficult, as can be seen  
212 from Hubbell's (2005) neutral theory of biogeography. By using simulations analogous to those we  
213 used to generate Fig. 2C, but with many more potential species, Hubbell (2005) generated local  
214 communities that varied over a much larger metacommunity landscape. The overall analysis is very  
215 complicated, but the result of most relevance to spatial patterns is that this process led to similarity  
216 among local communities that decreased linearly with the log of distance. That is, the relationship of  
217 similarity (the complement of ecological distance) was nonlinear with distance, even though the  
218 process that generated that similarity was the same at each point.

219 It would appear easy to deal with this situation. We could carry out a Mantel test of the  
220 relationship between similarity and log distance, but transforming a distance matrix has complex  
221 implications for interpretation. The rules we use in mathematics generally conform to Euclidean  
222 geometry, but the geometry of curved surfaces is much more complex, and manipulation of such

223 geometry is not a trivial task, even for geniuses, such as Einstein (Mlodinow 2001). If the “effect of  
 224 distance” is not linear, the effect of a particular unit of distance (say the distance you walk from point  
 225 1 to point 2) depends on the position of the observer relative to those two points. This is the theory of  
 226 relativity, and not the sort of problem that most ecologists are thinking of when they ask “How much  
 227 does distance matter?”

228         The apparent effect of a secondary nonlinear process depends on the dispersal of the primary  
 229 units (those generating the secondary response). The points in Fig. 2A were widely scattered, and we  
 230 assumed that these were the only individuals in the population (i.e. not the only ones sampled).  
 231 Therefore, the secondary process of reproduction produced clumps of points that reflected the  
 232 autocorrelation. If the initial individuals were close together in relation to the extent of influence of the  
 233 secondary process (Fig. 2E), there may be no obvious clumping (i.e. the pattern is stationary) after the  
 234 action of the secondary process (Fig. 2F), even though the same mechanistic process generated the  
 235 data. Pattern may be useful to indicate the probable action of a secondary process, but the absence of  
 236 pattern is not necessarily evidence of the absence of that process. This is important because all spatial  
 237 analyses are about detecting clumping and trying to determine what caused that clumping so that  
 238 nuisance variables can be discounted (controlled) and interesting variables can be analyzed.

239         If clumps can be identified a priori, it may be possible to select the most probable hypotheses  
 240 and discard the most unlikely (Barnett et al. 2010). However, most stationary positive autocorrelation  
 241 processes will lead to an essentially uniform distribution of the dependent variable if left to act long  
 242 enough in a homogeneous landscape. Strong clumping is usually strong evidence that a stationary  
 243 positive autocorrelation process is not acting alone. Assumption of an autocorrelation process may  
 244 lead to erroneous biological conclusions when some other process causes clumping (Barnett et al.  
 245 2010).

246

## 247 **SPATIAL ANALYSIS**

248

### 249 *Clumping as an indication of the effect of space*

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251         Most hypotheses about ecological communities attempt to explain spatial patterns (clumping).  
 252 However, researchers seek independent evidence, and spatial proximity may cause pseudo-replication  
 253 (Hurlbert 1984). Therefore, researchers face the quandary of forming hypotheses due to spatial  
 254 clumping while attempting to avoid clumping to test those hypotheses. Space is not an ecological  
 255 variable, but rather reflects some process that varies spatially (Diniz-Filho et al. 2003). Clumping may  
 256 occur at any of a variety of scales, from large (Fig. 2A) to small (Fig. 2D) with many intermediate  
 257 possibilities (Legendre and Legendre 1998; Legendre et al. 2002). It may be illogical to try to study  
 258 many phenomena occurring at different scales in the same analysis (Fortin and Dale 2009), and all

259 spatial analyses can be considered attempts to isolate the effects of particular independent variables  
 260 from other processes that cause clumping.

261         General trends (which may be the only stationary patterns) might be excluded before  
 262 undertaking spatial analyses, or removing effects of local patterns might be necessary. Regardless, the  
 263 choice of which scales to study should be determined by the questions, not the analysis (Diniz-Filho et  
 264 al. 2007; Fortin and Dale 2009). There is no scale at which only endogenous autocorrelation can be  
 265 assumed, and endogenous autocorrelation does not necessarily occur only at one scale. Consider the  
 266 distribution of individuals of a species of plant that is dispersed passively by gravity and also by birds.  
 267 This will result in two scales of clumping, both of which are endogenous. If the extent of the study is  
 268 small in relation to the extent of endogenous autocorrelation, the autocorrelation may be manifest as a  
 269 broad-scale trend across the study area (Beale et al. 2010). Removal of such a trend to obtain  
 270 “stationarity”, as is frequently recommended in time-series analyses, may be totally inappropriate.

271         The first step in an investigation of the role of space in ecology is exploratory data analysis  
 272 (EDA). In this step we do not invoke process and must only investigate pattern. Therefore, we use the  
 273 definition of Legendre & Legendre (1998), which defines autocorrelation in terms of pattern, rather  
 274 than that of Peres Neto & Legendre (2010), which defines autocorrelation in terms of process, because  
 275 distinguishing endogenous from exogenous autocorrelation requires knowledge of the process. In this  
 276 step, we are asking questions, such as “Are my data spatially autocorrelated?” “Is the response  
 277 variable, the predictor variable, or both autocorrelated?” “If yes, what is the extent of autocorrelation?”  
 278 “Are model residuals autocorrelated?” “Should I use a spatial analysis to take autocorrelation into  
 279 account (see below)?” Measures of autocorrelation, such as Moran’s  $I$  and Geary’s  $c$  and their  
 280 correlograms are used to explore these questions. Correlograms are used to detect statistically  
 281 significant spatial structure (i.e, the pattern, not the process) and to describe its general features.  
 282 Combined with maps, they are used to assess the magnitude and the pattern of autocorrelation in data  
 283 sets (Legendre and Legendre 1998). However, it is not obvious what criteria should be used to indicate  
 284 when space needs to be taken into account, and several authors recommend the use of spatial analyses  
 285 on the basis that they will always improve interpretation (Dormann et al. 2007; Beale et al. 2007;  
 286 Beale et al. 2010).

287

288 *Why undertake spatial analyses?*

289

290         When nearby values of variables are more similar than expected at random, a pattern of  
 291 positive autocorrelation is assumed, and produces two major classes of problems in spatial analyses.  
 292 The first is conceptual and related to the structure of the causal interpretation of the model being  
 293 investigated. When we introduce "space" into the model, we are including it as surrogate for some  
 294 biological or physical process, which induces spatial autocorrelation. If it is only a surrogate for a  
 295 nuisance variable, then eliminating the effect of space will not affect our interpretation. However, if it



296 is also a surrogate for a variable we wish to investigate, removing the "problem" of space may  
 297 eliminate an effect that we wanted to study. Therefore, before analysis, it is necessary to decide which  
 298 aspects of space we want to include in the analysis, and which aspects we want to discard. This  
 299 decision is biological/conceptual and often very difficult when we know little about the functioning of  
 300 the biological systems. However, it is also the most important decision, because it will affect all of our  
 301 interpretations (Legendre 1993; Legendre et al. 2002).

302 The second class of problems is statistical/computational. Autocorrelated data can give the  
 303 wrong estimates of degrees of freedom for conventional statistical tests and consequently gives  
 304 inflated type I error rates (Legendre 1993). This effect is often called pseudoreplication, but it is very  
 305 different from the pseudoreplication caused by confounding variables described in the previous  
 306 paragraph. Spatial autocorrelation may also affect estimates of regression coefficients due to red shifts  
 307 caused by spatial autocorrelation (Lennon 2000).

308 Discussion of the points alluded to in the preceding paragraphs (mainly the one related to  
 309 coefficient shifts) is recent, and filled with controversies (Lennon 2000; Diniz-Filho et al. 2003;  
 310 Hawkins et al. 2007; Bini et al. 2009). The second class of problems has been the focus of most of the  
 311 recent discussions in the literature (Diniz-Filho et al. 2003; Dormann et al. 2007; Beguería and Pueyo  
 312 2009; Bini et al. 2009), but these aspects are also related to the practice of partitioning variance  
 313 between interesting predictor variables and the possibly confounding factor "space" (Borcard et al.  
 314 1992; Legendre 1993; Legendre and Legendre 1998). Partitioning variance between "space" and  
 315 ecological predictor variables is the focus of research on niche versus neutral models of community  
 316 dynamics (Peres-Neto et al. 2006; Legendre et al. 2009a; Legendre et al. 2009b; Peres-Neto and  
 317 Legendre 2010), and the question of whether area or habitat is more important for reserve design.

318 Before deciding which spatial analysis to use, one must answer the following conceptual  
 319 questions:

320 1) Do we only want to remove the possible effects of other variables that are spatially  
 321 confounded with the predictor variable?

322 2) Do we want to partition the variance in the response variable into that which appears to be  
 323 associated only with the predictor variable(s) and that which may be associated with the predictor  
 324 variable and/or other variable(s) that are confounded with spatially-structured environmental  
 325 variation?

326 3) Do we only want to use a spatial analysis to remove spatial autocorrelation in order to be  
 327 able to use standard statistical tests?

328 4) Do we want to describe spatial patterns in response and predictor variables, relating them to  
 329 a specific spatial scale where they are most affected by autocorrelation?

330 Some analyses do more than one of these simultaneously, but it is important that we recognize  
 331 which problems are being resolved, because there is no general method that can solve all the  
 332 conceptual and statistical problems simultaneously.

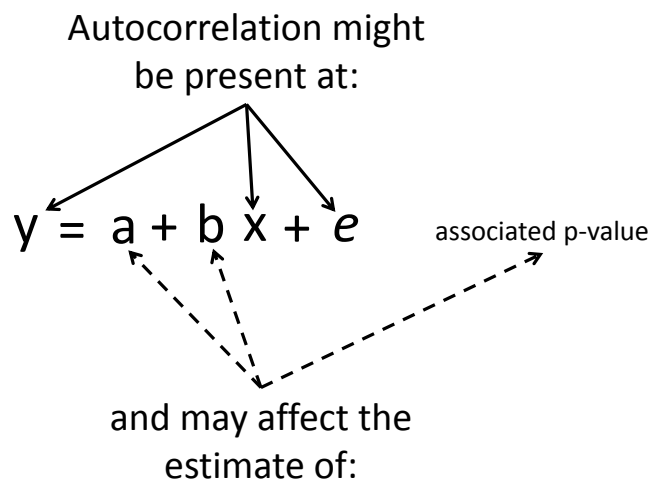
333 *Where is space in my model?*

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335 In general, the construction of an ecological model is a trade-off between complexity and  
 336 utility (Levins 1966). In the best-case scenario, the predictor variables should be orthogonal to space  
 337 and therefore not autocorrelated; however this rarely occurs in observational studies. In the simplest  
 338 form of statistical tests, inclusion of spatial variables decreases spatial autocorrelation in the residuals,  
 339 but reduces degrees of freedom. When modeling, our data might have autocorrelation patterns in the  
 340 response variable, in the predictor variables, and/or in the errors (residual) of the model (Fig. 3).

341 An assumption of most statistical tests is that the errors are independent and identically  
 342 distributed (the so called I.I.D. of errors), and it is common practice to say that residuals results from  
 343 all factors not included in model; e.g. soil pH, land use history (Diniz-Filho et al. 2003). The  
 344 assumption of I.I.D. of residuals (errors) is necessary to generate the distributions of statistics under  
 345 null hypotheses for most tests. In the "error model," residuals may be independent (first i in I.I.D.). In  
 346 "residual" (ecological) models, residuals are known not to be independent because they have causal  
 347 relationships with variables not included in model. At most, we can hope that they are independent of  
 348 the variables included in the model. One of the external variables traditionally relegated to the residual  
 349 variation is "space."

350



351

352 **Figure 3.** The basic structure of a linear-regression equation. Autocorrelation might be present  
 353 in the response ( $y$ ) and/or in the predictor ( $x$ ) variables, as well as in the errors ( $e$ ). When present,  
 354 autocorrelation might affect the estimate of p-values, though the existence of shifts in the estimates of  
 355 the intercept ( $a$ ) and the slope ( $b$ ) is debatable (Lennon 2000; Diniz-Filho et al. 2003; Hawkins et al.  
 356 2007).

357

358 When "space" affects variables in the analysis, the residuals may have a spatial pattern.  
 359 Consequently, the decision to use spatial methods may come as a result of an evaluation of residuals.  
 360 If residuals are autocorrelated then spatial analysis is used. However, statistical tests are compromised

361 only when both the predictor and response variables are autocorrelated (Legendre et al. 2002).  
362 Therefore, residuals can be spatially structured without inducing statistical bias (P.R. Peres-Neto  
363 *Personal Communication*). In fact, the residuals may remain autocorrelated even after the use of the  
364 appropriate spatial analysis (Beale et al. 2010). Therefore, the choice of the appropriate test should not  
365 be based only on analyses of residuals, but by assessing whether both response and predictor variables  
366 are spatially structured.

367         Several solutions have been proposed to manage the spatial autocorrelation in ecological data.  
368 We distinguish among two groups of solutions: i) removers - autocorrelation is a problem that should  
369 be removed from data; and ii) includers - autocorrelation is a natural process that should be understood  
370 and studied as an ecological phenomenon, not as a statistical problem. Generally, "the removers" tend  
371 to delete sampling sites until the data are no longer autocorrelated (Legendre and Legendre 1998,  
372 describe this process, but do not recommend it, pp 14), or to apply some type of correction to obtain  
373 the geographically effective degrees of freedom (Dutilleul 1993; Dutilleul et al. 2008). "Removers" do  
374 not necessarily try to take out all of the autocorrelation, but may restrict analyses to data grouped in  
375 scales relevant to the question, and in which it is unnecessary to account for autocorrelation at other  
376 scales. The "inclusive methods" are based on statistical procedures that take spatial autocorrelation  
377 into account (Dormann et al. 2007), changing the way that the data are analyzed and interpreted  
378 (Legendre 1993).

379

## 380 **SIMULATIONS**

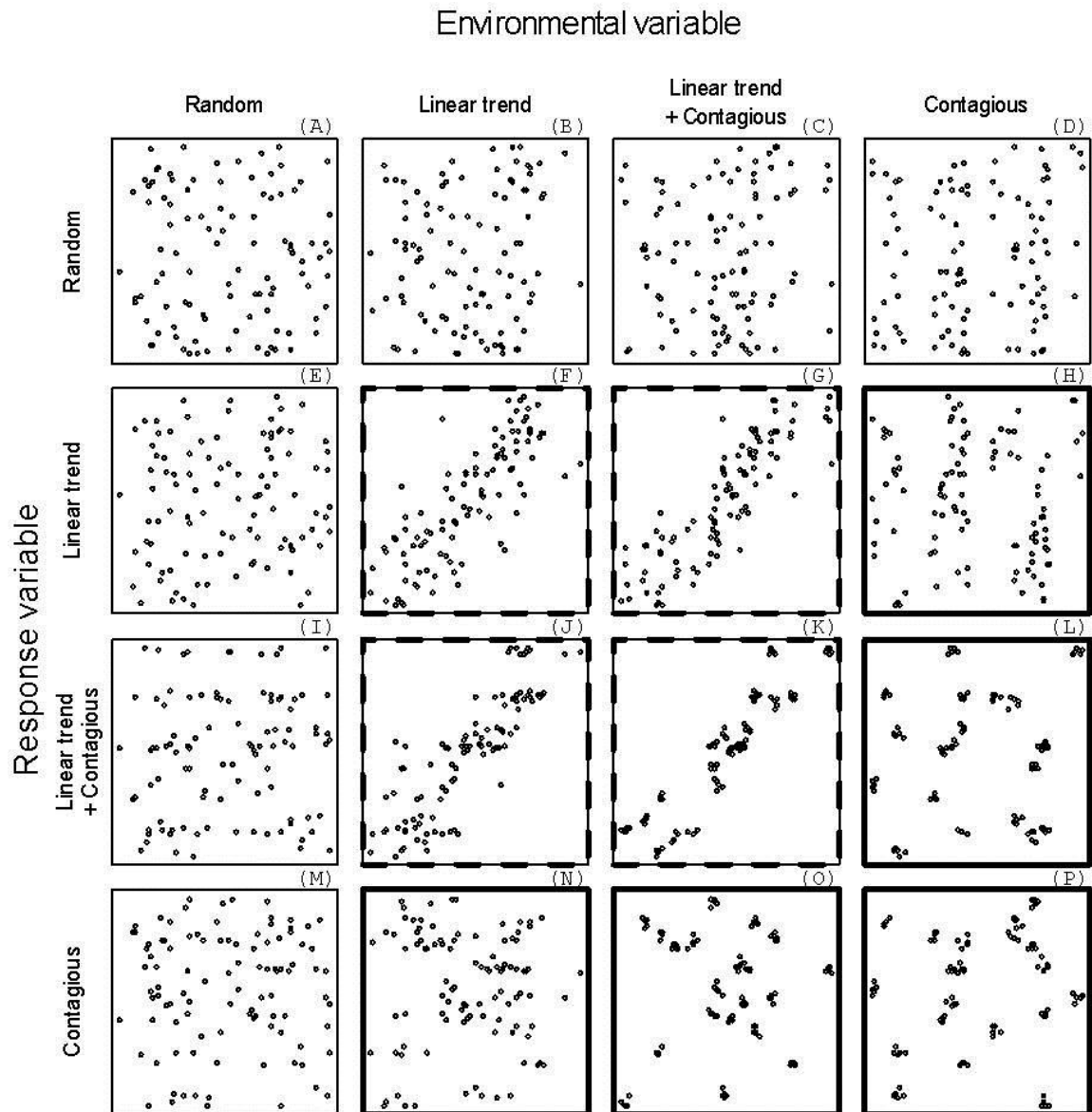
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### 382 *What the simulations mean*

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384         In the following sections we will use simple models with space represented by a single  
385 dimension (distance along a transect) to illustrate the results of some of the simulations in the  
386 literature, and their implications for different types of analyses. Basically we will generate 16 types of  
387 simulated data (Fig 4) and analyze these data using simple Ordinary Least Squares (OLS) regressions,  
388 Simultaneous Autoregressive (SAR) models (error, lagged, and mixed), Generalized Least Squares  
389 (GLS), and Spatial Filtering Techniques (using three different procedures to choose spatial filters to  
390 use in the model). Details of simulations and analysis are in the supplementary material. The effects of  
391 spatial autocorrelation on our interpretations depend on its strength and extent (Beale et al. 2010). We  
392 will discuss that later, and start with simple combinations of large-scale (a linear trend across the  
393 transect – Fig. 2A), small-scale autocorrelation generated by local processes (such as in Fig. 2D), and  
394 no autocorrelation (random association with space). Either or both of the dependent and independent  
395 variables may have no, large-scale, small-scale, or large- and small-scale autocorrelations. The  
396 possible combinations and resulting patterns in the relationships between dependent and independent  
397 variables are shown in Figure 4.

398 We can group the 16 graphs in three general scenarios: (1) Autocorrelation in either the  
 399 dependent or predictor variable, but not in both (Fig 4. B, C, D, E, I, M). (2) Both the dependent and  
 400 independent variables are spatially autocorrelated, but they are orthogonal (independent in the sense  
 401 that information on one relationship does not allow prediction of values generated by the other), and  
 402 spurious relationships are unexpected for purely geometrical reasons (Fig 4 H, L, N, O, P). (3) Both  
 403 variables are linearly related to space, resulting in a spurious relationship between them due to their  
 404 common relationship with space. (Fig. 4 F, G, J, K).



405

406

407 **Figure 4.** Sixteen combinations that can result from sampling different combinations of the  
 408 structures described in Fig. 2A-D. We sampled 200 equidistant points, spaced by 5 units, along the  
 409 transect.

409

410 These data were generated to avoid a causal relationship between the dependent and  
 411 independent variables. That is, information about the independent variable was not used to generate  
 412 the dependent variable. Therefore, the ideal statistical test would not indicate a relationship between  
 413 the dependent and independent variables. If we apply a test of the relationship between the dependent  
 414 and independent variables many times (we used 1000 times in our simulations), they should give an  
 415 apparently significant result only once in twenty times, if we use the conventional critical level to  
 416 reject the null hypothesis of 0.05. While we do not recommend an arbitrary 0.05 “significance” level,  
 417 it is commonly used to estimate the frequency of type I error (how often the null hypothesis is rejected  
 418 erroneously).

419 Scenario 1. – All of the combinations in scenario 1 involving autocorrelation in the dependent  
 420 variable (Fig. 4. A, B, C, D, E, I, M) induce autocorrelation in the residuals of a regression of the  
 421 dependent variable on the independent variable (Table 1), but conventional statistical tests produce  
 422 about the correct level of type I error (0.05). This is expected because statistical tests are compromised  
 423 only when both the predictor and response variables are autocorrelated (Legendre et al. 2002).  
 424 However, advocates of spatial analyses claim that spatial analyses should be carried out always  
 425 because spatial autocorrelation may affect the analyses even when statistical tests do not detect  
 426 autocorrelation at the appropriate significance level. We will not enter into this debate, but it clearly  
 427 would be beneficial to have diagnostic statistics to indicate when autocorrelation in the variables is  
 428 likely to lead to compromised statistical tests.

429

430 **Table 1:** Results of ordinary least squares (OLS) regression models for 1000 simulation runs  
 431 combining samples taken from our four scenarios (Fig. 4). Type I error rate / rate of times that  
 432 the residuals were autocorrelated at the first distance class among 1000 simulation runs.

		Environmental			
		Random	Linear	Linear+Contagious	Contagious
Response	Random	0.059/0.065	0.045/0.04	0.047/0.041	0.054/0.053
	Linear	0.056/1.0	1.0/0.713	1.0/0.543	0.387/1.0
	Linear+Contagious	0.049/1.0	1.0/0.986	1.0/0.937	0.407/1.0
	Contagious	0.05/0.911	0.353/0.867	0.385/0.875	0.412/0.924

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434

435 Scenario 2. – Both the dependent and independent variables are autocorrelated, but the  
 436 processes that lead to autocorrelation are independent for each variable, such that we would not expect  
 437 a relationship between them for geometric reasons (i.e. they are geometrically orthogonal, Fig 4 H, L,  
 438 N, O, P). This situation is probably rare in nature (Betts et al. 2009), and is not what worries most  
 439 ecologists. However, this scenario has been used in simulations by most modelers (Dormann et al.

440 2007; Betts et al. 2009; Beale et al. 2010) because it gives a good example of how autocorrelation can  
 441 give spurious statistical results, despite apparently orthogonal geometry. In this scenario, the null  
 442 hypothesis of no relationship between the dependent and independent variables is true, but ordinary  
 443 least squares (OLS) regressions indicate significant relationships (Table 1). Of the eight spatial  
 444 methods frequently recommended, only three, those related to SAR methods, returned type I error  
 445 rates close to the nominal 0.05 level (Table 2).

446 Scenario 3. – Both the dependent and independent variables have spatial relationships that  
 447 lead to a spurious relationship between them (Fig 4 F, G, J, K). This is probably the most common  
 448 case confronting ecologists and conservationists. If all clumping (autocorrelation pattern) in the  
 449 dependent variable is due to the effects of independent variables, there is no statistical problem due to  
 450 the autocorrelated pattern (Beale et al. 2010). However, with real data, the cause of clumping is being  
 451 inferred, and is not known before analysis. The clumping could be due to endogenous autocorrelation  
 452 (a process affecting only the dependent variable), due to independent variables included in the model,  
 453 or other independent variables not included in the model. Researchers tend to assume that the spatial  
 454 autocorrelation is totally attributed to endogenous processes (i.e. not due to habitat). However, that is a  
 455 very sweeping assumption that should be supported by strong natural-history justifications.

456

457 **Table 2:** Proportion of simulation runs that had a p-value  $\leq 0.05$  out of 1000. Row names are  
 458 the analysis used and column names are the variables used in the model. Y indicates a  
 459 response variable and X a predictor one. Subscript c indicates contagious, l indicates linear,  
 460 and l + c indicates linear plus contagious.

	$Y_c - X_l$	$Y_c - X_{l+c}$	$Y_c - X_c$	$Y_{l+c} - X_c$	$Y_l - X_c$
OLS	0.504	0.561	0.564	0.565	0.513
SAR <sub>error</sub>	0.051	0.047	0.054	0.05	-
SAR <sub>lagged</sub>	0.064	0.058	0.062	0.08	0.07
SAR <sub>mixed</sub>	0.053	0.046	0.054	0.061	0.051
GLS	0.241	0.409	0.417	0.405	0.399
ME	0.577	0.618	0.653	0.685	0.6361
SF	0.566	0.659	0.657	0.669	0.7746
PCNM	0.573	0.832	0.837	0.708	0.102

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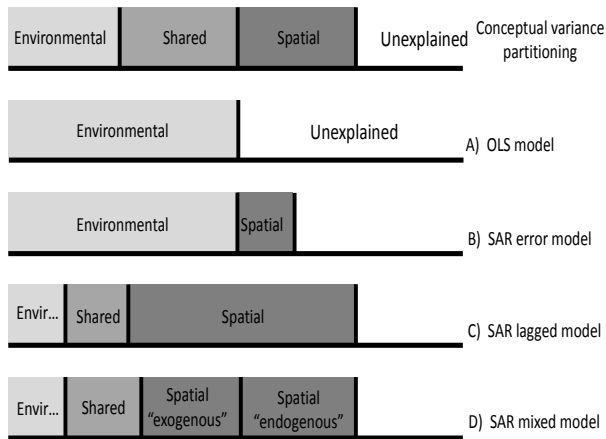
462 We used spatial confounding with a large-scale trend because it is easier to visualize, but  
 463 confounding can result when autocorrelation is on a similar scale for the dependent and independent  
 464 variables, independent of the scale of the autocorrelation. The problem of incorrectly estimated  
 465 probabilities remains along with the extra problem of confounded effects. Hurlbert (1984) referred to  
 466 the action of an unrecognized confounding variable as “demonic intrusion”. If the objective of spatial

467 analyses is to evaluate the possible effects of all spatially confounding variables by including them in  
468 the model as “space”, then space represents demonic intrusion. As we have seen, “space” is what we  
469 use to represent clumping. By including the effects of clumping, we are including the effects of all  
470 confounding variables that cause clumping.

471 In this case, the most we can do is to separate the variability in the dependent variable into  
472 parts that are generated by different processes. Part can be unambiguously attributed to the non-spatial  
473 independent variables included in the model, and part can be unambiguously attributed to spatially  
474 aggregated effects, which could be due to endogenous processes, such as limited dispersal of  
475 organisms, or spatially aggregated predictor variables not included in the model. Part of the variability  
476 cannot attribute to anything (residual), and the rest could be due to either the spatial predictors or the  
477 other independent variables included in the model (Fig. 5). To separate the effects of space and  
478 predictor variables, we must model autocorrelation in the independent variable that corresponds to  
479 autocorrelation in the dependent variable. Borcard and Legendre (2002) has pioneered this type of  
480 analysis, mainly using a technique called Principal Coordinates of Neighbourhood Matrix - PCNM  
481 (see also Dray et al. 2006; Legendre et al. 2009a). However, any of the methods that take spatial  
482 autocorrelation into account in the independent variable may be used (Table 2).

483 The down-side of taking into account the potentially confounding effect of space is that when  
484 we take out “space” we may be removing a true effect of the independent variable. This will affect our  
485 estimates of the regression coefficient for the independent variable. We have seen that, even when the  
486 effects of space and the independent variable are orthogonal, many of the spatial techniques, including  
487 PCNM, may provide unbiased estimates of the slope of the regression, but with great cost in precision  
488 (Fig. 6). This is important, because an imprecise estimate of the regression coefficient will lead to  
489 imprecise variance partitioning (i.e. the amount of potential confounding). Because researchers  
490 normally do one or a few studies, and have only one or a few estimates of the regression coefficient, it  
491 may not be very relevant that if they had done 1000 studies, the mean estimate of the regression  
492 coefficient would have been close to correct. Worse still, some of the best methods for dealing with  
493 the statistical problem of high rates of type I error for scenario 2 (e.g. autorregressive models) produce  
494 strongly biased estimates of the regression coefficient in scenario 3.

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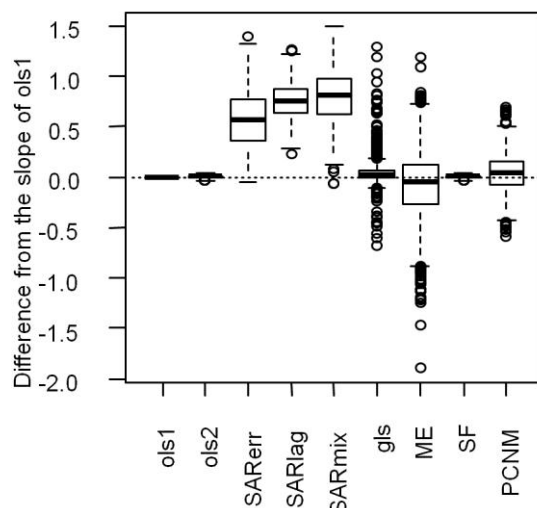
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**Figure 5.** Conceptual variation partitioning of OLS and SAR models. The first is the conceptual variation partitioning diagram, showing the environmental-only component, the environmental shared with the spatial component, the spatial-only component, and the unexplained variation. The remaining partitions are for A) OLS models, in which there is considered to be only the environmental component and the unexplained variance; B) SAR error, in which a spatial variable is created to account for the autocorrelated errors, so this model conceptually has no shared component; C) SAR lagged, in which a spatial variable is created to explain spatial patterns of the response variable, so there is a shared component between environmental variables and the spatial component; and D) SAR mixed models, in which two spatial variables are created in a way that the spatial component might be interpreted as two spatial only components, one related to the endogenous autocorrelation  $\rho_{WY}$ , and the other related to the exogenous autocorrelation  $\gamma_{WX}$ .



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**Figure 6.** Boxplots representing the differences found in the slope (standardized coefficients) between OLS1 estimated parameters from the other analysis run after the data being “pseudoreplicated”. The line inside the boxes is the median, the box indicates the first and third quartiles and whiskers which extend to the minimum and maximum values (points are outliers further from the mean than 1.5 times the box length).



515           There is also a conceptual problem with the exercise of attributing proportions of variance to  
516 “space”. Beside the fact that the result will be biased if there is a miss match between the scale of  
517 sampling and the scale of effect of predictor variables (de Knegt et al. 2010), the answer must be scale  
518 specific. The amount of variance due to any variable is not a characteristic of the biological system, it  
519 is a characteristic of the sampling scale. Any discussion of the proportion of variance attributable to  
520 factors causing endogenous autocorrelation should be prefaced by an explanation of why that  
521 particular scale is of interest for the conservation problem in hand.

522

### 523 *More complex simulations*

524

525           Beale et al. (2010) have carried out comprehensive simulations that are extensions of scenario  
526 2, with collinear predictor variables, model selection algorithms and application of regression  
527 techniques designed to address problems derived from the violation of assumptions. In general, their  
528 conclusions are similar to those presented here, although some methods that work well under simple  
529 scenarios are not improved by use of model selection algorithms. Model selection for collinear  
530 variables is an extremely complex subject and perhaps more polemical than selection of spatial  
531 techniques (Taper and Lele 2004). The two most complex scenarios presented by Beale et al (2010)  
532 were the scenarios in which none of the methods worked well and are useful to illustrate the  
533 limitations of spatial analyses in general.

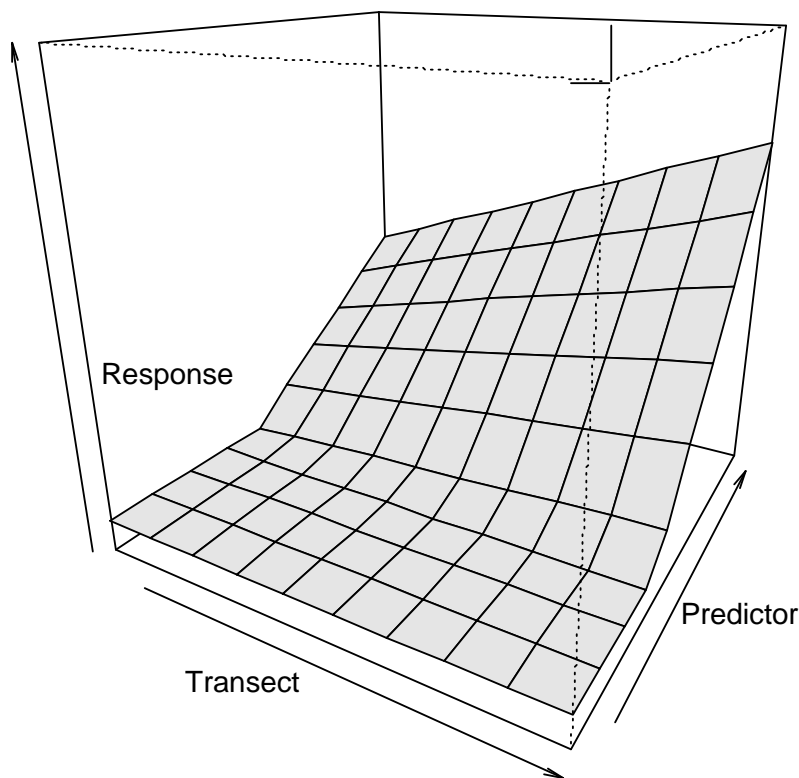
534           The first situation is where the relationship between the dependent and independent variables  
535 is nonstationary. As in Beale et al. (2010), we simulated no relationship between the dependent and  
536 independent variables on one side of the space (in our case, on one side of the transect) and a strong  
537 relationship on the other side (Fig. 7). The lines in Figure 7 illustrate the relationship we are trying to  
538 describe. It is clear why a global model cannot describe this situation. The regression coefficient is not  
539 a constant, and any model that ignores that will be misleading. This is independent of the possible  
540 autocorrelation in the residuals or any other statistical problem. The model is so badly specified that it  
541 is meaningless to compare the utility of the different methods.

542           The second situation, which Beale et al. (2010) surprisingly considered worse than the first, is when  
543 the general model is correct, but the autocorrelation in the residuals is nonstationary. They modeled an  
544 increase in the extent of the autocorrelation across their spatial coordinates. This relationship is  
545 illustrated in one dimension in Figure 8. This situation is analogous to breaking the assumption of  
546 homogeneity of variance (heteroscedasticity) in a simple regression situation, with well-known  
547 consequences (incorrect estimates of type I errors). The estimate of the regression coefficient is  
548 generally not badly affected by heteroscedasticity in a simple regression, but estimates of slopes with  
549 collinear predictor variables and heteroscedasticity may be very inaccurate (Beale et al. 2010).  
550 Although we agree with Beale et al. (2010) that nonstationarity of the autocorrelation in the residuals  
551 is a grave problem, we believe that, unlike the error in model specification described above, it is not

552 inherently unsolvable, and, where individual clumps can be recognized, analyses such as those  
 553 described by Barnett et al. (2010), which include different variances for each level of the predictor  
 554 variable, may lead to improved spatial analyses, as they do for repeated-measures analyses.

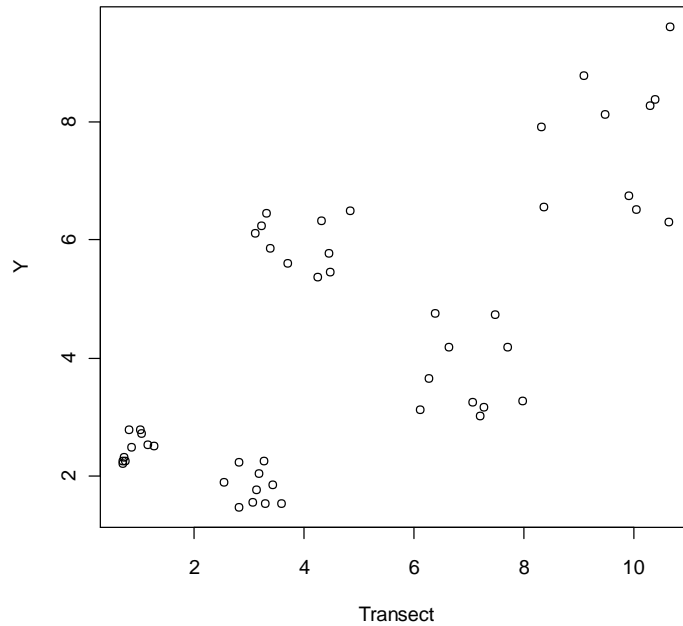
555 Most of the techniques we have discussed assume isotropy (the effect of distance is  
 556 independent of direction). When the effect of distance depends on direction (usually), this needs to be  
 557 taken into account in the analysis. Spatial filters are designed to capture any form of clumping, but  
 558 most other analyses need information on the form and direction of the autocorrelation. Dendritic  
 559 systems usually have connections that are not well modeled by Euclidean distance (Peterson & Ver  
 560 Hoef 2010). Those authors describe how to take into account different forms of connectivity  
 561 (dispersal), but as with most of the papers reviewed here, they only treated autocorrelation in the  
 562 residuals, and not in the predictor variables (pseudoreplication sensu Hurlbert, 1984). We can expect  
 563 further advances in modeling anisotropic systems in the near future.

564



565

566 **Figure 7.** Example of a situation in which there was no relationship between the dependent  
 567 and independent variables (response [e.g. regression slope] = 0) on one side of the space (in our case,  
 568 on one side of the transect) and there is a strong relationship on the other side.



569

570

571 **Figure 8.** An example where the extent of autocorrelation is non-stationary, which might  
 572 occur in a situation where dispersal is more limited on one end of the transect. This results in points  
 573 clumps being more aggregated at small distances along the transect.

573

574 **CONCLUSIONS**

575

576 *Where to go from here?*

577

578

579 Conservation biologists want to use the most powerful method, and recent studies of spatial  
 580 analyses conclude that applying some of the techniques they describe is better than doing nothing  
 581 (Dormann et al. 2007; Bini et al. 2009; Beale et al. 2010). However, conservation biologists must be  
 582 clear about their objectives. Spatial autocorrelation is generally advantageous for specific normative  
 583 studies, because it permits land-use zoning and the inclusion of considerations relating to costs of land  
 584 acquisition and control of access (Watts et al. 2009). Many of the most promising spatial methods in  
 585 conservation biology described in the introduction do not involve statistical problems of  
 586 autocorrelation in the residuals, which has been the focus of much of the recent debate. It would be  
 587 foolish to try to remove the effect of spatial aggregation before undertaking these studies.

588

589 Although conservation biologists may be concerned about the possibility of unmeasured and  
 590 unknown confounding variables (demonic intrusion) leading to spurious conclusions, this has not been  
 591 the focus of most of the recent debate. Simulations were specifically designed to create autocorrelation  
 592 in the residuals without collinearity between “space” and the independent (predictor) variables (de  
 593 Knecht et al. 2010). If the researcher is worried about confounding variables, they should use  
 594 techniques that model space in the dependent or independent variables. However, no particular

593 advantage may be obtained in allocating variance between “space” and environment, because, at most  
594 spatial scales of interest to conservation biologists, “space” generally just represents unknown  
595 environmental variables in the analysis. If a specific process, such as reproduction or dispersal, is  
596 thought to cause autocorrelation, it may be better to model that process, rather than calling it “space.”  
597 We have focused on simple examples, and assumed that sampling was undertaken at the scale  
598 appropriate for the questions. However, autocorrelation in the residuals is likely to be caused by  
599 sampling at a scale inappropriate to the question (de Knecht et al. 2010). In this case, removing  
600 autocorrelation from the residuals instead of using it to redefine the question will result in analyses  
601 that are as biased and inappropriate as OLS regression.

602         If the researcher can assume that “space” does not represent confounding variables, and only  
603 wants to carry out valid statistical tests and estimate parameters (that cannot also be variables), then  
604 spatial techniques that focus on the residuals are the most appropriate and may greatly improve  
605 estimates (Beale et al. 2010 and references therein). Although we agree with Beale et al. (2010) that  
606 nonstationarity of the autocorrelation in the residuals is a grave problem, we believe that, unlike the  
607 model misspecification described in the previous paragraph, it is not inherently unsolvable, and, it may  
608 be possible to use covariates to model the residual structure (Zuur et al. 2009). Where individual  
609 clumps can be recognized, analyses such as those described by Barnett et al. (Barnett et al. 2010) may  
610 lead to improved spatial analyses, as they do for repeated-measures analyses.

611         Recent studies in landscape ecology suggest that the configuration of landscape elements may  
612 be important in itself, and there may be nonlinear “threshold” effects (Metzger 2006). There has been  
613 only limited progress in landscape ecology because of the difficulty of replicating landscapes. Internal  
614 validation (such as standard statistical tests) assumes that the ecological relationships are well known  
615 (and generally linear) and can be extrapolated to other landscapes. However, real-world landscapes are  
616 generally so complex, and with so many nonlinear relationships, that extrapolation to other systems  
617 based on past knowledge of a particular system is risky because of the likelihood of essentially  
618 unpredictable phenomena (“black swans” in the terminology of Taleb 2007). Conservation biologists  
619 should seek more substantive replication (i.e. the repetition of the study by other researchers in other  
620 landscapes) in order to have confidence in their models.

621

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623

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627

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2  
3 **Spatial eigenfunction analyses in stream networks: do watercourse and overland**  
4 **distances produce different results?**

5  
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18  
19 Abbreviated title: Watercourse or overland distances?

20 Keywords: Stream networks, overland, watercourse, dispersal, community

21

## 22 SUMMARY

23

- 24 1. The use of spatial variables is a common procedure in ecological studies. The technique is based  
25 on the definition of a connectivity/distance matrix that conceptually defines the dispersal of  
26 organisms. The shortest distance between two points is a straight line. Despite the fact that a  
27 straight line may not represent the easiest dispersal path for many kinds of organisms, straight  
28 line distances are often used to detect patterns. We argue that other types of  
29 connectivity/distance matrices will better represent dispersal paths, such as the watercourse  
30 distance for aquatic organisms (e.g. fish, shrimps).
- 31 2. We used empirical and simulated community data to evaluate the usefulness of spatial variables  
32 generated from watercourse and overland (straight-line) distances.
- 33 3. Spatial variables based on watercourse distances captured patterns that straight-line distances  
34 did not, and provided better representations of the spatial patterns generated by dispersal along a  
35 dendritic network.
- 36

## 37 Introduction

38

39 Understanding the factors controlling the distribution of lotic organisms is one of the main  
40 objectives of stream ecology. Traditionally, stream ecologists have related the biota to environmental  
41 predictors (e.g. physicochemical measurements and substrate characteristics) in order to understand  
42 and predict species distribution patterns (Cummins & Lauff, 1968; Townsend & Arbuttle, 1997; Buss  
43 *et al.*, 2004; Yoshiyuki & Hajime, 2007). Recently developed statistical techniques allow us to study  
44 community distribution in relation to spatial predictors as well as environmental predictors (Borcard &  
45 Legendre, 2002; Griffith & Peres-Neto, 2006; Peres-Neto & Legendre, 2010). These have been pivotal  
46 to the study of metacommunities (Leibold *et al.*, 2004; Holyoak, Leibold & Holt, 2005) because  
47 spatial connectivity among communities is a key aspect of metacommunity analyses. Additionally, the  
48 use of spatial predictors allows researchers to quantify, albeit indirectly, the role of dispersal in  
49 shaping beta-diversity patterns, an issue often overlooked when only environmental models are used  
50 (Bunn & Hughes, 1997).

51 Spatial eigenfunction analyses are frequently used to represent the variable “space” in  
52 ecological studies, with the main objective of partitioning variance in response variables into that  
53 attributable to measured environmental variables, pure space, and shared effects of environment and  
54 space (Borcard & Legendre, 2002; Peres-Neto *et al.*, 2006; Peres-Neto & Legendre, 2010). Spatial  
55 eigenfunction analysis comes under a variety of names (although they are all variations of the same  
56 theme; see Dray, Legendre & Peres-Neto, 2006 *et al.*, 2006), including Principal Coordinates of  
57 Neighbour Matrices (PCNM), Distance-based Eigenvectors Maps and Moran's Eigenvector Maps.  
58 However, it is not always clear what space represents, and spatial eigenvectors represent any set of  
59 variables that causes clumping in the distribution of values of the response variable(s). Space is often  
60 meant to represent dispersal limitation or some other process that is largely independent of  
61 environmental predictors, such as those proposed in neutral models of community assembly (Hubbell,  
62 2001; 2005). However, space and environment are also highly interrelated (Tobler's first law of  
63 geography: “Everything is related to everything else, but near things are more related than distant  
64 things”; e.g., Bjorholm *et al.*, 2008). This spatial dependency decreases our ability to identify the main  
65 processes (i.e. niche based vs. dispersal processes) and underlying patterns of community structure  
66 (Gilbert & Lechowicz, 2004). Therefore, because clumping may also result from unmeasured  
67 environmental variables, the attribution of observed patterns to dispersal processes must be done  
68 cautiously (Diniz-Filho, Bini & Hawkins, 2003; Hawkins *et al.*, 2007).

69 Spatial eigenvector methods decompose the spatial variability into a set of explanatory spatial  
70 variables that represents independent propositions of how local communities are interlinked (Ramette  
71 & Tiedje, 2007). As the created variables are statistically orthogonal, they are not collinear. Standard  
72 methods to construct spatial variables (e.g. PCNM) are generally based on the use of a Euclidean  
73 distance matrix between sampling sites. This distance matrix is then submitted to a Principal

74 Coordinate Analysis whose axes (eigenvectors) are used as spatial explanatory variables in univariate  
75 or multivariate analyses (see Borcard & Legendre, 2002 for more details about PCNM). The  
76 eigenvectors associated with high eigenvalues represent broad scale patterns of relationships among  
77 sampling units, whereas those with low eigenvalues represent fine scale patterns (Griffith & Peres-  
78 Neto, 2006). Euclidean distances may be appropriate for aquatic organisms that migrate over land,  
79 such as flying aquatic insects (Bilton, Freeland & Okamura, 2001). On the other hand, many  
80 organisms, such as fish and immature stages of aquatic insects, are mostly unable to migrate in this  
81 way. For these groups, the distance between two sites might be better defined by the length of the  
82 watercourse between two points (i.e., the distance along the network pathway; Ganio, Torgersen &  
83 Gresswell, 2005; Chaput-Bardy *et al.*, 2009; Brown & Swan, 2010). In fact, several types of  
84 connectivity matrices among stream sites can be generated (Fullerton *et al.*, 2010).

85         Space per se cannot be considered an explanation of ecological variability (Leduc *et al.* 1992).  
86 Thus, a significant relationship between spatial variables (eigenvectors) and raw species data tables  
87 could indicate the existence of an underlying abiotic or biotic process with a spatial component. From  
88 an ecological point of view, a set of spatial variables derived from overland distances is likely to  
89 represent a large-scale gradient in climatic conditions and other abiotic factors, whereas a set of spatial  
90 variables derived from watercourse distances is more likely to relate to dispersal limitation.

91         In order to increase our understanding of how spatial processes regulate biological  
92 communities, and increase the variance explained by statistical models, new analytical methods have  
93 been proposed to incorporate other kinds of connectivity among sites in stream networks, such as  
94 autocovariance models (Peterson & Ver-Hoef, 2010) and asymmetric eigenvector maps (Blanchet,  
95 Legendre & Borcard, 2008). It could be argued that the results of two analyses of variance  
96 partitioning, the first one based on spatial variables generated by using overland distances and the  
97 second by using watercourse distances (e.g. Beisner *et al.*, 2006; Nabout *et al.*, 2009), would be  
98 equivalent due to the flexibility of eigenfunction spatial analyses (Griffith & Peres-Neto, 2006). This  
99 is expected because, in both cases, several spatial variables with different spatial structures are  
100 generated. However, the equivalence of different types of connectivity matrices for spatial  
101 eigenfunction analyses has not been demonstrated.

102         We investigated whether spatial variables derived from watercourse distances explain more of  
103 the variance in community structure than spatial variables based on overland distances for two groups  
104 of aquatic organisms (fish and immature stages of caddisflies) in first to third order streams in a  
105 tropical forest. We also generate artificial communities, in which spatial patterns were caused only by  
106 dispersal limitation, to evaluate whether spatial variables based on watercourse distances explain more  
107 of the variance in community structure than those based on overland (Euclidean) distances, when the  
108 model is essentially neutral (no effects of environmental variables).

109

## 110 Methods

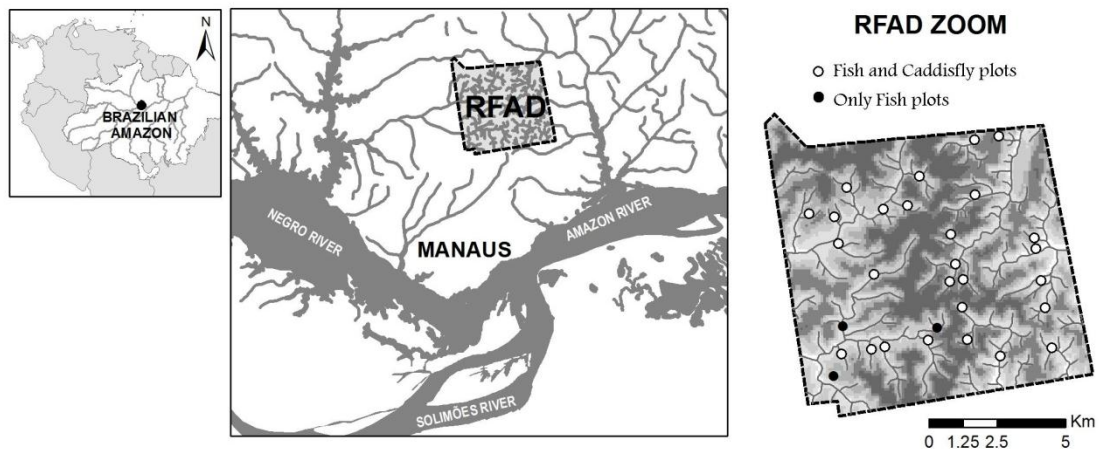
111

### 112 *Empirical Field Data*

113

114 We used four sets of field data gathered in streams in Ducke Reserve (02°53`S, 59°58`W; near  
 115 the city of Manaus, Central Amazon, Brazil). Three data sets include fish samples taken from 30  
 116 stream sites (Fig. 1) on three sampling dates (Espírito-Santo *et al.*, 2009). Six physicochemical  
 117 variables were also measured: pH, conductivity, width, depth, dissolved oxygen and water velocity.  
 118 Sampling details can be found in Espírito-Santo *et al.*, (2009).

119 The fourth data set concerns caddisfly samples (Pes, 2005) taken at 27 of the same sites (Fig.  
 120 1), with three benthic sample units of 2.25 m<sup>2</sup>, separated by at least 5 m, at each site. Larvae were  
 121 collected using a d-net and/or a Surber sampler (both with mesh size of 250 µm) and individuals  
 122 attached to bedrock or stones were removed using tweezers and spatulas. Available substrate in the  
 123 sample units was assessed, collecting leaves, sand and macrophytes using d-nets, and storing in plastic  
 124 bags with 80 % ethyl alcohol (except stones and large woody debris). In the laboratory, the larvae  
 125 were identified to morphospecies or, when possible, species. The same physicochemical variables  
 126 were measured as for the fish datasets, except for dissolved oxygen.



127

128 **Figure 1.** Location of the Ducke Reserve (RFAD) and of the sampling plots. Fish  
 129 were sampled at 30 sites and caddisfly at 27.

130

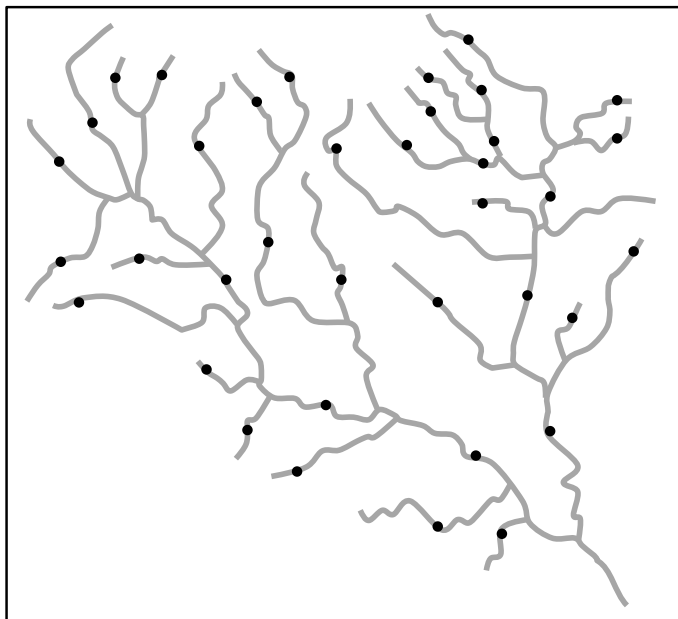
### 131 *Simulated Data*

132

133 We drew manually an artificial stream network where 37 sites were placed haphazardly (Fig.  
 134 2). The shape of this network is commonly observed in nature, including many branches and  
 135 confluences, and has properties adequate for our objectives. The relationship between matrices  
 136 generated using overland and watercourse distances among the sites was weak, and the correlation

137 between Euclidean and watercourse distances was relatively low, as observed for streams in the Ducke  
 138 Reserve network (see Peterson & Ver-Hoef, 2010 for other ways to generate artificial stream  
 139 networks). In our simulation, there was no difference between the capacities to disperse upstream or  
 140 downstream.

141 We used a spatially explicit, individual-based (see Zurell *et al.*, 2010 for examples) simulation  
 142 procedure to produce artificial community data. First we defined a pool of 50 species for the entire  
 143 network and then randomly assigned  $S$  species to each site. Each site had a fixed carrying capacity of  
 144 500 individuals that were equally distributed among the  $S$  species present at the beginning of the  
 145 process. At each time step, each individual could give birth to a single offspring with a probability  $b$   
 146 and could die with a probability  $d$ . Each new individual could migrate to any site within a threshold  
 147 distance, defined as the minimum distance along the network to keep all sites connected (minimum  
 148 spanning tree; Legendre & Legendre, 1998). The probability of colonizing a new site was inversely  
 149 proportional to the distance from the source site. The distances among sites considered in these  
 150 simulations were watercourse distances. Thus, dispersal processes were restricted to follow the  
 151 network pathways. We ran the simulation for 1000 time steps. At the end of each time step and when  
 152 the total number of individuals (in any given site) was larger than 500, randomly selected individuals  
 153 were removed from sites until the local population was reduced to 500.



154

155 **Figure 2.** Artificial stream network used to simulate community data. Sampling sites were  
 156 haphazardly placed. Watercourse and overland distances were calculated and used in the simulation  
 157 process. The probability of colonization of a given site was inversely proportional to the distance from  
 158 the source site through the watercourse corridor.

159

160 *Data analysis*

161

162 Data on fish and caddisfly species composition were analyzed in relation to the six and five  
163 physicochemical variables, respectively, and in relation to two sets of spatial variables generated from  
164 watercourse and overland distances. All analyses were carried out in the R environment (R  
165 Development Core Team, 2009). PCNM was used to generate spatial variables, using the *pcnm*  
166 function from the *vegan* package (Oksanen *et al.*, 2010). We used partial redundancy analyses (pRDA;  
167 Borcard, Legendre & Drapeau, 1992; Legendre & Legendre, 1998) to quantify the relative importance  
168 of environmental and spatial variables in explaining the variation in community composition. For  
169 these analyses, we employed the function *varpart* from the *vegan* package. We used a stepwise  
170 selection procedure to select spatial variables (eigenvectors) and environmental variables using the  
171 *ordistep* function from *vegan*. Community data were transformed prior to analysis using the Hellinger  
172 transformation (Legendre & Gallagher, 2001).

173 The threshold value used in the PCNM analysis was the minimum distance that kept all  
174 sampling sites connected using a minimum-spanning-tree procedure. However, a plateau at the centre  
175 of the Ducke Reserve separates two drainage basins. The eastern basin is connected to the streams of  
176 the western basin only by long watercourse distances, passing through the Amazon and Negro rivers  
177 (Fig. 1). This long distance may act as a barrier for dispersal of organisms from streams of one basin  
178 to streams of the other. Conventional PCNM procedure connects streams of both sides of the reserve,  
179 so we used a second truncated connectivity matrix based on the Euclidean distances, in which the  
180 western and eastern basins were “manually” unconnected. We also used a watercourse distance matrix  
181 to generate the PCNM variables.

182 Hereafter, the sets of spatial variables generated by the PCNM analysis, and which were based  
183 on the overland, overland with separation of the basins, and watercourse distance matrices will be  
184 referred as overland, overland-unconnected and watercourse eigenvectors, respectively. To evaluate  
185 the unique contributions of the PCNM variables generated by using these three distance matrices, we  
186 ran three partial RDA models for each of the three fish and caddisfly datasets, using environmental  
187 data and each set of eigenvectors as explanatory variables.

188 We analyzed the simulated data using partial RDA in which spatial variables generated by  
189 watercourse and overland distances were used as two sets of explanatory variables. To quantify the  
190 shared variance explained by the two sets of spatial variables, we ran two stepwise selection  
191 procedures using the *ordistep* function to retain watercourse and overland eigenvectors to be used in  
192 the partial RDA. It is important to note that this procedure was used only to quantify the shared  
193 variance explained by the two sets of spatial variables.

194

195 **Results**

196

197 The correlations between overland and watercourse and between overland and overland-  
 198 unconnected distance matrices were 0.49 and 0.46, respectively. The correlation between overland-  
 199 unconnected and watercourse distance was 0.62. In our artificial network the correlation between  
 200 overland and watercourse distance matrices was 0.58.

201

202 *Empirical Field Data*

203

204 For all three fish databases, analyses based on watercourse distances produced adjusted  $R^2$   
 205 higher than those based on Euclidean (overland) distances (Table 1). RDA models applied to caddisfly  
 206 data produced lower adjusted- $R^2$  than the RDA models applied to fish data. In general, models based  
 207 on overland-unconnected distances (i.e. east and west basins unconnected) produced higher adjusted-  
 208  $R^2$  than connected inter-basin overland distances. More spatial variables were retained in the analyses  
 209 using watercourse distances, and these generally represented spatial structures at finer scales (i.e.  
 210 eigenvectors with low eigenvalues).

211

212 **Table 1.** Table of variance partitioning for fish and caddisfly data. Spatial variables represent spatial  
 213 structures varying from broad (eigenvectors associated with high eigenvalues) to fine (low  
 214 eigenvalues) scales. Spatial variables are shown in the order they were retained in the stepwise  
 215 procedure (low numbers (e.g. 1, 2, etc.) represent variables with high eigenvalues). Values for each  
 216 explained fraction are adjusted  $R^2$ . Fractions are [a] pure environmental, [b] shared, and [c] pure  
 217 spatial. Overland-U represents the spatial variables generated by using a Euclidean distance matrix in  
 218 which east and west basins are unconnected.

Data	Distance	Spatial variables retained	Environmental variables retained	Fractions		
				[a]	[b]	[c]
Fish dry season 1	Overland	17,8	Depth, Oxygen dissolved, Width	0.178	0.075	-0.015 <sup>ns</sup>
	Overland-U	1,17		0.152	0.101	0.035
	Watercourse	1,12,22,4		0.098	0.155	0.081
Fish rainy season	Overland	17	Depth, Oxygen dissolved, pH, Velocity	0.307	0.03	-0.004 <sup>ns</sup>
	Overland-U	1		0.297	0.04	0.035
	Watercourse	22,1,19,4,3,9,25		0.138	0.199	0.082
Fish dry season 2	Overland	17	Depth, pH	0.202	0.047	-0.017 <sup>ns</sup>
	Overland-U	1,3,17,20		0.159	0.091	0.062
	Watercourse	12,1,22,9,4,20,19		0.077	0.172	0.088
Caddisfly	Overland	1,3	pH, Depth, Conductivity	0.073	0.014	0.024
	Overland-U	1,11		0.028	0.059	0.011 <sup>ns</sup>
	Watercourse	1,11		0.035	0.052	0.022

219 <sup>ns</sup> Non significant fraction ( $p > 0.05$ ); all other testable fractions were significant at  $P \leq 0.05$ .

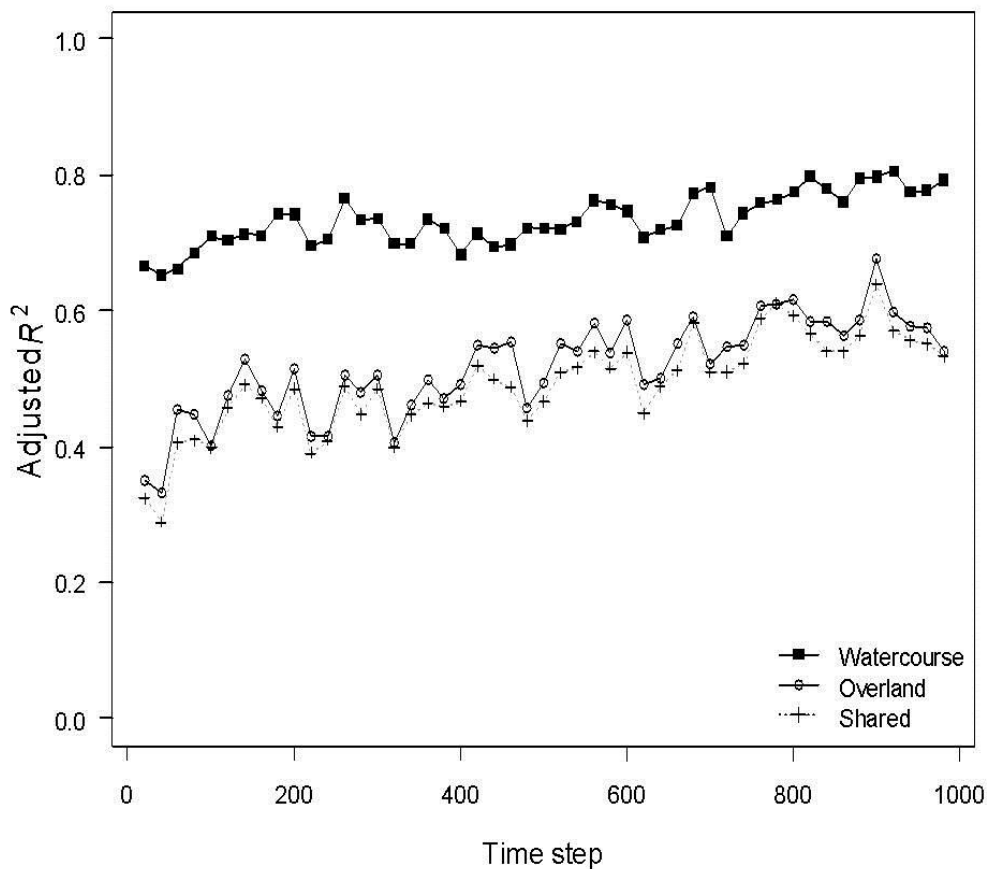
220



221 *Simulation*

222

223 The high value for adjusted  $R^2$  (0.75) obtained by RDA is an indication that the simulation  
 224 procedure was effective for our objectives (i.e., we were able to generate communities with spatial  
 225 patterns related to our distance matrices). There was a considerable difference between the adjusted  $R^2$   
 226 obtained with the spatial variables generated using overland and watercourse distances. Some spatial  
 227 variables were redundant, but about 35% of the total variance explained was exclusively attributable to  
 228 the spatial variables generated using watercourse distance (the distance used in the simulation). Only  
 229 about 3 % of the variance was exclusively attributable to the overland eigenvectors (Fig. 3).



230

231 **Figure 3.** Variation partitioning of simulated data. Shown are the adjusted  $R^2$  from three  
 232 separate RDA models. The first included only watercourse eigenvectors, while the second included  
 233 only overland eigenvectors. The third series of values was obtained by a partial RDA that included  
 234 both watercourse and overland eigenvectors to obtain the shared fraction. Note that the exclusive  
 235 portion of variation explained by overland eigenvectors was minimal (ca. 3%). Simulations were run  
 236 for 1000 time steps and values are plotted in intervals of 20 time steps.

237

## Discussion

Stream communities are affected by processes operating at different scales, from local to regional (Heino, Louhi & Muotka, 2004; Mykrä, Heino & Muotka, 2007; Roque *et al.*, 2010). The long watercourse distance between the two Ducke Reserve basins might represent a physical barrier and constrain the dispersal of organisms. Such an effect was not detected by simple overland distances, and spatial variables generated by a watercourse-distance based eigenvector procedure explained much more of the fish community structure than the same procedure applied to overland distances.

In contrast, caddisflies have flying adults that are able to disperse over land (Collier & Smith, 1998; Wilcock *et al.*, 2007) and, in their case, the spatial variables based on overland distances accounted for more of the variability in community structure. Moreover, the proportion of variability in caddisfly communities that was uniquely explained by spatial variables derived from watercourse distances was slightly lower than that for fishes.

Although our results showed that watercourse eigenvectors explained much more variance than overland eigenvectors, the unconnected-overland eigenvectors also explained a significant fraction of the variance in fish data. However, this explained variance was almost completely shared with watercourse eigenvectors as shown by a partial RDA using both sets of spatial predictors (variance purely attributable to unconnected-overland was 0.4 % for the first dry season, < 0.1 % for the rainy season, and 4.9 % for the second dry season). Thus, because overland and watercourse distance matrices are correlated to some extent (0.49 to 0.62), both distance matrices provide spatial variables that are also correlated, causing a detectable shared component. For aquatic insects that have different dispersal modes (i.e., drifting along the watercourse during immature stages and flying overland at adult stages; Poff *et al.*, 2006), the use of both types of distances might be necessary to explain species distributions. However, currently there is no tool to tease apart the shared component, so we cannot be confident if the variation explained by one of the two distances is spurious or not. It is important to keep this in mind when evaluating processes related to different types of distance matrices, as it is in the evaluation of gene flow by different dispersal routes (Chaput-Bardy *et al.*, 2009).

Peres-Neto and Legendre (2010) discussed the influence of the number of spatial variables on the power to detect the exclusive effect of environmental predictors in a variation-partitioning framework. Although our results also highlight this effect (i.e., a reduction in the relative contribution of the environment), they were stable in relation to the number of variables in the sense that we detected a significant environmental fraction ([a], Table 1) in most cases. Most importantly for our discussion, however, the variability of the environmental fraction was also dependent on the type of distance matrix used. Thus, our results demonstrate that the number of spatial variables and the type of distance matrix used to generate spatial variables have a profound effect on the interpretation of

275 metacommunity models. For instance, the use of a simple overland distance matrix would suggest that  
276 a species-sorting model would be most appropriate (see Table 1), as found in several studies (e.g.  
277 Cottenie 2005; Vanschoenwinkel *et al.*, 2007; Van der Gucht *et al.*, 2007). On the other hand, the  
278 importance of dispersal-related processes in driving metacommunities structure increased  
279 conspicuously when the watercourse distance matrix was used (Table 1; see also Beisner *et al.*, 2006  
280 for another analysis with fish data). In these cases, the results were consistent with a mixed (species-  
281 sorting + mass effects) metacommunity, a pattern found in 29% of the 158 data sets analyzed by  
282 Cottenie (2005).

283         Dispersal limitation appears to be the principal endogenous cause of spatial autocorrelation  
284 that is of interest to ecologists (Bahn, Krohn & O'Connor, 2008; Shurin, Cottenie & Hillebrand, 2009),  
285 and most of the discussion on the effect of “space” is in regard to dispersal limitation. However,  
286 spatial variables generated by eigenfunction analyses do not measure this directly, and much of the  
287 variance attributed to space may be due to the effects of unmeasured environmental variables (Diniz-  
288 Filho *et al.*, 2003; Hawkins *et al.*, 2007). Also, Smith & Lundholm (2010), using simulated data,  
289 raised concerns about the use of variation partitioning as a method to tease apart the effects of niche  
290 and neutral processes, mainly due to the effects of the degree of dispersal limitation on both pure  
291 environmental and pure spatial variance fractions. When dispersal limitation is the primary mechanism  
292 creating species distribution patterns of lotic species, as in our simulations, spatial variables based on  
293 watercourse distances do explain more of the observed variance than spatial variables based on  
294 straight-line distances (i.e. overland eigenvectors).

295         In the simulation study, about 60% of the variance explained was attributable to the shared  
296 component (i.e., the variability that either watercourse or overland eigenvectors was able to explain),  
297 but the exclusive variance explained by watercourse eigenvectors (note that simulated data were  
298 generated using an algorithm of dispersion only along watercourse corridors) was about 35%, while  
299 the exclusive variance explained by the overland eigenvectors was only about 3%, showing the  
300 importance of using the correct distance or connectivity matrix for eigenfunction spatial analyses.

301         In this study, we assumed that dispersal limitation among sites was a simple function of  
302 distance along the watercourse. However, dispersal is not necessarily as easy in an upstream direction  
303 compared to downstream (Blanchet *et al.*, 2008), or in small streams compared to large streams. If  
304 more were known about the natural history of the species, it might be possible to use more realistic  
305 distances and connectivity matrices. Even when organisms do not disperse along channel segments,  
306 other functions could represent matrix permeability, and account for differences in environmental  
307 conditions that could affect dispersal. For instance, Ver-Hoef *et al.* (2006) and Peterson *et al.* (2007)  
308 showed that spatial models that incorporate flow direction, as well as stream distance, were more  
309 adequate than models that only use stream distance. In an application of these models, Isaak *et al.*  
310 (2010) showed that spatial models significantly outperformed their nonspatial counterparts in  
311 predicting thermal habitats of salmonids.

312 We conclude that the use of Euclidean distances, despite their simplicity of definition, might  
 313 not be the best choice for creating spatial predictors for eigenfunction spatial analyses. This is  
 314 particularly important for aquatic systems, but may well apply to terrestrial systems depending on the  
 315 environmental setting (e.g. fragmented or topographically variable landscapes) and on the vagility of  
 316 the taxonomic group under study.

317

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319

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329

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331

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### Capítulo 3

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Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O., Magnusson, W.E. 2011. Environmental and spatial factors controlling caddisfly (Trichoptera) species distribution: spatial extent, environmental heterogeneity and raw-data vs distance-based approaches. Manuscrito Formatado para *Freshwater Biology*



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3 Environmental and spatial factors controlling caddisfly (Trichoptera) species  
4 distribution: spatial extent and environmental heterogeneity

5  
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19 Running head: Environmental and spatial factors controlling caddisfly species

20  
21 **Keywords:** Distance-based approach; Neotropical streams; Raw-data approach; Redundancy analysis;  
22 Spatial analysis;

23

24 **SUMMARY**

- 25 1. Many recent studies have quantified the relative importance of environmental variables and  
26 dispersal limitations in shaping the structure of stream communities. The effect of scale on the  
27 importance of these two factors has seldom been evaluated and the effect of niche properties,  
28 represented by substrate characteristics and stream properties, depend on environmental  
29 heterogeneity, which increases with the increase in spatial extent. Spatial processes causing  
30 spatial patterns, such as dispersal limitation, also depend on the scale of the study.
- 31 2. We analyzed the distribution of caddisfly species in 89 Amazonian streams in relation to  
32 stream characteristics and spatial variables representing overland dispersal routes. The streams  
33 are distributed in three regions differing in spatial extent and environmental characteristics.  
34 We analyzed the data using partial Redundancy Analysis with two predictor datasets, one  
35 environmental and one spatial, to evaluate the variation in assemblage composition. We also  
36 separated caddisflies into good and bad dispersers to evaluate possible differences in  
37 responses of these two groups.
- 38 3. The environmental component explained a higher proportion of variance in the assemblage  
39 composition than the spatial component. Spatial effects were evident only when analyzing  
40 data from the three regions together, although, the exclusive spatial fraction was quite low.  
41 Good dispersers responded similarly to the whole community, while poor dispersers were  
42 related to environmental variables only in one region and also were not related to spatial  
43 variables.
- 44 4. Caddisflies were most affected by niche factors. The large environmental effect and small  
45 spatial effect conform to the use of these stream insects as good indicators of site properties  
46 and disturbances in monitoring programs.

47

48

## 49 Introduction

50

51 Most streams are environmentally heterogeneous at multiple spatial scales, from whole biomes to local  
 52 substrates (Mykrä, Heino & Muotka 2007), and this heterogeneity generally regulates the patterns of  
 53 distribution and abundance of stream organisms (Heino, Louhi & Muotka 2004). Substrate,  
 54 limnological factors, biotic interactions, and frequency of spates are important factors influencing  
 55 stream biota at all spatial scales (Bond & Downes 2000; Clausen & Biggs 1997; Heino *et al.*, 2004;  
 56 Olsen, Townsend & Matthaei 2001; Pringle 2001; Roque *et al.*, 2010). In addition, due to higher, on  
 57 average, connectivity, streams within drainages may be more biologically similar than streams in  
 58 different drainages. The high similarity among communities inhabiting nearby streams may be due to  
 59 both environmental similarity and the limited ability of species to disperse to distant streams in a  
 60 metacommunity context.

61 Two main types of factors can affect community compositions at local and regional scales.  
 62 Local processes relate to species interactions and local environmental conditions, while regional  
 63 processes are related to dispersal of organisms between communities in addition to environmental  
 64 variables describing regional properties. In this context, two main frameworks have been used to  
 65 discuss the control of species distribution (Brown *et al.*, 2011). The idea that communities are  
 66 principally structured in relation to niche properties is usually called species sorting (Cottenie 2005).  
 67 Neutral theories treat individuals of all species as ecologically equivalent with identical dispersal  
 68 capacity. According to this perspective, differences in distributions are created by random processes of  
 69 mortality and colonization (Hubbell 2001). Determining the relative contributions of species sorting  
 70 and neutral processes is currently the objective of many ecological studies (Logue *et al.*, 2011).

71 Variation partitioning analysis is frequently used to infer the relative importance of  
 72 environmental factors and spatial variables in explaining the structure of biological assemblages  
 73 (Peres-Neto & Legendre 2010 and references therein ; e.g. Peres-Neto *et al.*, 2006). Partitioning the  
 74 variation in assemblage data uses the species-data table as the response variable and environmental  
 75 and spatial variables as predictors. Space is usually represented by a symmetric geographic distance  
 76 matrix **D** containing  $n(n-1)/2$  elements (where  $n$  is the number of sites). This matrix can be analyzed  
 77 directly using partial Mantel tests (distance approach; Tuomisto & Ruokolainen 2006; Tuomisto &  
 78 Ruokolainen 2008), but it is also possible to convert this matrix into orthogonal variables of length  $n$ ,  
 79 allowing the analysis of the species-assemblage data in its original form (the raw-data approach;  
 80 Legendre, Borcard & Peres Neto 2005). The raw-data approach is usually based on eigenfunction  
 81 analysis (e.g. Griffith & Peres-Neto 2006; Landeiro & Magnusson 2011; Peres-Neto & Legendre  
 82 2010), which is considered the most flexible way to recover spatial patterns in the data (but see  
 83 Landeiro *et al.*, 2011).

84 Eigenfunction analysis produces eigenvectors associated with large, intermediate, and small  
 85 eigenvalues that represent, respectively, landscape wide trends (e.g., global), medium scales (e.g.,

86 regional), and fine scales or patchiness (e.g., local). This flexibility comes with a cost for  
87 interpretation, but these methods are well suited to generate proxy spatial variables to represent  
88 dispersal and/or unmeasured environmental variables, which may be structured at different spatial  
89 scales (Blanchet, Legendre & Borcard 2008b; Landeiro *et al.*, 2011).

90 Aquatic insects are often used as indicators of environmental impacts, and this raises the  
91 question of whether differences in assemblage structure are due to the environment or are simply the  
92 consequence of the distances among sites. The expected effect of distance on differences among  
93 biological assemblages is nonlinear if one assumes a pure neutral model (Diniz *et al.*, 2012; Hubbell  
94 2001; Hubbell 2005; Rosindell, Hubbell & Etienne 2011), so the effect of distance depends on the  
95 scale of the investigation. There are many questions that can be approached with distance analyses  
96 (Landeiro & Magnusson 2011), but the objective in environmental impact studies is simply to remove  
97 the confounding effect of space so that valid tests can be made concerning environmental impacts.

98 Caddisfly (Trichoptera) larvae frequently have been used in monitoring programs and as  
99 bioindicators of organic pollution (e.g. Couceiro *et al.*, 2007) and are important components of  
100 Amazonian streams, playing an important role in food webs (Walker, Henderson & Sterry 1991) and  
101 ecological processes, such as leaf breakdown (Landeiro *et al.*, 2010; Landeiro, Hamada & Melo 2008).  
102 Landeiro *et al.* (2011) concluded that species of Trichoptera have good local dispersal abilities as  
103 adults, because community structure was related to Euclidean (overland) distances rather than  
104 watercourse distances in a single, relatively small (100 km<sup>2</sup>) region. Caddisflies are commonly used as  
105 bioindicators due to their relationships with environmental conditions (Rosenberg & Resh 1993), and  
106 because they are good dispersers at local scales (Bilton, Freeland & Okamura 2001; Collier & Smith  
107 1998), which might minimize distance effects and spatial pattern. However, the effects of distance  
108 depend on the scale of the study, which in turn determines the length of many environmental gradients  
109 (Gilbert & Lechowicz 2004). Environmental impacts may be limited to local scales, or may affect  
110 large regions. Therefore, the relative effects of distance and environment on community similarity  
111 should be evaluated over multiple spatial scales (Brown *et al.*, 2011).

112 We investigated the effects of spatial scale on the structure of assemblages of caddisfly larvae in  
113 89 Amazonian streams in three regions near Manaus (Brazil). These regions vary in spatial extent and  
114 in the spatial arrangement of sampling sites. We hypothesized that the importance of environmental  
115 and spatial variables would be higher in the analyses including all data than in analyses of the data for  
116 each region separately. We expected that the region with the lowest spatial extent would have low  
117 environmental heterogeneity and that assemblage composition would be poorly predicted by spatial  
118 variables. Conversely, data sampled at broader scales should reveal higher environmental  
119 heterogeneity and higher spatial effects (the latter due to increased effects of dispersal limitation). We  
120 also classified caddisflies into good and bad dispersal classes, predicting that good dispersers are more  
121 related to environmental variables and that bad dispersers are more related to spatial variables. We  
122 show that variation in species composition of Amazonian caddisfly is better predicted by

123 environmental than by spatial variables, even when only species considered poor dispersers were  
124 included in the analysis. These results are in agreement with the statements that caddisflies are reliable  
125 indicators of environmental impact in this region that holds so much of the world's biodiversity.

126

## 127 **Methods**

128

### 129 *Study area*

130

131 The data used in this study were obtained from 89 stream sites, between April 2002 and February  
132 2003, in Central Amazonia (see Fittkau 1964 for more details on Central Amazonia). We sampled  
133 black-water streams (i.e. streams with dark waters caused by the humic and fulvic acids leaching from  
134 decomposing leaves leaves) in areas that are not seasonally flooded (called "*terra firme*" forests in the  
135 Amazonian literature). In general, streams in Central Amazonia are characterized by nutrient poor,  
136 acid waters, and low daily and annual variation in water temperature, with annual and daily means  
137 close to 25 °C (Sioli 1984).

138 We sampled immature caddisflies at 89 sites distributed in three regions (Fig. 1). The first  
139 region included 39 sites in the Ducke Reserve (hereafter DR; 03°00'00"S; 59°52'40"W), a 10 × 10 km  
140 reserve on the edge of Manaus City. The second region is maintained by the Biological Dynamics of  
141 Forest Fragments Project (BD hereafter) located about 70 km north of Manaus (02°26'02"S;  
142 59°46'32"W). The BD comprises areas of old-growth and regrowth forests, as well as pastures. We  
143 obtained samples from 20 streams in the BD region. The third region was Presidente Figueiredo  
144 County (hereafter called PF), located about 120 km north of Manaus (02°01'02"S; 60°01'30"W), where  
145 we sampled 30 streams. The spatial extents, as defined by the most widely spaced sites in the regions,  
146 were about 10 km at DR, 40 km at BD, and 100 km at PF region (Fig. 1).

147 Most streams in DR and BD have sandy bottoms, while those in PF have bedrock and stones  
148 (boulders, cobbles, pebbles, and gravel) in addition to sand. Streams in PF have fast-flowing waters  
149 and many waterfalls due to an ancient Tertiary plateau that is responsible for the sloped relief in  
150 relation to the more geologically recent, low-elevation, Quaternary formations underlying BD and DR.

151

### 152 *Sampling details*

153

154 Before sampling, the proportion of each substrate type (woody debris, leaves, roots, sand,  
155 macrophytes, stones [cobbles, pebbles, and gravel], and bedrock) was visually estimated following the  
156 method described by McCreadie & Colbo (1991). We took three sample units of 2.25 m<sup>2</sup> at least 5 m  
157 apart within a stream reach of 50 m, and sampled all substrate available in each of the three sample  
158 units using a D-net (mesh size of 250 µm). In some cases, where the main substrate was composed by  
159 bedrock we used a Surber-sampler with the same mesh size. Caddisflies attached to bedrock and

160 stones were removed using tweezers and spatulas. Samples were stored in plastic bags and fixed in  
161 96% ethyl alcohol. In the laboratory, the caddisflies were separated under a stereomicroscope and  
162 designated to morphospecies or, when possible, to species.

163 Physicochemical variables were also measured at each site. Water temperature was measured  
164 using a hand-held thermometer. Conductivity and pH were measured with a portable conductivity and  
165 pH meter. Water velocity ( $V$ ; cm/sec) was estimated using the method described by Craig (1987).  
166 Stream discharge ( $D$ ) was estimated as  $D = W \times D \times V$ , where  $W$  is stream width (m) and  $D$  is stream  
167 depth (m).

168

#### 169 *Data analysis*

170

171 To test whether environmental heterogeneity differed among regions, we used analysis of  
172 homogeneity of multivariate dispersions (hereafter PERMDISP). PERMDISP is a multivariate  
173 analogue of Levene's test for homogeneity of variances and the statistic (average distance of group  
174 members to the group centroid) is tested by permutation (Anderson 2006). In addition, we tested  
175 whether the environmental characteristics differed among the regions using a non-parametric  
176 multivariate analysis of variance (npMANOVA; Anderson 2001). Environmental data (except pH)  
177 were log-transformed before analysis. Data in percentages were transformed to arcsine square root.  
178 Afterward, we standardized all variables to mean zero and unit variance. The Euclidean distances  
179 based on standardized environmental data were used in the PERMDISP and npMANOVA.

180 Using the  $\log(x+1)$  abundance data we calculated the Bray–Curtis index to represent the  
181 dissimilarity in species composition among streams. When using assemblage dissimilarities, the  
182 average distance to group centroid (i.e. multivariate dispersion) is a measure of overall species  
183 turnover, or beta diversity in the region (Anderson, Ellingsen & McArdle 2006). Therefore, we used  
184 the PERMDISP to evaluate if beta diversity differed among the regions (i.e. differences in multivariate  
185 dispersions). Tukey's test was used for pairwise comparisons between regions. We also used  
186 npMANOVA to test whether species composition differed among regions.

187 Caddisflies migrate overland in the adult stages and, although in-stream migration through larval  
188 drift and upstream adult flight are well recognized for caddisflies (e.g. Petersen *et al.*, 2004), a matrix  
189 of Euclidean (overland) distances between sample sites provides adequate descriptors of dispersal  
190 routes and spatial patterns (Landeiro *et al.*, 2011). We analyzed the data using the raw data approach  
191 (Legendre *et al.*, 2005), through a partial Redundancy Analysis (pRDA), to evaluate the relative  
192 contributions of environmental and spatial variables to assemblage patterns. The spatial variables used  
193 in the pRDA were obtained by means of an eigenfunction analysis using Principal Coordinates of  
194 Neighbor Matrices (PCNM; Borcard & Legendre 2002). The PCNM approach uses a truncated matrix  
195 of geographic distances in a principal coordinate analysis to generate the spatial variables that  
196 represent spatial patterns ranging from broad (low order PCNMs) to fine scales (high order PCNMs).

197 After the creation of the spatial variables, we ran separate RDA models for environmental and spatial  
 198 variables and evaluated the significance of these models. In the cases where the full model was  
 199 statistically significant (as indicated by 9999 Monte Carlo permutations) we used a forward selection  
 200 procedure (Blanchet, Legendre & Borcard 2008a) to retain only the spatial and environmental  
 201 variables most related to caddisfly-assemblages to be used in the pRDA. By using pRDA, we obtained  
 202 the components of variance explained exclusively by the environmental variables [a], by the  
 203 environmental variables that are spatially structured [b], uniquely by the spatial variables [c] and the  
 204 unexplained variance [d]. We ran the pRDA and variance partitioning for data from all regions  
 205 combined, and separately for each region. Values of variance partitioning reported for pRDA are  
 206 adjusted  $R^2$  (Peres-Neto *et al.*, 2006). Someone might argue that rare species have great effects on  
 207 results of community analyses; therefore, we analyzed the data removing species that occurred in one  
 208 to ten streams to evaluate possible effect in the results.

209 In addition, we attempted to account for dispersal limitation of species classifying them as good  
 210 and poor dispersers. The optimal way to classify species as good or poor disperser is based on genetic  
 211 variation of population across geographic distance. However, this information is lacking for many  
 212 parts of the world and generally is done for a few species. Our solution was to classify species  
 213 exclusive to each region as poor dispersers and species occurring in all regions as good dispersers.  
 214 Then we also analyzed the data of each area considering the dispersal ability of species.

215 All analyses were done using the vegan (Oksanen *et al.*, 2011) and packfor (Dray, Legendre &  
 216 Blanchet 2009) libraries available for the R environment for statistical computing (R Development  
 217 Core Team 2011).

218

## 219 **Results**

220

221 We collected a total of 98 morphospecies (Appendix 1), 69 from DR, 85 from PF, and 69 from BD.  
 222 The average number of species per stream was 22.5 species, ranging from 2 to 39. On average, DR  
 223 streams had a higher number of species per stream than PF and BD (Table 1). The number of  
 224 exclusive species (considered poor dispersers) was highest at PF (18), and much lower in DR (8) and  
 225 BD (4). Fifty one species occurred in the three areas and were considered good dispersers.

226

### 227 *Environmental and biological differences among the regions*

228

229 Assemblage composition and environmental characteristics differed among regions (npMANOVA;  
 230  $F_{2,86} = 8.07$ ,  $F_{2,86} = 29.82$ , respectively,  $p < 0.001$ ). Environmental variability (Fig. 2A) also differed  
 231 among the regions (PERMDISP,  $F_{2,86} = 8.30$ ,  $p < 0.001$ ), where PF was the region with the highest  
 232 environmental variability (average distance to centroid), followed by BD and DR (Table 1). However,  
 233 PF and BD did not differ significantly in their environmental variability (Tukey post-hoc tests;  $p =$

234 0.91), indicating that these regions are equally heterogeneous, while DR, the region with lower  
 235 average distance to group centroid (i.e. less environmental heterogeneity), differed in environmental  
 236 conditions from PF (Tukey;  $p < 0.001$ ) and from BD (Tukey;  $p < 0.013$ ).

237 The average distance to group centroid based on assemblage dissimilarities (i.e. species turnover  
 238 or beta diversity) also differed among the regions (PERMDISP,  $F_{2,86} = 14.73$ ,  $p < 0.001$ , Fig. 2B). PF  
 239 had the highest average distance to group centroid, followed by BD and DR (Table 1). PF differed  
 240 significantly from BD and DR in average distance to group centroid (Tukey post-hoc test;  $p = 0.005$ ;  
 241  $p < 0.001$ ; respectively), but DR and BD did not differ significantly.

242

#### 243 *Variation in assemblage composition*

244

245 In line with the results provided by npMANOVA, Principal Coordinate Analysis showed a clear  
 246 pattern differentiating the caddisfly assemblage composition in PF streams from the other regions (Fig.  
 247 2B). For the pooled dataset, the full environmental and the full spatial models (i.e. including all  
 248 variables) were significant. The forward selection procedure retained 10 environmental variables and  
 249 eight spatial variables in the reduced models (Table 2). At this large scale (the three regions together),  
 250 24.3% of the variance was explained by the predictor variables. The exclusive fraction explained by  
 251 the environment [a] was 11% and the spatially structured environmental variation [b] accounted for  
 252 9.5%. There was a significant relationship with the spatial variables, but they accounted for only 3.8%  
 253 of the variance in assemblage composition. The caddisflies were sensitive to substrate type, and the  
 254 streams with large areas of bedrock and macrophytes were distinct from other streams in the same  
 255 region. The DR and BD streams differed in other environmental features (Fig. 2A), but these  
 256 differences were not important in predicting assemblage composition.

257 The full spatial model was not significant for data from individual regions analyzed separately  
 258 (i.e. there is no significant spatial patterns within regions). The full environmental model was  
 259 significant in all regions. At DR, three environmental variables (discharge, conductivity, and  
 260 percentage of stones) were retained in the reduced model, which explained 16.6% of the variance in  
 261 assemblage data. At BD two environmental variables (depth and temperature) were retained and  
 262 accounted for 14.3% of the variance in assemblage data. At PF, stream depth, width, temperature, and  
 263 conductivity were the variables retained, accounting for 14.6 % of the variance. The variance  
 264 explained exclusively by the environment was higher within regions (DR = 16.6%, BD = 14.3%, PF =  
 265 14.6) than for pooled data (11%). However, the fraction [a+b] (environment [a] plus spatially  
 266 structured environment [b]) was higher for the pooled data (Table 2). The removal of rare species did  
 267 not caused great changes in the overall results (Table S1).

268 The result of analysis including only common species (i.e. good dispersers) were similar to the  
 269 results above, in which environmental patterns are significant and lack of spatial patterns (Table 3). On



270 the other hand, exclusive species (i.e. poor dispersers) were related to environmental variables only in  
271 DR and spatial patterns were not significant in any region (Table 3).

272

## 273 Discussion

274

275 The three regions differed in environmental characteristics and caddisfly assemblages, and both beta-  
276 diversity and environmental variability were related to spatial extent. Thus, as predicted by Anderson  
277 (2006), there was a positive association between biological and environmental variability. This  
278 association was mediated by spatial extent, because the relative importance of abiotic factors changes  
279 across spatial scales (Jackson, Peres-Neto & Olden 2001). However, assemblage structure was not  
280 better explained by environmental and spatial variables in PF, the region with largest spatial extent and  
281 environmental heterogeneity. For all regions, assemblage structure was better explained by  
282 environmental descriptors than by spatial variables. When the analysis were done taking into account  
283 dispersal abilities of species the results were similar to those for the whole assemblage, although the  
284 environmental patterns were significant only in DR region for poor disperser assemblage. Therefore, it  
285 appears that, at the scales we studied, caddisfly species are more dependent on species sorting factors  
286 (i.e. relationship between the environmental gradients and species composition) than on dispersal  
287 processes. Similar results have been obtained for other freshwater organisms, such as  
288 macroinvertebrates (Mykrä *et al.*, 2007), snails (Hoverman *et al.*, 2011), and bacterial community  
289 composition (Van der Gucht *et al.*, 2007), as well as for terrestrial organisms, such as and plants  
290 (Gilbert & Lechowicz 2004; Ruokolainen *et al.*, 2007; Tuomisto, Ruokolainen & Yli-Halla 2003),  
291 highlighting the “power of species sorting” mechanisms (Leibold *et al.*, 2004; Van der Gucht *et al.*,  
292 2007).

293 Geomorphological and hydrological features may account for the differences in assemblage  
294 composition between regions in our study. For instance, most streams in the PF region contain  
295 bedrock and free stones as the main available substrates, whereas most BD and DR streams have  
296 sandy bottoms. Stream substrate has been recognized as an important factor controlling the  
297 distribution of caddisflies in other regions (Urbanic, Toman & Krusnik 2005; Wiggins 1996), as well  
298 as other aquatic insects (Boyero 2003; Buss *et al.*, 2004; Siqueira *et al.*, 2012). In our study, spatial  
299 patterning observed in the analysis using all data might be due to the lack of environmental variables  
300 describing regional patterns, while regional patterns were well described by the spatial variables  
301 generated with PCNM analysis. Indeed, the PCNMs retained for the pRDA model were those  
302 representing broad spatial scales (first order PCNMs; Borcard & Legendre 2002). However, given the  
303 lack of spatial patterns within areas, it is unlikely that the inclusion of spatially patterned variables  
304 would increase the coefficient of determination of our models.

305 The dispersal modes of caddisflies are dependent on their life cycle stage. Larval stages disperse  
306 by drifting downstream, mainly during spate events where the dispersal distance is dependent on spate

307 intensity. Adults are known to disperse upstream by lateral flight to other streams, varying among  
308 species. We expected to observe spatial patterns caused by dispersal limitation in PF area because its  
309 high spatial extent, however, spatial patterns were not observed.” The lack of spatial effects in the PF  
310 region might be related to the hydrological characteristics of that area. In PF, streams are wider, with  
311 more rapids and higher water velocity, factors that increase the intensity of disturbances during spate  
312 events. Spate events might carry organisms for long distances and obscure the relationship between  
313 niche factors and dispersal ability trait. At DR and BD, the streams are smaller and streams overflow  
314 laterally during spates, rather than rushing downstream (Espírito-Santo *et al.*, 2009; Pazin *et al.*, 2006).

315 Some streams sampled in PF are wider and have lower canopy cover than the other two regions,  
316 allowing high light availability and algal proliferation (Vannote *et al.*, 1980). Accordingly, most  
317 species found in PF feed on algae, such as six species of the family Hydroptilidae and three species in  
318 the genus *Smicridea* [Hydropsychidae] (Merritt & Cummins 1996; Oliveira & Froehlich 1996; Pes,  
319 Hamada & Soares 2008) that were found only in PF streams. *Atopsyche* sp. [Hydrobiosidae] and  
320 *Synoestropsis* sp. [Hydropsychidae] also found only in PF, are generally associated with bedrock  
321 substrates in wider streams in Central Amazonia.

322 Recognizing the role of niche and spatial effects in community composition is currently one of  
323 the main goals of several branches of ecology. According to Logue *et al.*, (2011) “species-sorting is  
324 the only paradigm that can clearly be distinguished, metacommunities characterized by species-sorting  
325 processes can, however, be further scrutinized for high and limited dispersal; the origin of spatial  
326 variation can be difficult to assess”. Variation partitioning is affected by the lack of important spatially  
327 structured environmental predictors, which causes an overestimation of the pure spatial component [c],  
328 precluding its use as an absolute indicator of neutral processes (Laliberté *et al.*, 2009).

329 We used only environmental variables describing the variation at local scale (stream reaches),  
330 and inclusion of regional variables could improve understanding of species distributions and increase  
331 the percentage of variance explained (Roque *et al.*, 2010). Galbraith *et al.* (2008) found that 22.4% and  
332 24.2% of the explained variance in caddisfly species distribution in Oklahoma and Arkansas streams  
333 was accounted for exclusively by regional environmental variables and by regional spatially-structured  
334 variables (shared component), respectively. However, the spatial variables generated with PCNM are  
335 expected to form clumps similar to those formed by regional environmental variables. The high  
336 variance explained exclusively by regional variables in the study of Galbraith *et al.* (2008) might be  
337 due the use of trend-surface analysis, a technique less flexible than PCNM to recover spatial patterns  
338 at local scales (Borcard & Legendre 2002; Griffith & Peres-Neto 2006). The lack of spatial component  
339 observed within regions indicates that inclusion of regional variables would probably not help to  
340 explain caddisfly species distribution within regions. However, the stronger spatial patterns for the  
341 data pooled from the three regions, indicate that inclusion of regional properties, such as drainage  
342 basins or geological formations, may be an appropriate strategy where potential environmental  
343 impacts cross regional boundaries.

344           The percentage of variance in species composition explained by environmental variables did not  
345 increased with the increase in environmental heterogeneity, but was similarly predicted by species  
346 sorting mechanisms (sensu Leibold *et al.*, 2004). However, spatial effects, or dispersal limitation, were  
347 not observed even in PF, the area with high spatial extent. This was unexpected mainly for poor  
348 disperser assemblage, considering that PF covered a much larger area than the other regions. The  
349 strength of association between geographical distance and assemblage dissimilarity depends on the  
350 grain size and on the spatial extent. In general, large spatial extents should produce stronger  
351 relationships between assemblage dissimilarity and geographical distance (Nekola & White 1999).  
352 Brown & Swan (2010) and Heino *et al.* (2011), in studies carried out at a similar spatial extent (~100  
353 km ), observed low spatial effects and attributed their findings to the possibility that the study regions  
354 were too small in spatial extent for the detection of strong dispersal limitation. Thompson &  
355 Townsend (2006) and Maloney & Munguia (2011) also analysed data on macroinvertebrates at similar  
356 spatial extent, and found higher spatial effects, but Astorga *et al.*, (2012) found that freshwater  
357 organisms are more controlled by environmental factors than by limited dispersal over distances up to  
358 1100 km in Finland, though the species with low dispersal abilities were more related to spatial  
359 distance.

360           A possible reason for these different results is the differences in the dispersal ability of the fauna  
361 sampled in each region. In addition, there are other species traits, such as life-history and dispersal  
362 capacity, that should be accounted for in attempts to disentangle niche versus dispersal processes.  
363 Information on such traits is generally lacking for Amazonian caddisflies, and studies of genetic  
364 variation of populations might give the information on dispersal abilities. Another possible  
365 explanation is that these studies focused on the entire community rather than on a small subset of the  
366 freshwater community, for example, subsets of species with similar dispersal abilities (Brown *et al.*,  
367 2011). Recognizing the role of niche and spatial effects in community composition is currently one of  
368 the main goals of several branches of ecology. There are several analytical issues that need further  
369 development, but more knowledge of species traits and genetic variability among populations could  
370 help to disentangle spatial and niche processes. Such species traits should ideally be incorporated into  
371 metacommunity analysis, however, this kind of information is lacking for many parts of the world,  
372 including the Amazon. Empirical studies of dispersal would provide the information necessary to  
373 adequately include dispersal processes in stream metacommunity ecology (Brown *et al.*, 2011).  
374 Studying dispersal abilities through genetic measures might be the solution, but it is quite difficult and  
375 expensive, generally done with a few number of species (Miller, Blinn & Keim 2002; Wilcock *et al.*,  
376 2007).

377

378           *Conclusion*

379

380 Before a particular taxon can be used as an environmental indicator it is important to evaluate  
 381 the effects of spatial scale and environmental heterogeneity on differences among assemblages. The  
 382 movement of aquatic insects via different dispersal routes has received considerable attention (Bilton  
 383 *et al.*, 2001; Collier & Smith 1998). Downstream drift, upstream flight, and between-stream  
 384 migrations through lateral migrations (Miller *et al.*, 2002) increase genetic homogeneity and similarity  
 385 of species composition among streams and stream reaches (i.e. decrease beta diversity). In the absence  
 386 of environmental effects, dispersal ability of species is a major control of the turnover. Our results  
 387 show that community composition was related to spatial processes when all sites are analyzed jointly.  
 388 However, when we analyzed the data from each region separately, community composition were  
 389 unrelated to spatial processes (even in PF that have spatial extent of more than 110 km, similar to the  
 390 longer distance of the pooled data). Even when there were significant effects of spatial variables,  
 391 environmental properties explained much more variation than spatial one. In temperate regions,  
 392 caddisflies are considered to be useful indicators for biomonitoring due their sensitivity to aquatic  
 393 conditions (Rosenberg & Resh 1993). In view of the higher environmental control (i.e. species sorting)  
 394 observed, our results support the use of caddisflies as an indicator of water quality and environmental  
 395 conditions, even in megadiverse tropical regions such as the Amazon.

396

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406

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- 585
- 586

587 **Table 1:** Results for the analysis of homogeneity of multivariate dispersions. Shown are the mean  
 588 ( $\pm$ SD) distances to the group centroid. Last row shows the average number of species per stream at  
 589 each region.

	DR	BD	PF
Spatial extent (decimal degress)	0.03 $\pm$ 0.01	0.10 $\pm$ 0.07	0.19 $\pm$ 0.17
Environmental dispersion	2.15 $\pm$ 0.86	2.96 $\pm$ 1.39	3.08 $\pm$ 0.91
Assemblage composition dispersion	0.45 $\pm$ 0.05	0.49 $\pm$ 0.07	0.56 $\pm$ 0.08
Mean number of species per stream	24.6 $\pm$ 6.0	20.1 $\pm$ 7.1	21.6 $\pm$ 6.9

590

591 **Table 2:** Variation partitioning results based on partial RDA analysis. The final pRDA model using  
 592 only the variables retained with the forward selection procedure is shown. Numbers for spatial  
 593 variables indicate their order, where lower orders represent broad scale patterns. P spat and P env give  
 594 the significance for the full spatial and full environmental models (i.e. using all variables available).  
 595 The spatial and environmental variables are shown in the order they were retained in the forward  
 596 selection procedure. [a] = environmental fraction; [b] = shared fraction; [c] = spatial fraction. The  
 597 significance values for the environmental and spatial fractions are given. The full spatial models for  
 598 DR, BD, and PF are not significant, therefore, the forward selection was not done.

Datase t	Full model significance		Variables retained		Fractions		
	P env	P spat	Spatial	Environmental	[a]	[b]	[c]
All	0.001	0.001	1,2,6,9, 3,18,7,24	Width, sand, depth, litter, temperature, pH, stone, conductivity, macrophytes, bedrock	0.11*	0.09 5	0.038*
DR	0.001	0.34	-	Discharge, conductivity, stone	0.166*	-	-
BD	0.008	0.1	-	Depth, temperature	0.143*	-	-
PF	0.001	0.56	-	Width, depth, temperature, conductivity	0.146*	-	-

599 \* p < 0.001; - The forward selection was not done

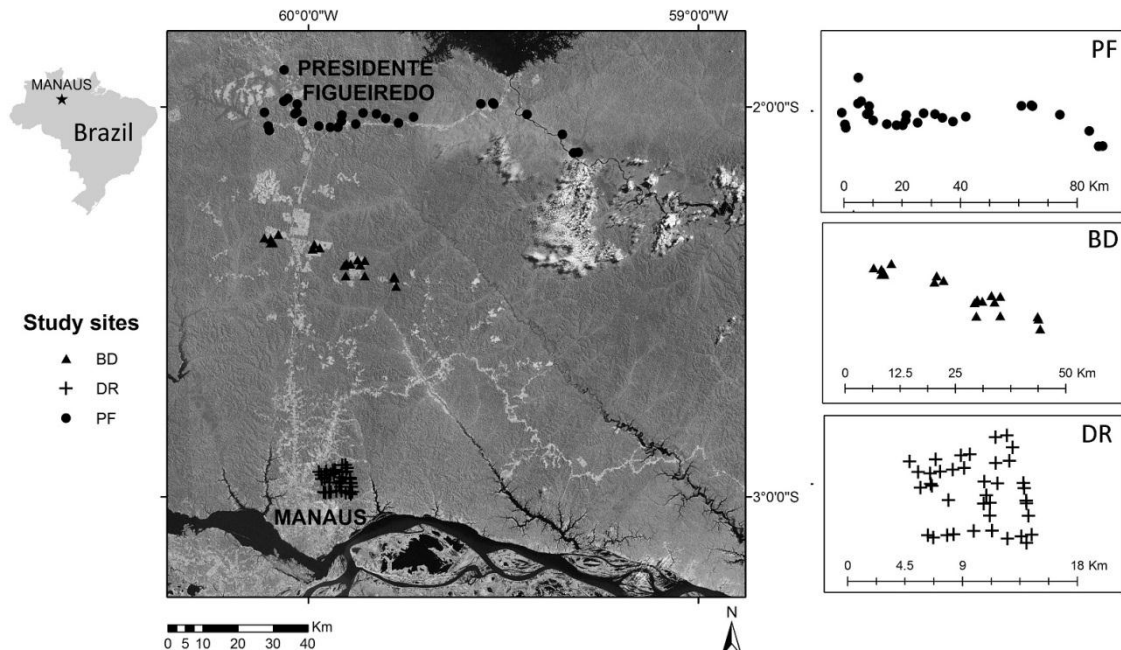
600

601 **Table 3:** Variation partitioning analysis of species tables divided into exclusive species and species  
 602 common to all regions. Results based on partial RDA analysis. The final pRDA model using only the  
 603 variables retained with the forward selection procedure is shown. P spat and P env give the  
 604 significance for the full spatial and full environmental models (i.e. using all variables available). The  
 605 spatial and environmental variables are shown in the order they were retained in the forward selection  
 606 procedure. [a] = environmental fraction; [b] = shared fraction; [c] = spatial fraction. The significance  
 607 values for the environmental and spatial fractions are given.

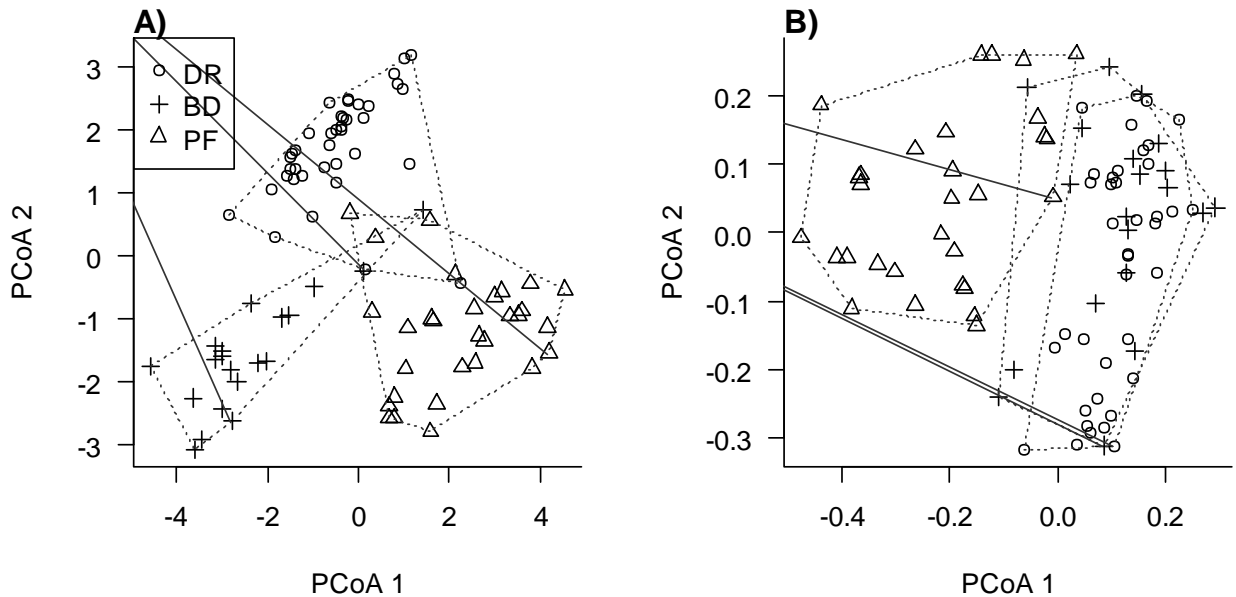
Dataset	Region	Full model significance		Variables retained		Fractions		
		P env	P spat	Spatial	Environmental	[a]	[b]	[c]
Exclusive species	DR	0.040	0.235	-	Width, conductivity	0.227*	-	-
	BD	0.161	0.362	-	-	-	-	-
	PF	0.231	0.626	-	-	-	-	-
Common Species	DR	0.001	0.370	-	Discharge, conductivity	0.160*	-	-
	BD	0.031	0.198	-	Depth, temperature	0.178*	-	-
	PF	0.002	0.511	-	Depth, width, sand	0.160*	-	-

608 \*p < 0.001; - The forward selection was not done

609



610  
 611 **Figure 1:** Map of Brazil and geographical location of sampling sites. Ducke Reserve (DR), Presidente  
 612 Figueiredo (PF), and the reserves of the Biological Dynamics of Forest Fragments Project (BD).



613  
 614 **Figure 2:** Principal Coordinate Analysis (PCoA), used in the PERMDISP procedure, illustrating the  
 615 differences in A) environmental conditions and B) assemblage composition. The assemblage  
 616 composition observed in PF differed statistically from those of DR and BD. The environmental  
 617 dissimilarity matrix used in the PCoA was calculated using the Euclidean distance on standardized  
 618 environmental data. The assemblage dissimilarity matrix used in the PCoA was calculated on

619 abundance data ( $x$ ) transformed to  $\log(x + 1)$ . Polygons delimitate samples from the same sample  
620 region.  
621  
622

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Victor Lemes Landeiro V.L., Waldez F., Menin M. 2011. Spatial and environmental factors controlling frog assemblages with aquatic and terrestrial reproduction. Submetido a *Biotropica*

1 LRH: Landeiro *et al.*

2 RRH: Factors Controlling Amazonian Frog Assemblages

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10 Spatial and Environmental Factors Controlling Frog Assemblages with Aquatic and  
11 Terrestrial Reproduction

12

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1 **ABSTRACT:**

2 Anurans are one of the most endangered biological groups, and their sensitivity to environmental  
3 changes makes them a useful tool for biomonitoring programs. Species with close relationships to  
4 environmental variables are those more threatened by environmental changes. However, species  
5 without environmental associations that show patterns more related to spatial factors, such as dispersal  
6 limitation, might be less affected by environmental changes and less threatened by global warming.  
7 We evaluated the distribution of anurans in 72 plots in central Amazonia, relating them to  
8 environmental factors and other factors that induce spatial clumping. We predicted that species with  
9 aquatic reproduction would be more dependent on environmental conditions than species with  
10 terrestrial reproduction, which we predicted to be more affected by factors that induce spatial patterns  
11 unrelated to known environmental predictors. Combining all species in the same analysis, the spatial  
12 pattern was stronger than that induced by the environmental factors included in the analysis. However,  
13 the observed pattern was highly dependent on the reproductive mode of species. Species with aquatic  
14 reproduction were more related to the environmental variables, while species with terrestrial  
15 reproduction showed strong spatial patterns. These findings are relevant to development of  
16 conservation strategies and biological monitoring programs. Because species strongly influenced by  
17 environmental controls may be more sensitive to specific threats, such as conversion of riparian areas,  
18 whereas species that do not have restrictive needs for reproduction, but which show strong  
19 associations with forests could be better indicators of general environmental degradation associated  
20 with climate change or selective timber harvesting.

21 *Key words:* anuran assemblages; Central Amazon; dispersal limitation; Neotropics; niche control;  
22 spatial patterns; variance partitioning, redundancy analysis

23

24



1 **RESUMO:**

2 Anuros são um dos grupos biológicos mais ameaçados e sua sensibilidade às mudanças ambientais os  
3 torna uma ferramenta útil para programas de biomonitoramento. Espécies com distribuição  
4 relacionadas às variáveis ambientais são as mais ameaçadas por mudanças ambientais. Entretanto, as  
5 espécies sem associações ambientais e que mostram padrões mais relacionados a fatores espaciais,  
6 como dispersão limitada, podem ser menos afetadas por mudanças ambientais e menos ameaçadas  
7 pelo aquecimento global. Avaliamos a distribuição de anuros em 72 parcelas na Amazônia central,  
8 relacionando-os a fatores ambientais e a fatores que induzem agregação espacial. Previmos que  
9 espécies com reprodução aquática seriam mais dependentes das condições ambientais que espécies  
10 com reprodução terrestre, que previmos ser mais afetadas por fatores que induzem padrões espaciais  
11 alheios aos fatores ambientais. Combinando todas espécies na mesma análise, o padrão espacial foi  
12 mais forte do que o produzido pelas variáveis ambientais incluídas nas análises. Entretanto, o padrão  
13 observado depende muito do modo reprodutivo das espécies. Espécies com reprodução aquática foram  
14 relacionadas com as variáveis ambientais, enquanto espécies com reprodução terrestre mostraram  
15 padrões espaciais. Estes resultados são relevantes para o desenvolvimento de estratégias de  
16 conservação e para os programas de controle biológico. Pois as espécies fortemente influenciadas pelo  
17 ambiente podem ser mais sensíveis a ameaças específicas, como a conversão de matas ciliares, ao  
18 passo que espécies sem necessidades ambientais restritivas para a reprodução, mas que mostram  
19 associações fortes com as florestas, podem ser melhores indicadores de degradação ambiental, em  
20 geral associadas a alterações climáticas ou a extração seletiva de madeira.  
21

1

2 AMPHIBIAN SPECIES ARE THREATENED BY MANY FACTORS INCLUDING habitat loss, habitat  
3 fragmentation, diseases and pollution throughout the Neotropics (Loyola *et al.*, 2008; AmphibiaWeb,  
4 2011). About 32 percent of amphibian species are threatened or extinct (IUCN, 2010). Amphibian  
5 species are considered sensitive to environmental changes (e.g. Vallan, 2000), generally  
6 associated to their strong endemism and physiological constraints. Climate change is a major threat to  
7 amphibian biodiversity (Hero *et al.*, 2006) and management actions are urgent (Shoo *et al.*, 2011).

8         The distribution of anurans is known to be affected by many biotic and abiotic factors, such as  
9 availability of breeding habitats (Zimmerman & Bierregaard, 1986), litter cover (Heinen, 1992),  
10 vegetation structure (Pearman, 1997), and structural diversity of habitats (Ernst *et al.*, 2006). In  
11 tropical rainforests, topography, soil, leaf litter depth and vegetation are considered the major factors  
12 affecting anuran species distribution (Lieberman, 1986; Fauth *et al.*, 1989; Allmon, 1991; Giaretta *et*  
13 *al.*, 1999; Vonesh, 2001). However, anuran species with different developmental modes might respond  
14 to habitat disturbance in different ways (Loyola *et al.*, 2008). In Amazon forests, the abundance of  
15 terrestrial breeding species is affected by topography and soil features (Menin *et al.*, 2007), whereas  
16 the abundance and occurrence of aquatic breeding species are affected mainly by the distance from  
17 streams (Menin *et al.*, 2011).

18         In general, as in most studies with other taxa, only environmental constraints have been  
19 evaluated in analysis of anuran species distribution. However, spatial factors related to dispersal  
20 ability have been evaluated for a few species (Jones *et al.*, 2006). Neutral theory of biogeography and  
21 biodiversity posits that the patterns of abundance and distribution of species can be understood by  
22 models that consider individuals as if they were equivalent in birth, death and dispersal rates, and in  
23 their competitive abilities. Therefore, species spatial distribution patterns, such as the distance decay  
24 of similarity in ecological communities, would be the result of stochasticity in dispersal limitation  
25 rather than to species niche properties (Hubbell, 2001; Rosindell *et al.*, 2011). Therefore, spatial  
26 aggregations may occur for reasons other than direct environmental influences. Many authors have  
27 included spatial factors in their models, trying to tease apart the effects of niche properties from those  
28 of spatial patterns not directly related to the measured environmental factors through variance  
29 partitioning techniques (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006). It is important to emphasize that  
30 neutral theory tries to explain why there is so little variation among communities at local scales, while  
31 studies of variance partitioning focus only on that part of the community that varies spatially.  
32 Although many recent studies on metacommunity dynamics have investigated the role of spatial  
33 processes in light of the predictions given by the neutral theory (Linares-Palomino & Kessler, 2009;  
34 Bonada *et al.*, 2011), few have done that with a special focus on conservation biology.

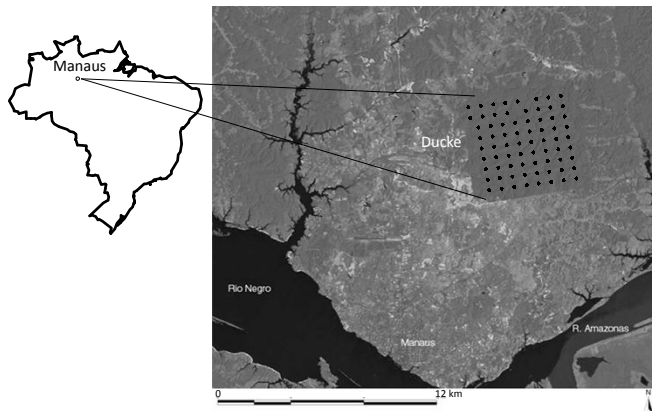
1 Here, we evaluate the environmental and spatial processes controlling anuran species  
 2 assemblages at 72 plots in an Amazon forest. Besides estimating the relative role of these processes in  
 3 controlling overall assemblages we separated the species with aquatic reproduction from those with  
 4 terrestrial reproduction to evaluate whether they respond to the same factors. Because anurans are very  
 5 sensitive to environmental changes we hypothesized that the environmental control would be higher  
 6 than the spatial control, and that species with different types of reproduction would differ in their  
 7 relationships with environmental and spatial variables. More specifically, we predicted that species  
 8 with terrestrial reproduction would be more affected by spatial constraints, because their distribution is  
 9 more restricted by dispersal limitation than by dependence on water resources, and that species with  
 10 aquatic reproduction would be more controlled by niche factors associated with water availability.

## 11

## 12 METHODS

13

14 **STUDY AREA.**—Our study was undertaken in the Reserva Florestal Adolpho Ducke (RFAD, 02°55'  
 15 and 03°01'S, 59°53' and 59°59'W), adjacent to the city of Manaus, Amazonas state, Brazil (Fig. 1).  
 16 The reserve covers 10,000 ha of *terra firme* (non-flooded) rainforest, a well-drained forest not subject  
 17 to seasonal inundation. The forest is characterized by a 30-37 m tall closed canopy, with emergents  
 18 growing to 40-45 m (Ribeiro *et al.*, 1999). The understory contains abundant sessile palms  
 19 (*Astrocaryum* spp. and *Attalea* spp.; Ribeiro *et al.* 1999). The climate is characterized by a rainy  
 20 season from November to May and a dry season during the rest of the year (Marques Filho *et al.*,  
 21 1981). Mean annual temperature is approximately 26° C (Marques Filho *et al.*, 1981) and mean annual  
 22 rainfall between 1985 and 2004 was 2489 mm.



23

24 **FIGURE 1:** Location of Ducke Reserve adjacent to the city of Manaus in the Brazilian Amazon.  
 25 Points indicate 1 km equidistant sample plots.

1 BIOLOGICAL DATA.—We sampled anurans during three diurnal samples (November–December  
2 2002, February–April 2003 and January–February 2004) and five nocturnal samples (November–  
3 December 2002, March–May 2003, November–December 2003, January–March 2004 and April–May  
4 2004). Data were collected in 72 plots systematically distributed over a 64-km<sup>2</sup> grid formed by 8-km  
5 long trails (Fig 1, see also Menin *et al.*, 2007; 2008 for more information). Each plot was at least 1 km  
6 distant from any other. Plots were 250 m long and positioned to follow altitudinal contour lines, and  
7 thus minimized altitudinal and soil variation within each plot (Magnusson *et al.*, 2005a). All plots  
8 were at least 1 km distant from the reserve edges. Surveys occurred only during the rainy season  
9 (November to May).

10 Diurnal surveys lasted about 2 h per plot and were conducted between 08:00 and 16:00 h by two  
11 people walking along a 250 m x 1 m plot. Observers visually scanned and gently turned over the leaf-  
12 litter, detecting individuals by visual encounter. The two first surveys were conducted by the same  
13 person (FW and field assistant), but in the third survey, a member was changed (two field assistants  
14 with a lot of field experience). Nocturnal samples were carried out by using simultaneous visual  
15 encounter surveys and auditory sampling (Heyer *et al.*, 1994). We sampled each plot for about one  
16 hour between 18:30 and 22:00 h. The two observers stopped every 5 m and recorded the number of  
17 calling individuals of each species and searched the litter and vegetation for anurans. All individuals  
18 located visually or by their call within 20 m of the center line of the plot were recorded. All nocturnal  
19 surveys were conducted by the same two people (MM and field assistant). We produced separate  
20 datasets of abundance of anurans for diurnal and nocturnal surveys, then pooled the datasets from the  
21 two periods to form a single dataset. We also separated the species into those with aquatic  
22 reproduction and those with terrestrial reproduction, comprising thus tree datasets: all species, species  
23 with aquatic reproduction, and species with terrestrial reproduction.

24  
25 ENVIRONMENTAL AND SPATIAL PREDICTORS—We included the following environmental  
26 variables in our analysis: average slope across the plot, percentage soil clay content, number of trees in  
27 the plot, litter depth, distance to the nearest stream, and soil pH (see Menin *et al.*, 2007 for more  
28 details). All data used in this work is freely available at <http://ppbio.inpa.gov.br>, where detailed  
29 metadata describing each data set can be found, including more detailed information on sample  
30 methods and measurements.

31 Spatial variables were generated through a technique called Principal Coordinates of Neighbor  
32 Matrices (Borcard & Legendre, 2002). PCNM was based on a Euclidean distance matrix between  
33 sampling plots in which this distance matrix is submitted to a Principal Coordinate Analysis (PCoA)  
34 and the eigenvectors with positive eigenvalues are extracted. These eigenvectors (usually called  
35 PCNMs or spatial filters; Diniz-Filho & Bini, 2005; Griffith & Peres-Neto, 2006) represent distinct

1 spatial patterns that are mutually orthogonal – they were used as our spatial predictor variables.  
2 PCNMs have been used as proxies representing spatial structures generated by environmental  
3 autocorrelation and biotic processes, such as dispersal, in studies on metacommunity dynamics  
4 (Nabout *et al.*, 2009; Landeiro *et al.*, 2011). PCNMs with high eigenvalues (i.e., PCNMs of low order)  
5 represent broad-scale patterns of relationships among sampling sites, whereas those associated with  
6 low eigenvalues (i.e., PCNMs of high order) represent fine-scale patterns.

7  
8 DATA ANALYSIS.—The environmental data was transformed to  $\log(x + 1)$ , except pH, and  
9 standardized to zero mean and unit variance before analysis. To evaluate the effects of environmental  
10 and spatial variables on the distribution of anuran species we used partial Redundancy Analysis  
11 (Peres-Neto & Legendre, 2010). The biotic dataset was transformed using the Hellinger  
12 transformation, following recommendations for this kind of analysis (e.g. Peres-Neto & Legendre,  
13 2010). The spatial variables were generated using Principal Coordinates of Neighbor Matrices  
14 (Borcard & Legendre, 2002). We used a forward selection procedure (Blanchet *et al.*, 2008a) based on  
15 10,000 permutations to retain only the most important environmental and spatial variables affecting  
16 the distribution of anuran assemblages.

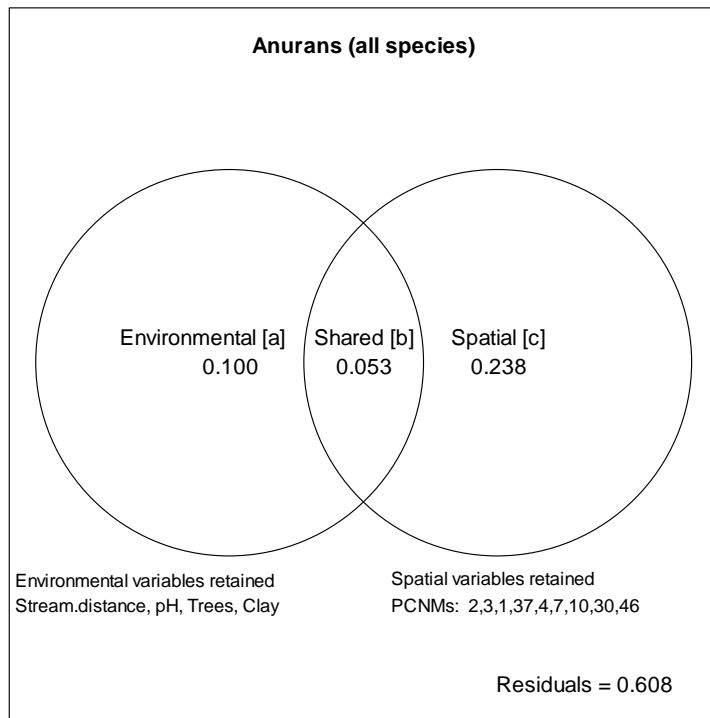
17 Because models with a high number of variables (*i.e.* more variables retained in the forward  
18 selection procedure) has, artefactually, higher explanatory power than models with few variables,  
19 results of partial Redundancy Analysis were based on adjusted fractions of variation (Peres-Neto *et al.*,  
20 2006). The total variation in the anuran assemblages was divided into four fractions: variation  
21 explained exclusively by environmental variables [a], explained variation that is shared between  
22 environmental and spatial variables [b], variation explained exclusively by spatial variables [c], and  
23 the unexplained variance [d]. All analysis were run using R functions (R Development Core Team,  
24 2011) available in vegan (Oksanen *et al.*, 2011) and packfor (Dray *et al.*, 2009) R libraries.

## 25 26 **RESULTS**

27  
28 We collected 29 species of anurans, of which 20 species have aquatic reproduction and 9 have  
29 terrestrial reproduction. Seven species with aquatic reproduction were found only sporadically (*i.e.* in  
30 less than four sites) and were removed from the analysis. Therefore, we analyzed only 13 species with  
31 aquatic reproduction.

32 About 39 percent of the variation of anuran assemblages was explained by the environmental  
33 and spatial variables (Fig. 2). Both environmental [a] and spatial [c] fractions were significant  
34 ( $p < 0.001$ ). The spatial component was higher than the environmental component (23.8% and 10%  
35 respectively) and the shared component was 5.3 percent. The environmental variables related to

1 anuran assemblages were distance to the nearest stream, soil pH, number of trees in the plot, and soil  
 2 clay content. Nine spatial variables were retained for the partial RDA model.



3

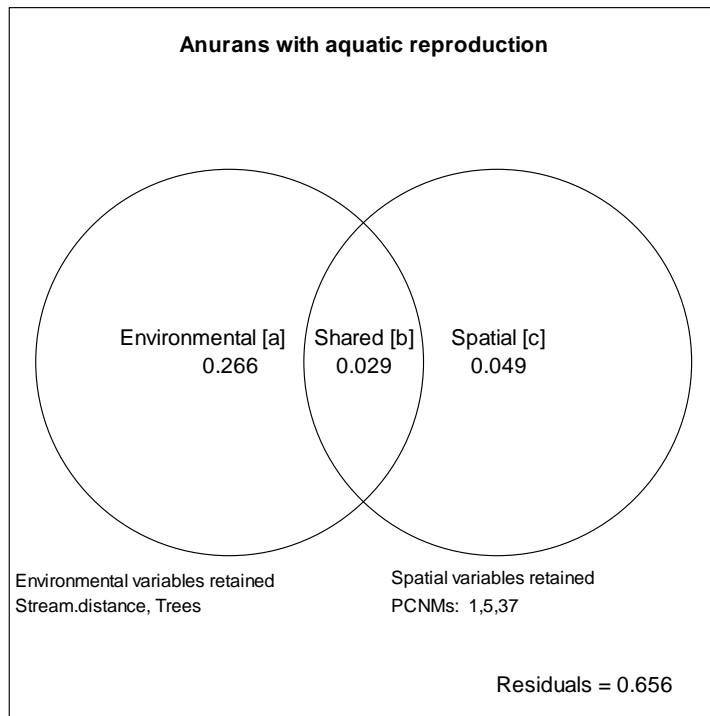
4 **FIGURE 2:** Variation partitioning results for anuran assemblages (all species). Results based in  
 5 a partial Redundancy Analysis and values shown are adjusted  $R^2$ .

6

7 About 34 percent of the variation in the assemblage of anurans with aquatic reproduction was  
 8 explained by both set of predictors (Fig. 3). Both environmental [a] and spatial [c] fractions were  
 9 significant ( $p < 0.001$ ). Most of the variation (26.6%) in the assemblages of anurans with aquatic  
 10 reproduction was explained exclusively by environmental variables (distance to the nearest stream and  
 11 number of trees). Only three spatial variables were retained and accounted for only 4.9 percent of the  
 12 variation. The shared variation was equal to 2.9 percent.

13

14 About 40 percent of the variation in the assemblage of anurans with terrestrial reproduction was  
 15 explained by the spatial and environmental variables (Fig. 4). Environmental [a] and spatial [c]  
 16 fractions were significant ( $p < 0.001$ ). In contrast to the anurans with aquatic reproduction, the variation  
 17 in the assemblages of anurans with terrestrial reproduction was better explained by spatial variables  
 18 (eight spatial variables retained), accounting for 30.3 percent of the variation. The two environmental  
 19 variables retained (soil clay content and pH) accounted for only 5.4 percent of the variation and the  
 20 shared fraction was equal to 3.6 percent.



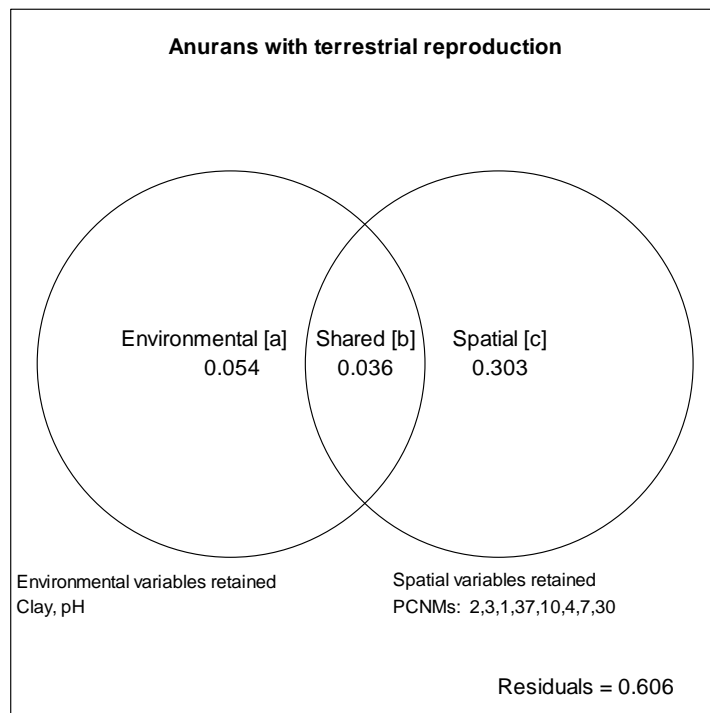
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FIGURE 3: Variation partitioning results for assemblages of anurans with aquatic reproduction.

3

Results based in a partial Redundancy Analysis. Values shown are adjusted  $R^2$ .



4

5

FIGURE 4: Variation partitioning results for assemblages of anurans with terrestrial

6

reproduction. Results based in a partial Redundancy Analysis. Values shown are adjusted  $R^2$ .

7

## 1 DISCUSSION

2  
3 Our models explained about 35 percent of the between-plot variation in anuran assemblages. When all  
4 species were pooled, the spatial patterns were stronger than the effects of the environmental variables  
5 included in the analyses. However, the pattern was highly dependent on the reproductive mode of  
6 species. Species with aquatic reproduction were more associated with variation in environmental  
7 factors (*i.e.* probable niche control), whereas species with terrestrial reproduction showed spatial  
8 patterns that were not associated with the environmental variables included in the analyses.

9 The environmental patterns are easily interpreted because they are associated with  
10 environmental variables included in the analyses. However, spatial patterns may arise from two main  
11 sources. Some spatially structured environmental variables, important for anurans, may not have been  
12 measured and, consequently, were not included in the models (Diniz-Filho *et al.*, 2003; Landeiro &  
13 Magnusson, 2011). That is, in the absence of an important environmental variable in the analysis, the  
14 variation in species distribution due to that environmental variable will be attributed exclusively to  
15 spatial variables. Another possibility is that species are really not dependent on environmental  
16 constraints and the observed spatial patterns are due to dispersal limitation or other endogenous  
17 process such as differential reproduction (Fortin & Dale, 2005; Landeiro *et al.*, 2011). Here, we  
18 measured environmental variables commonly found to affect anuran species distribution, so we  
19 believe that the spatial pattern observed in species with terrestrial reproduction is more related to  
20 intrinsic dispersal processes than to the lack of important environmental variables.

21 In the Neotropical region, the main environmental characteristics that have been found to affect  
22 anuran distributions are vegetation structure, leaf litter depth, topography and soil features, such as pH  
23 and clay content. Some studies reported positive relationships between litter layer development and  
24 species richness or abundance of many species (Fauth *et al.*, 1989; Giaretta *et al.*, 1999; Vonesh,  
25 2001), probably related to a greater number of microhabitats (Fauth *et al.*, 1989) or refuges  
26 (Lieberman, 1986), whereas other studies find no such effect on the anuran litter community (Allmon,  
27 1991; Menin *et al.*, 2007). Here, we found no relationship between litter depth and anuran  
28 assemblages in the Ducke Reserve. Topographic characteristics, such as slope, are related to the  
29 abundance or occurrence of three of the anuran species with terrestrial reproduction we found in this  
30 study (Menin *et al.*, 2007). However, this does not create a general pattern for the whole terrestrial-  
31 breeding assemblage.

32 In our study, terrestrial breeding anurans were related to soil features. Soil pH also influenced  
33 the abundance of terrestrially breeding anuran species when each species was analyzed independently  
34 (Menin *et al.*, 2007). The early developmental stages of some species of amphibians can be severely  
35 affected by low pH because it affects ionic regulation of embryos (Pierce, 1985). Therefore, although



1 relationships with pH were not detected for all species when the analysis was run on each species  
2 independently, it appears that the distributions of terrestrially anurans are dependent on natural  
3 variation in soil pH. Effects of soil clay content in the abundance of some anuran species has been  
4 detected in Costa Rica (Watling, 2005), Australia (Woinarski *et al.*, 1999) and Amazonia (Menin *et*  
5 *al.*, 2007). Soils with high clay content are found distant from streams margins (riparian zones) and  
6 retain high water and moisture, allowing the reproduction of species in terrestrial nests. On the other  
7 hand, aquatic breeding anurans were affected by distance from streams and number of trees.

8 Vegetation structure is generally assumed to be an important characteristic affecting riparian  
9 anuran species (Parris & McCarthy, 1999). The density of trees influences species richness and  
10 composition of terrestrial and arboreal anuran species in some tropical sites (Pearman, 1997; Parris &  
11 McCarthy, 1999; Ernst & Rödel, 2005; Ernst, 2006; Keller *et al.*, 2009). In Central Amazonia, a high  
12 density of small trees was found in bottomlands (Castilho *et al.*, 2006). Distance to the nearest stream,  
13 soil clay content and the slope of the terrain in the plot is related to the water availability, and sites  
14 near streams with low clay content and flatter terrains (through pond formation) can provide more  
15 oviposition sites for anurans (Keller *et al.*, 2009; Menin *et al.*, 2011).

16 The conservation of anuran species can be highly dependent on life-history traits, such as the  
17 type of reproduction (Loyola *et al.*, 2008). The inclusion of anuran developmental modes in analyses  
18 aimed to choose priority areas for anuran conservation results in a clear gain in comprehensiveness of  
19 the selection process. When compared to usual analyses that do not consider these life-history traits,  
20 the conservation of species that require an aquatic habitat for their reproduction is improved.  
21 Otherwise, priority area setting exercises tend to favor species with terrestrial development (Loyola *et*  
22 *al.*, 2008).

23 As the severity and frequency of droughts affecting the Amazon region are expected to increase  
24 (Lewis *et al.*, 2011), associated with other potential environmental changes caused by global warming,  
25 the effects on anuran species might be severe for species dependent on aquatic habitats to reproduce,  
26 and for species that rely on humid soils for terrestrial reproduction. Most terrestrial-breeding frogs  
27 occur in humid areas (Duellman, 1995; 1999). Our results showed that species with aquatic  
28 reproduction are highly related to environmental conditions, mainly the distance to the nearest water  
29 source, indicating that their occupation in the landscape will be affected by changes in the availability  
30 of water sources. In addition, little of the beta diversity observed in terrestrially breeding frogs  
31 assemblages is associated with habitat variation (Menin *et al.*, 2007).

32 Zimmerman & Bierregaard (1986) suggested that frogs are not good indicator species for  
33 fragmentation studies because their distributions are largely determined by the presence of water  
34 bodies suitable for reproduction. However, that generalization does not apply to the terrestrially  
35 breeding species (Menin *et al.*, 2007). The effects of climate change are likely to be different for

1 aquatic-breeding and terrestrial-breeding frogs. Whereas the distribution of aquatic-breeding frogs  
 2 across the landscape are likely to be influenced by changes in the distribution of water bodies, aquatic-  
 3 breeding species are not likely to become locally extinct until almost all water bodies are lost, and they  
 4 could potentially be maintained by artificial water sources. This probably explains why aquatic-  
 5 breeding species are common in the driest areas of Amazonia (Duellman, 1988). In contrast, there are  
 6 few or no terrestrial-breeding species in the drier parts of Amazonia, suggesting that their limited  
 7 dispersal abilities associated with requirements for humid climates might result in their being pushed  
 8 completely off the landscape. Considerations about vulnerability of different species will have to take  
 9 into account differences in the requirements of the guilds and the scale of the changes.

10 These findings are relevant to development of conservation strategies and biological monitoring  
 11 programs, because species strongly influenced by environmental controls may be more sensitive to  
 12 specific threats, such as conversion of riparian areas. On the other hand, species that do not have  
 13 restrictive needs for reproduction, but that show strong associations with humid forests could be better  
 14 indicators of general environmental degradation associated with climate change or activities such as  
 15 selective timber harvesting.

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4               analysis of taxonomic surrogacy, taxonomic sufficiency and numerical  
5                               resolution in a megadiverse region  
6

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25 **ABSTRACT**

26

27         The need for biodiversity conservation is increasing at a rate much faster than the acquirement  
28 of knowledge on biodiversity, such as descriptions of new species and mapping species distribution.  
29 As global changes are winning the race against the acquisition of knowledge, many researchers resort  
30 to the use of surrogate groups to aid in conservation decisions. Reductions in taxonomic and numeric  
31 resolution are also desirable, because they could speed up the acquisition of data using less effort, if  
32 little important information is lost. In this study, we evaluate the congruence in species composition  
33 among 22 taxonomic groups to evaluate if any of these groups could be used as surrogates for the  
34 others in monitoring programs. We also evaluated if the taxonomic or numeric resolution of possible  
35 surrogates can be reduced without greatly reducing the overall congruence. Congruence among plant  
36 groups was high, while the congruence among most animal groups were very low, except for anurans  
37 in which congruence values were only slightly lower than for plants. Liana (Bignoniaceae) was the  
38 group with highest congruence, even using genera presence-absence data. The congruence among  
39 groups was related to the environmental factors, specially soil clay and phosphorous contents. Several  
40 groups showed strong spatial clumping, but this was unrelated to the congruence among groups. The  
41 high congruence of lianas with the other groups suggests that it may be a reasonable surrogate group,  
42 mainly for the other plant groups analyzed. Although difficult to count and identify, the number of  
43 studies on the ecology of lianas is increasing. Most of these studies have concluded that lianas are  
44 increasing in abundance in tropical forests. Beyond the high congruence, lianas are worth monitoring  
45 in their own right because they are sensitive to global warming and the increasing drought frequency  
46 and severity in tropical regions. Our findings suggest that data on surrogates groups with relatively  
47 low taxonomic and numerical resolutions can be reliable shortcuts for biodiversity assessments,  
48 especially in megadiverse areas with high rates of habitat conversion where lack of biodiversity  
49 knowledge is pervasive.

50

51 **Keywords:** Amazonia, Congruence, Mantel, Procrustean rotation, Spatial patterns, Surrogate groups

52

53

## 54 **1. Introduction**

55

56         Reliable biodiversity data allowing the use of systematic conservation planning procedures  
57 (Margules and Pressey, 2000) are available only for a few areas worldwide. Conversely, most of the  
58 species-rich areas are plagued by the absence of biological information (e.g. Hopkins, 2007; Schulman  
59 et al., 2007). Brown & Lomolino (1998) and Lomolino (2004) coined the terms “Linnean shortfall”  
60 and “Wallacean shortfall” to summarize this problem. The first term refers to the lack of information  
61 about species identities, whereas the second is related with the lack of data on the spatial distribution  
62 of the species (see also Whittaker et al., 2005).

63         The world is experiencing severe human-induced impacts (e.g. Hansen et al., 2000;  
64 Vörösmarty et al., 2010), so we may not have time to solve the Linnean and Wallacean shortfalls  
65 before the impacts on biodiversity become irreversible. In addition, carrying out inventories of all  
66 biodiversity of megadiverse regions of the planet, apart from being expensive and time-consuming,  
67 may be a quixotic task (Magurran and Queiroz, 2010). The huge diversity found in the Amazon would  
68 require an inordinately large number of taxonomists for a minimally reliable inventory of this diversity  
69 (Hopkins, 2007), and many tropical areas are still inaccessible, especially in the Amazon region  
70 (Schulman et al., 2007).

71         Because of the Linnean and Wallacean shortfalls, most proposed systematic conservation  
72 plans are based on surrogate taxa, which are selected by the availability of data (Rodrigues and  
73 Brooks, 2007). However, the decisions taken for a particular surrogate group may not be the best for  
74 the conservation of all (unknown) biodiversity in a given area (Franco et al., 2009) and the  
75 effectiveness of these decisions are also scale dependent. Because of the uncertainty about the  
76 efficiency of the surrogacy approach, the number of studies testing for community congruence (cross-  
77 taxon congruence) is increasing conspicuously (e.g. Paszkowski and Tonn, 2000; Su et al., 2004;  
78 Macía et al., 2007). Two communities are said to be concordant when beta-diversity or community  
79 structures exhibited by these communities are correlated (Lopes et al., 2011). Similar response to  
80 major environmental gradients is the most common mechanism underlying community congruence  
81 (Heino et al., 2003). A good surrogate group should be easy to sample, identify, and have a  
82 distribution pattern congruent with those of other taxonomic groups. Independently of other  
83 requirements, although rarely tested, concordance is a necessary property for the reliable use of  
84 surrogate groups.

85         Besides the analysis of community congruence, a different set of studies has focused on how  
86 well biodiversity patterns, obtained with species-level data, can be reproduced by data on higher taxa,  
87 in order to improve the cost-effectiveness of monitoring programs and community analyses in general  
88 (e.g. Attayde and Hansson, 2001; Bertrand et al., 2006). The effects of taxonomic resolution on

89 biodiversity patterns can be tested by merging species into coarser taxonomic classes and by  
90 evaluating the similarity between ordination patterns depicted by both species-level and lower-  
91 resolution data (Melo, 2005; Anderson et al., 2005). If the patterns are similar, then higher taxa data  
92 can be used to substitute species-level data (e.g. Terlizzi et al., 2003) that is more expensive and time  
93 consuming to obtain. The effects of numerical resolution (e.g., transforming abundance data into  
94 presence-absence data) on biodiversity patterns can be analyzed similarly (Melo, 2005; Carneiro et al.,  
95 2010). The reliability of higher taxa data for conservation planning is also scale dependent and, in  
96 general, the effectiveness of surrogates increases with the increase of the spatial extent of the area  
97 under study (La Ferla et al., 2002; ter Steege et al., 2006).

98         Studies in the Amazon region have found cross-taxon correlations between similarity matrices  
99 derived from plant groups (Vormisto et al., 2000; Ruokolainen et al., 2007; Macía et al., 2007), but  
100 studies evaluating the congruence between floristic and faunistic data are largely lacking (see Paavola  
101 et al., 2006; Qian and Ricklefs, 2008 for studies in other regions). Variation in faunistic similarity  
102 might be better predicted by floristic similarity than by environmental similarity matrices (Oliver et  
103 al., 1998). This is so because data on plant species composition integrate a number of important  
104 environmental factors and because of the direct relationships among animal and plants (Schaffers et  
105 al., 2008).

106         Here we used comprehensive data on composition of different communities in a 100 km<sup>2</sup>  
107 Amazonian reserve to evaluate the congruence in the distribution pattern of 22 taxonomic groups. For  
108 those groups that could be used to predict the distribution of others, we also evaluated the degree to  
109 which biomonitoring assessments undertaken at this spatial scale can be simplified by using surrogate  
110 groups and reducing the taxonomic and/or numeric resolution. To the best of our knowledge, no  
111 previous study has examined the adequacy of surrogate groups, taxonomic and numerical resolution in  
112 the same study.

113

## 114 **2. Material and methods**

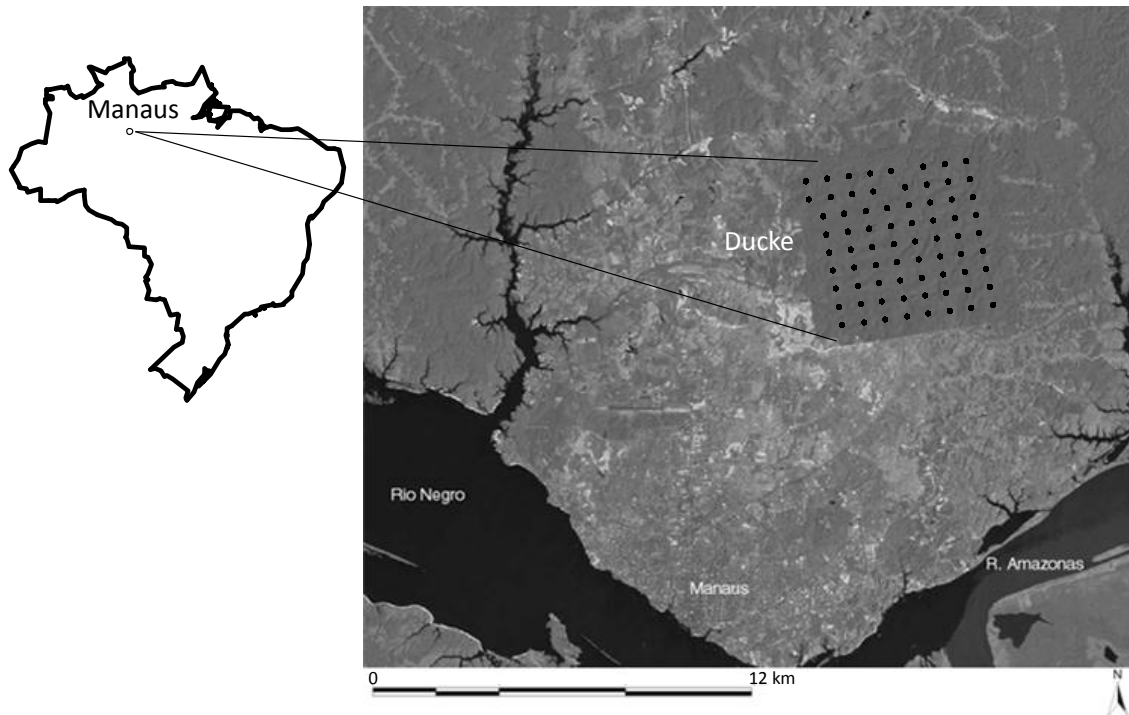
115

### 116 *2.1 Study area*

117

118         This study was undertaken using data on 22 taxonomic groups collected at the Ducke Reserve  
119 of the Instituto Nacional de Pesquisas da Amazônia (INPA), located 26 km north-west of Manaus  
120 (Fig. 1). The area corresponds to site 1 of the Brazilian Long-Term Ecological Research Program  
121 (PELD), and is part of the Biodiversity Research Program (PPBio) of the Brazilian Ministry of  
122 Science and Technology (MCT). The reserve covers 10,000 (10×10 km) hectares of terra-firme  
123 tropical rain forest, with a closed canopy 30–37 m high and emergents growing to 40–45 m (Ribeiro et

124 al., 1999). A central plateau splits the reserve into two drainage systems (Espírito-Santo et al., 2009)  
 125 with altitude ranging from 40 to 110 m asl. The mean annual temperature is 26°C and the mean annual  
 126 rainfall is 2362 mm. Soils in the reserve are composed of marine sediments of the tertiary,  
 127 representing a continuum from clayey soils at higher altitudes to sandier soil at lower altitudes (i.e.  
 128 stream valleys).



129  
 130 **Figure 1.** Location of Ducke Reserve in the Brazilian Amazon. Points indicate 1 km equidistant  
 131 sample plots.

132

## 133 2.2 Sampling design and datasets

134

135 All datasets used in this study were gathered by research teams working in PPBio (see  
 136 Magnusson *et al.* 2005 and <http://ppbio.inpa.gov.br/Eng>). The basic sampling design used in this  
 137 program is based on the RAPELD protocol with a system of trails and permanent plots in which a  
 138 diverse range of taxa can be sampled (see Magnusson *et al.*, 2005; Costa and Magnusson, 2010 for a  
 139 detailed description of the sampling design). The RAPELD grid in Ducke Reserve is a rectangle with  
 140 sides of 8 by 9 km, resulting in 64 km<sup>2</sup> of trails in which 72 plots separated by 1 km are spread (Fig.  
 141 1). Each sample plot is 250 m long, with width varying according to the taxa or life stage being  
 142 sampled. The center line of each plot follows an elevation contour line, thus minimizing altitudinal  
 143 variation within plots. A detailed description of the sampling protocols used to collect the data on

144 composition and abundance of the different taxonomic groups can be found in the metadata available  
 145 together with individual datasets in the PPBio website (<http://ppbio.inpa.gov.br/Eng>).

146 Most of the 22 datasets used were of plant groups: [of trees of Burseraceae,  
 147 Chrysobalanaceae, Euphorbiaceae, Fabaceae, Lauraceae, Lecythidaceae, Moraceae, Myristicaceae and  
 148 Sapotaceae; Palms; Angiosperm Herbs; Ferns; shrubs of Piperaceae in the genus *Piper* and Rubiaceae  
 149 in the genus *Psychotria*; and lianas (Bignoniaceae)]. Seven datasets were of animal groups: [diurnal  
 150 anurans; nocturnal anurans; lizards; bees; ants; soil-and-litter meso-invertebrates; and mites of the  
 151 Suborder Oribatida].

152 All organisms were identified to species or morphospecies, except for soil and litter meso-  
 153 invertebrates, which were identified to Class, Order or Family. Samples were taken in the same plots;  
 154 but some groups were not sampled in all plots (30 to 72 plots were sampled for each group).  
 155 Environmental variables are also available from the PPBio data repository (<http://ppbio.inpa.gov.br>).  
 156 In this study, we used five environmental variables (soil clay, silt and phosphorus (P) contents, terrain  
 157 slope and number of trees in the plot) that PPBio researchers found to be the most important in  
 158 explaining patterns in community structure of the different groups analyzed in this study (e.g. Costa et  
 159 al., 2005; Kinupp and Magnusson, 2005).

160

### 161 *2.3 Analysis of congruence*

162

163 We first analyzed the congruence among all datasets using species abundance data.  
 164 Abundance data were transformed into  $\log(x+1)$  prior to analyses to reduce the influence of outliers.  
 165 To reduce the dimensionality of each dataset, we conducted a principal coordinate analysis (Legendre  
 166 and Legendre, 1998) using the Bray-Curtis distances among sampling plots. The level of community  
 167 congruence (between any two ordination solutions; i.e., between the eigenvectors extracted from the  
 168 Bray-Curtis distance matrices) was quantified and tested for statistical significance by the Procrustean  
 169 superimposition method and a Monte Carlo procedure (with 5000 permutations), respectively. The  $m^2$   
 170 values (the goodness-of-fit statistic that measures the level of congruence between two ordination  
 171 configurations) were transformed to Procrustes correlation ( $r$ ) by calculating the square root of their  
 172 complements ( $r = \sqrt{1 - m^2}$ ) (Oksanen et al., 2011).

173 Mantel tests are also commonly used in studies of community congruence (see Table 2 of  
 174 Heino, 2010). For this reason, we also evaluated the levels of community congruence by estimating  
 175 the standardized Mantel correlation ( $r_M$ ) between pairs of Bray-Curtis distance matrices. The  
 176 significance level of each Mantel statistic was determined by comparing the observed value of  $r_M$  with  
 177 those obtained after 5,000 Monte Carlo simulations. Results from this test were similar and are  
 178 presented in the Appendix. We present the results from Procrustean approach in the body of the paper

179 because it has been shown to have higher power and lower type I error rates than the Mantel test  
180 (Peres-Neto and Jackson, 2001).

181 We submitted the matrix of congruence (pair-wise congruence) to a second-stage Non-Metric  
182 Multidimensional Scaling (NMDS) analysis to construct a plot to further examine the congruence  
183 between datasets. We calculated the average congruence that each group had with the others and the  
184 group with the highest mean was considered the best surrogate.

185

#### 186 *2.4 Putative causes of congruence*

187

188 We used a partial Redundancy Analysis (pRDA, Peres-Neto et al., 2006) to evaluate spatial  
189 and environmental patterns in each dataset (species abundance, using the Hellinger transformation).  
190 For this analysis, we used the five variables presented above as environmental predictors, while the  
191 spatial variables were the eigenvectors extracted, using an eigenfunction analysis (PCNM), from a  
192 matrix of geographic distances between plots (Borcard and Legendre, 2002). We used a forward  
193 selection procedure (Blanchet et al., 2008) to retain spatial and environmental variables to be used in  
194 the pRDA. The results of variation partitioning were based on adjusted fractions of variation (Peres-  
195 Neto et al., 2006). Detailed descriptions of variation partitioning based on RDA can be found in Peres-  
196 Neto & Legendre (2010) and references therein.

197 Multivariate partitioning techniques have been extensively used to infer the relative roles of  
198 spatial and niche processes in structuring biological communities (Cottenie, 2005). However, these  
199 approaches were recently challenged by Gilbert & Bennet (2010), who indicated that different  
200 versions of these techniques produced biased estimates of the relative importance of spatial and  
201 environmental signals, and by Smith and Lundholm (2010), who showed that identical levels of  
202 migration and environmental control can produce very different variance components. We believe that  
203 these recent criticisms to multivariate partitioning techniques have raised an important debate, which  
204 is far from being settled. Thus, we used these techniques here cautiously and only as a way to detect  
205 either environmental or spatial signals, instead of trying to measure their relative importance in  
206 community structuring. We predicted that datasets with high environmental and/or spatial signals  
207 would have higher congruence between themselves than between datasets with low environmental  
208 and/or spatial patterns. We predicted that datasets with high environmental and/or spatial signals  
209 would have higher congruence between themselves than between datasets with low environmental  
210 and/or spatial patterns.

211 We also regressed the mean level of congruence of each group with the environmental fraction  
212 [ab] and with the spatial fraction [bc] of the variance partitioning analysis. This regression enabled us

213 to determine how much of the congruence patterns were associated with shared responses to  
214 environmental and spatial factors and how much were simply due to other unstudied factors.

215

## 216 *2.5 Impacts of reducing taxonomic and numerical resolution*

217

218 After identify the taxonomic group with highest congruence with the others, we evaluated the  
219 impact of decreasing the numeric and taxonomic resolution of data on the levels of congruence. To  
220 accomplish this, we pooled species to genera (except for meso-invertebrates, *Psychotria* and *Piper*  
221 datasets) and/or converted abundance to presence-absence data. We used the Sorensen distance for  
222 presence-absence data in the association matrix for the PCoA that was used in the Procrustes and  
223 Mantel analyses. The same procedures were used to measure the levels of congruence between the  
224 group with the highest mean congruence (after reducing the taxonomic and numerical resolution) and  
225 all other groups.

226

## 227 *2.6 Computational tools*

228

229 All analyses were run in the R environment for statistical computing (R Development Core  
230 Team, 2011). Protest, Mantel tests, redundancy analysis, and variation partitioning analysis were all  
231 run using the functions *protest*, *mantel*, *rda* and *varpart* available in vegan package (Oksanen et al.,  
232 2011).

233

## 234 **3. Results**

235

### 236 *3.1 Analysis of congruence*

237

238 The highest level of congruence we found was between palms and lianas ( $r = 0.87$ ;  $P < 0.005$ ),  
239 while the lowest was between Burseraceae and mesofauna ( $r = 0.04$ ;  $P = 0.99$ ). In general, congruence  
240 was higher among plant groups (mean  $r = 0.51 \pm 0.16$  SD) than among animal groups (mean  $r = 0.24$   
241  $\pm 0.12$  SD) and lianas was the group with the highest mean level of congruence (mean  $r = 0.60 \pm 0.23$   
242 SD, Fig. 2, see also Table A1 in The Appendix). The second stage NMDS represented well the  
243 relationships in the procrustean congruence among groups (Fig. 3), where groups with higher  
244 congruence were placed together. Almost all plant groups are close together in a cluster in which the  
245 groups with higher congruence form the center. Two plant groups (Euphorbiaceae and Lauraceae),  
246 which were poorly correlated with the other plant groups are spread around, together with the animal  
247 groups.

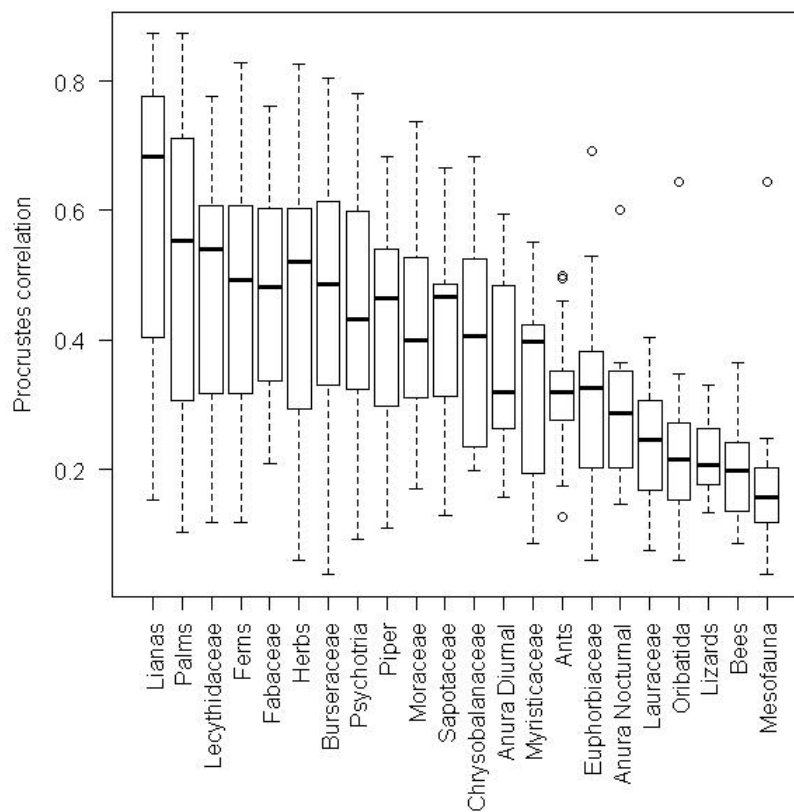
248 The ordination patterns generated by lianas (species abundance data) were virtually unchanged  
 249 after the conversion of abundance to presence and absence data (Protest,  $r = 0.975$ ,  $P < 0.001$ ), after  
 250 pooling species into genera (Protest,  $r = 0.857$ ,  $P < 0.001$ ) or when changing genera abundance data to  
 251 genera presence-absence data (Protest,  $r = 0.777$ ,  $P = 0.001$ ).

252

### 253 3.2 Putative causes of congruence

254

255 Most datasets of plants and those of anurans showed high environmental and/or spatial signals,  
 256 while invertebrates and lizards had no significant spatial or environmental signals (Table 1). Lianas  
 257 showed no spatial pattern, but had the second largest environmental signal ( $[a] = 0.253$ ), being mainly  
 258 associated with clay and P contents. The mean level of congruence, obtained for each group, was  
 259 highly related to the environmental fraction  $[ab]$  ( $r^2 = 0.56$ ,  $p < 0.001$ , Fig. 4-a), but the mean level of  
 260 congruence was not significantly related with the spatial fraction  $[bc]$  ( $r^2 = 0.07$ ,  $p = 0.24$ , Fig. 4-b).



261

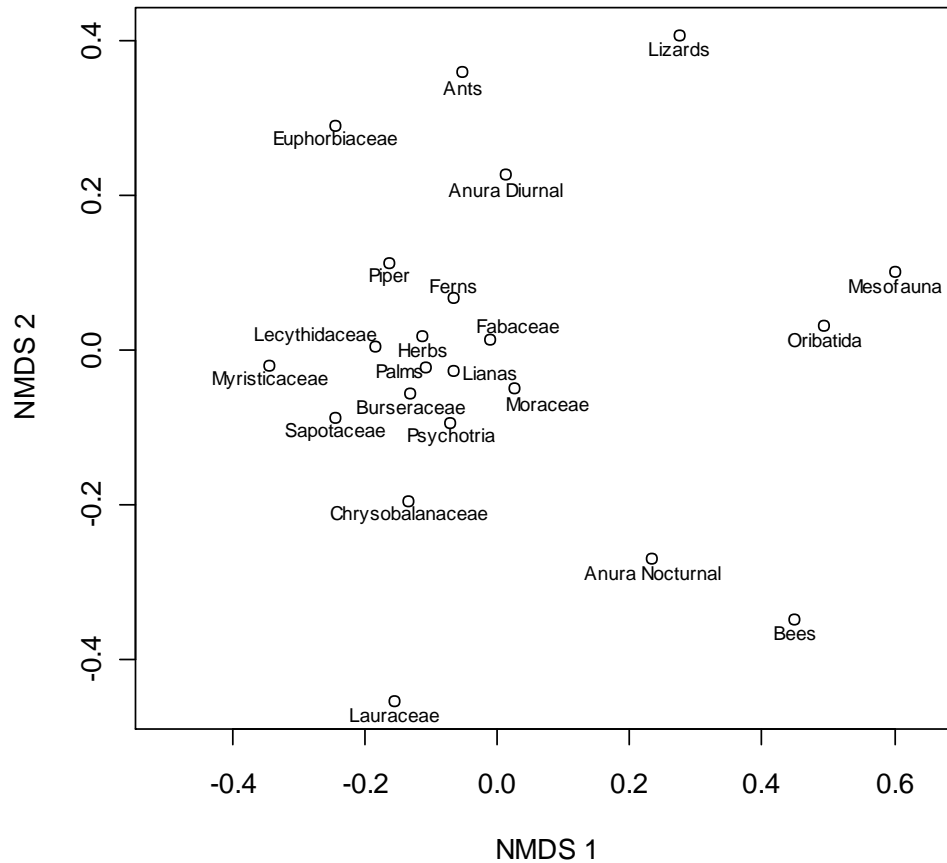
262 **Figure 2.** Procrustean rotation results for species abundance data (5000 permutations).  
 263 Congruence among 22 community datasets was evaluated with the correlations in symmetric  
 264 Procrustean rotations. This figure was constructed using the values presented in Table A1 in the  
 265 Appendix.



266 **Table 1:** Variance partitioning analysis. Spatial filters (PCNMs) and environmental variables are shown in the  
 267 order they were retained in the forward selection procedure. [a] = environmental fraction; [b] = shared fraction; [c]  
 268 = spatial fraction; [a+b+c] = Total variance explained.

	Environment	PCNMs	[a]	[b]	[c]
Lianas	clay,P	-	0.289	-	-
Trees	clay,P,slope,trees	1,2,3,37,24,6,30,38,8	0.086	0.038	0.033
Palms	P,clay,slope,trees	30,1,2,38,8,42,31	0.262	0.152	0.025
Herbs	clay,slope,P,trees	34,33,29,11,2,4,1,7,6,31,40,26,8,36,35	0.109	0.143	0.114
Ferns	P,slope,clay,trees	11,32,33,29,34,1,25,30,10	0.185	0.165	0.105
Lecythidaceae	clay,P	1,24,2,37,3,6,13	0.148	0.042	0.068
Fabaceae	clay,P,slope	1,2,3,44	0.094	0.002	0.028
Burseraceae	P,clay,slope,trees,silt	2,28,37,48,3,8,38,1,14,26,13,30	0.11	0.068	0.081
<i>Psychotria</i>	P,clay,slope,trees	32,2,1,3,9,37,6,5	0.142	0.079	0.176
Sapotaceae	clay,P,trees	3,2,1,8,45,5,6	0.054	0.034	0.045
Moraceae	clay,trees,P	2,30,47,37,1	0.104	0.041	0.036
<i>Piper</i>	clay,slope,P	1,40,4,2,6,44	0.143	0.046	0.089
Chrysobalanaceae	P,Clay	24,2,10,48	0.048	0.005	0.031
Diurnal Anura	clay,slope,trees	1	0.218	0.005	0.053
Myristicaceae	clay,P,trees	-	0.112	-	-
Euphorbiaceae	P,slope	31,37,2,42	0.056	0.015	0.039
Ants	-	2	-	-	0.043
Noturnal Anura	P,silt,trees,Clay	2,3,37,1,4,7,10,30,46,12,48	0.098	0.111	0.214
Lauraceae	P,silt	35,4	0.02	0.001	0.013
Oribatida	Clay	1,6,34,7,2,30,25,18,49	0.008	0.01	0.078
Lizards	trees,Clay	7	0.048	-0.003	0.018
Bees	Silt	5,7,4	0.012	0.013	0.087
Mesofauna	-	16,15,35,6,3,27,7,2,1,19,8,20,12	-	-	0.219

269 - no variable was retained in the forward selection procedure.



270

271

272 **Figure 3.** An ordination plot from second-stage NMDS obtained from the matrix of  
 273 congruence (evaluated with the correlations in symmetric Procrustean rotation – see Table 1) among  
 22 community datasets. Stress = 20.41.

274

### 275 *3.3 Impacts of reducing taxonomic and numerical resolution*

276

277 Although not statistically significant (paired  $t$ -test = 1.087;  $df$  = 20;  $P$  = 0.29, mean of the  
 278 differences = 0.005), the levels of congruence between lianas (the surrogate group with highest overall  
 279 congruence) and other groups (especially herbs, palms, Chrysobalanaceae, Myristicaceae,  
 280 diurnal/nocturnal anurans, oribatid mites and bees) were even higher after transforming the liana-  
 281 abundance data into presence-absence data. However, the levels of congruence between lianas and the  
 282 other groups were statistically lower after grouping lianas species abundance data into genera-  
 283 abundance data (paired  $t$ -test = 3.389;  $P$  = 0.002, mean of the differences = 0.048) or after reducing  
 284 both the taxonomic and numerical resolution of the lianas dataset (i.e., using the genera presence-  
 285 absence data; paired  $t$ -test = 4.141;  $P$  < 0.001, mean of the differences = 0.080). However, even using  
 286 genera presence-absence data for lianas (i.e. the coarsest numeric and taxonomic resolutions), the  
 287 mean level of congruence (mean  $r$  = 0.516, Table 2) was still better than the mean congruence found  
 288 for palms (mean  $r$  = 0.515), the group with the second highest level of congruence (see Table A1 in

289 the Appendix). Thus, the ability of lianas to reproduce ordination patterns generated by other groups  
 290 was largely maintained after the reduction of numerical resolution (abundance to occurrence),  
 291 reduction of the taxonomic resolution (species to genera) or both (Table 2).

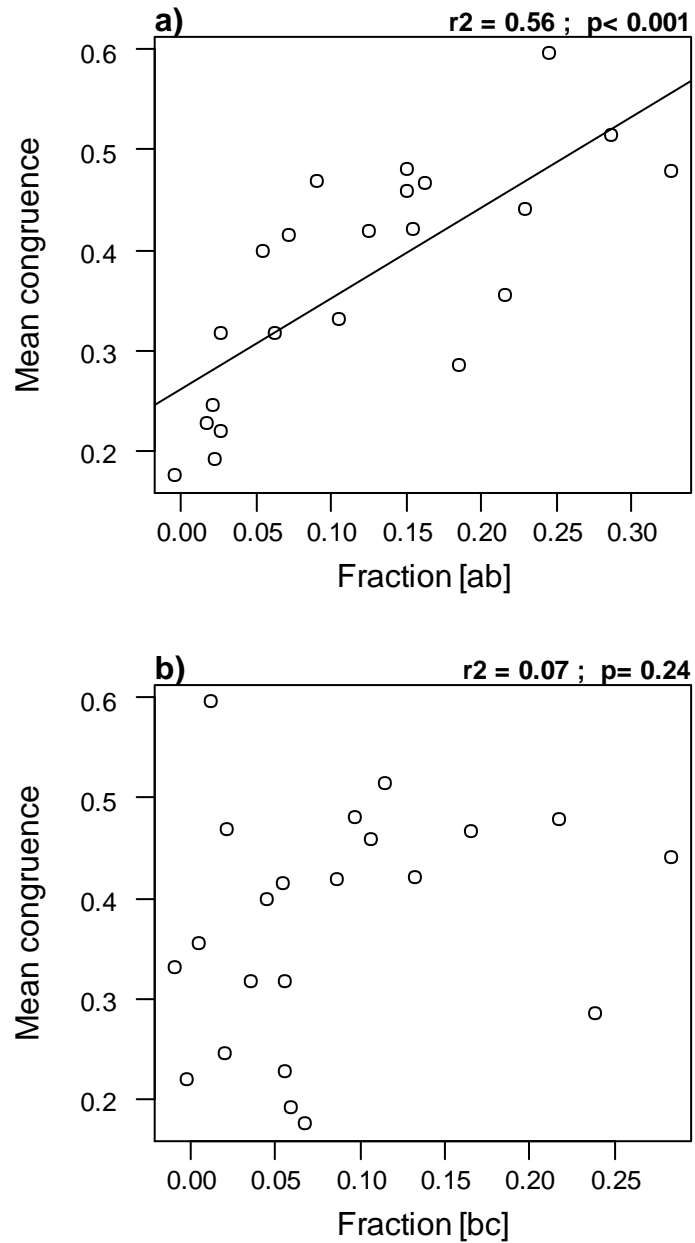
292 Similar results were obtained using Mantel tests to evaluate the patterns of congruence (see  
 293 Appendix 1).

294

295 **Table 2.** Congruence between Lianas, at different taxonomic and numeric resolutions, with  
 296 the other groups (species abundance, except for mesofauna). Congruence was evaluated using  
 297 Procrustean rotations (5000 permutations). The mean congruence was high for all combinations of  
 298 taxonomic resolution.

	Lianas			
	Species		Genera	
	Abundance	Ocurrence	Abundance	Ocurrence
Palms	0.87	0.88	0.83	0.77
Lecythidaceae	0.78	0.77	0.70	0.64
Ferns	0.83	0.82	0.63	0.59
Fabaceae	0.76	0.73	0.68	0.62
Herbs	0.83	0.85	0.73	0.72
Burseraceae	0.81	0.80	0.73	0.68
<i>Psychotria</i>	0.78	0.76	0.68	0.62
<i>Piper</i>	0.68	0.67	0.69	0.65
Moraceae	0.74	0.70	0.72	0.65
Sapotaceae	0.67	0.66	0.56	0.50
Chrysobalanaceae	0.68	0.69	0.68	0.65
Diurnal Anura	0.59	0.61	0.59	0.58
Myristicaceae	0.55	0.56	0.47	0.40
Ants	0.34 <sup>n</sup>	0.32 <sup>n</sup>	0.40	0.45
Euphorbiaceae	0.69	0.67	0.63	0.57
Nocturnal Anura	0.60	0.62	0.55	0.50
Lauraceae	0.40	0.40	0.34	0.33
Oribatida	0.35	0.36	0.31 <sup>n</sup>	0.29 <sup>n</sup>
Lizards	0.24 <sup>n</sup>	0.19 <sup>n</sup>	0.16 <sup>n</sup>	0.12 <sup>n</sup>
Bees	0.15 <sup>n</sup>	0.20 <sup>n</sup>	0.15 <sup>n</sup>	0.19 <sup>n</sup>
Mesofauna	0.18 <sup>n</sup>	0.17 <sup>n</sup>	0.30 <sup>n</sup>	0.32 <sup>n</sup>
Mean	0.60	0.59	0.55	0.52
SD	0.23	0.23	0.23	0.23

299 <sup>n</sup> Non-significant values ( $p > 0.05$ )



300

301

302

303

304

305

306

**Figure 4.** Relationship between the mean level of congruence values (Protest) calculated for each group with the environmental [ab] and with spatial [bc] fractions derived from the partial RDA analyses. [ab] and [bc] represent the adjusted  $R^2$  resulting from RDAs between the biological matrices and the environmental predictor matrix and between the biological matrices and the spatial predictor matrix, respectively.

## 307 **4. Discussion**

308

309         The distribution patterns of most of 15 plant group analyzed showed high congruence, while  
310 invertebrates and lizards had low congruence with other groups. Anurans showed high congruence  
311 with plants, but the values were slightly lower than those among plants. Based only on congruence,  
312 lianas (Bignoniaceae) would be the best candidate for a surrogate group. Although statistically  
313 significant, the decrease in the taxonomic and numeric resolution of lianas datasets did not greatly  
314 decreased the congruence with the other groups; the coarsest resolution of lianas (genera presence-  
315 absence) had higher congruence values than the finest resolution of palms (species abundance data),  
316 the group with the second highest congruence.

317

### 318 *4.1 Congruence among groups*

319

320         The congruence in distribution patterns might be highly dependent on the geographic location  
321 and spatial extent of analysis (McKnight et al., 2007; Cabeza et al., 2008). McKnight et al. (2007)  
322 found that the congruence in beta diversity among amphibians, birds and mammals were generally  
323 stronger within the Neotropical than within the Nearctic realm. Thus, extrapolation of our results to  
324 regions beyond the Amazon should be done with caution.

325         Based on Mantel tests, Ruokolainen *et al.* (2007) considered ferns (Pteridophytes) to be the  
326 best surrogate group for other plants. Our results based on Procrustean rotations (and Mantel, see  
327 Appendix A1) also identified ferns as a potential surrogate group, but several other groups of plants  
328 also had high values of congruence (e.g. palms, Lecythydaceae, ferns, Fabaceae, angiosperm herbs,  
329 Burseraceae), and lianas (Bignoniaceae) had the highest overall congruence.

330

### 331 *4.2 Putative causes of congruence*

332

333         Differences in distributional patterns between communities may be due to dissimilar responses  
334 to environment gradients, due to different dispersal abilities or both (Linares-Palomino and Kessler,  
335 2009). Conversely, similar responses to environmental gradients may be the main causes of  
336 congruence between groups of species (e.g. Paszkowski and Tonn, 2000). The high congruence among  
337 plant groups observed here might be explained by the environmental control because the variance-  
338 partitioning analysis indicated that the variance associated with environmental variables was related to  
339 the mean congruence of each group.

340         The main causes for the high congruence among plants might be associated with similar  
341 responses to soil characteristics. Variation in densities of most plants was associated with clay and P

342 content. Lianas showed the highest sensitivities to soil variation (28.9 % of the variance was explained  
343 by clay and P soil contents). In general, soil factors have been found to be better predictors of floristic  
344 patterns in the Amazon region than spatial factors (e.g. Tuomisto et al., 2003; Costa et al., 2005).  
345 Lianas generally have high dispersal ability (Macía et al., 2007), which might be responsible for the  
346 lack of spatial pattern observed.

347

#### 348 *4.3 Lianas as a potential surrogate group*

349

350 Although lianas are considered a weed in silvicultural activities (Gerwing, 2001) and are hard  
351 to sample and count in the field, they have many interesting ecological characteristics that may make  
352 them useful as a surrogate group. The importance of lianas might be increasing in tropical forests,  
353 where they comprise about 25% of the woody stem density and species richness, reaching values as  
354 high as 44% in the Amazon forests (Schnitzer and Bongers, 2002). Lianas contribute to diversity and  
355 community structure, exerting profound effects on other growth forms, such as altering tree growth,  
356 species composition and reducing fecundity, fundamentally changing the functioning and  
357 physiognomy of tropical forests (Schnitzer and Carson, 2010). In general, lianas are more abundant on  
358 rich soils (Putz and Chai, 1987) and related with tree structure (Nogueira et al., 2011) at small scales.  
359 At large scales, lianas are associated with the seasonality of rainfall, being more abundant and more  
360 species rich in regions with strong seasonal droughts (Schnitzer, 2005), and reduction in rainfall may  
361 be favoring lianas in some tropical forests (Swaine and Grace, 2007). Schnitzer (2005) showed that  
362 lianas can growth seven times more in height than trees during periods of reduced water availability.  
363 Gap formation (Schnitzer and Bongers, 2002) and forest fragmentation (Laurance et al., 2001) also  
364 may increase the abundance and diversity of lianas.

365 Proliferation of lianas may exacerbate biomass declines and seriously affect forest structure  
366 and functioning (Laurance et al., 2001) with considerable implications to the carbon cycle and for the  
367 biodiversity of tropical forests (Phillips et al., 2002). A volume of *Forest Ecology and Management*  
368 (vol. 190, 2004) was dedicated to discussion of the importance of lianas in tropical forest functioning,  
369 in which understanding the ecology of lianas was pointed out as crucial, not just for the understanding  
370 of basic ecological questions, but also for the management and conservation of tropical forests (Wright  
371 et al., 2004). Because the severity and frequency of drought events affecting the Amazon region are  
372 expected to increase (Lewis et al., 2011), the use of lianas as a surrogate group for other plants in the  
373 Amazon might be fruitful not just due to its surrogacy capability, but also because it is an indicator  
374 group for environmental changes.

375 While lianas may be useful surrogates for biological variation at local scales, or as surrogates  
376 for environmental changes, their potentially high dispersal and close association with environmental

377 factors may make them less suitable as surrogates at wider scales for groups that have more limited  
378 dispersal, or for groups, such as the animal groups in this study, that show less local variation  
379 associated with soil characteristics. Very often, it is the local endemics that are of greatest  
380 conservation concern, and not the species with high dispersal ability and high adaptability to  
381 disturbance. Programs, such as the PPBio (<http://ppbio.inpa.gov.br>), are just starting to accumulate  
382 integrated data on many taxa and environmental variables at wider scales, so selection of surrogates  
383 for wider scales should be made with great caution.

384

#### 385 *4.4 Effects of numerical and taxonomic resolution*

386

387 In our study, the reduction of the taxonomic resolution of lianas caused a significant decrease  
388 in the congruence of lianas with the other groups. However, the mean of the differences was low. In  
389 addition, even using low resolution data, the group composed by lianas was the best surrogate one (i.e.  
390 had the highest mean congruence). Therefore, the taxonomic and numeric resolution of lianas can be  
391 reduced without a greater loss of information, at least in the spatial scale of this study. These results  
392 are in line with previous studies showing that the use of data with low numerical and taxonomic  
393 resolutions may be reliable for plant groups (e.g. Prinzing et al., 2003; Torre-Cuadros et al., 2007) and  
394 for animal groups (e.g. Attayde and Hansson, 2001). Conversely, there is a tradeoff between the  
395 taxonomic resolution used and how clear cut the pattern is (e.g. the magnitude of the effect, Melo,  
396 2005) that should be taken into account before deciding what resolution to use.

397 There is high variability at the species level at local and regional scales. Increasing the  
398 taxonomic level decreases the variability at local scales, but at regional scales it remains high  
399 (Anderson et al., 2005). This is in agreement with the idea that coarser taxonomic resolution could be  
400 effectively used for conservation purposes, in which regions of rapid species turnover require  
401 increased attention to the placement and size of conservation areas in order to protect biodiversity  
402 (McKnight et al., 2007). Therefore, reducing the numerical and taxonomic resolution could reduce the  
403 labor and costs of biodiversity sampling without losing important information.

404

## 405 **5. Conclusions**

406

407 Our study provides information on the use of surrogate groups at local scales in the Amazon.  
408 Plant groups were highly congruent at the scale studied, while animal groups had low congruence with  
409 other animal datasets and with plant datasets. The use of lianas as surrogate group might have many  
410 fruitful properties other than those related to a surrogate group. Because lianas grows fast in new gaps  
411 and during drought periods, they might be used as an indicator group of global climate changes, such

412 as increased drought periods, while acting as a surrogate group for other purposes. In addition to the  
 413 use of lianas as a surrogate group to simplify monitoring assessments, the use of liana's presence-  
 414 absence data and genera level identifications also could reduce the costs and labor of monitoring  
 415 studies.

416

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418

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425

426

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**Appendix A1 - Results for Procrustean rotation and for Mantel tests**

**Table A1.** Procrustean rotation results for species abundance data (5000 permutations). Congruence among 22 community datasets was evaluated with the correlations in symmetric Procrustean rotations. This matrix was used to run the second stage NMDS. The last two rows show the mean and standard deviation of congruence values obtained for each taxonomic group. Columns and rows are ordered from the highest mean value to the lowest.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]	[17]	[18]	[19]	[20]	[21]	[22]
[1] Lianas																						
[2] Palms	0.87																					
[3] Lecythidaceae	0.78	0.71																				
[4] Ferns	0.83	0.74	0.69																			
[5] Fabaceae	0.76	0.67	0.67	0.58																		
[6] Herbs	0.83	0.79	0.64	0.69	0.6																	
[7] Burseraceae	0.81	0.78	0.6	0.6	0.62	0.67																
[8] <i>Psychotria</i>	0.78	0.77	0.6	0.62	0.63	0.57	0.61															
[9] <i>Piper</i>	0.68	0.62	0.54	0.61	0.52	0.58	0.54	0.5														
[10] Moraceae	0.74	0.62	0.59	0.53	0.59	0.52	0.63	0.48	0.46													
[11] Sapotaceae	0.67	0.55	0.61	0.48	0.48	0.48	0.49	0.47	0.48	0.46												
[12] Chrysobalanaceae	0.68	0.6	0.55	0.49	0.48	0.53	0.6	0.43	0.41	0.4	0.59											
[13] Anura-Diurnal	0.59	0.44	0.48	0.55	0.49	0.53	0.38	0.32	0.38	0.31	0.31	0.3										
[14] Myristicaceae	0.55	0.42	0.51	0.41	0.4	0.39	0.41	0.41	0.3	0.4	0.52	0.43	0.24									
[15] Ants	0.34 <sup>n</sup>	0.26 <sup>n</sup>	0.36	0.32 <sup>n</sup>	0.34 <sup>n</sup>	0.29 <sup>n</sup>	0.33 <sup>n</sup>	0.28 <sup>n</sup>	0.35 <sup>n</sup>	0.32 <sup>n</sup>	0.46	0.2 <sup>n</sup>	0.5	0.5								
[16] Euphorbiaceae	0.69	0.49	0.4	0.49	0.38	0.38	0.36	0.34	0.53	0.32	0.33	0.22 <sup>n</sup>	0.32	0.22 <sup>n</sup>	0.37							
[17] Anura-Noturnal	0.6	0.3	0.28	0.36	0.34	0.29	0.36	0.35	0.36	0.35	0.22 <sup>n</sup>	0.24	0.2 <sup>n</sup>	0.19 <sup>n</sup>	0.34 <sup>n</sup>	0.2 <sup>n</sup>						
[18] Lauraceae	0.4	0.31	0.32	0.25 <sup>n</sup>	0.29	0.3	0.23	0.31	0.21 <sup>n</sup>	0.17 <sup>n</sup>	0.4	0.38	0.29	0.16 <sup>n</sup>	0.28 <sup>n</sup>	0.12 <sup>n</sup>	0.17 <sup>n</sup>					
[19] Oribatida	0.35	0.26	0.29	0.31	0.24	0.17 <sup>n</sup>	0.12 <sup>n</sup>	0.33	0.12 <sup>n</sup>	0.2 <sup>n</sup>	0.26	0.24	0.22 <sup>n</sup>	0.15 <sup>n</sup>	0.18 <sup>n</sup>	0.06 <sup>n</sup>	0.16 <sup>n</sup>	0.08 <sup>n</sup>				
[20] Lizards	0.24 <sup>n</sup>	0.32	0.2 <sup>n</sup>	0.24 <sup>n</sup>	0.33	0.25	0.26	0.19 <sup>n</sup>	0.26	0.25	0.21 <sup>n</sup>	0.2 <sup>n</sup>	0.26	0.14 <sup>n</sup>	0.28 <sup>n</sup>	0.2 <sup>n</sup>	0.15 <sup>n</sup>	0.13 <sup>n</sup>	0.14 <sup>n</sup>			
[21] Bees	0.15 <sup>n</sup>	0.2 <sup>n</sup>	0.14 <sup>n</sup>	0.12 <sup>n</sup>	0.23 <sup>n</sup>	0.26 <sup>n</sup>	0.2 <sup>n</sup>	0.09 <sup>n</sup>	0.29 <sup>n</sup>	0.25 <sup>n</sup>	0.14 <sup>n</sup>	0.2 <sup>n</sup>	0.17 <sup>n</sup>	0.09 <sup>n</sup>	0.13 <sup>n</sup>	0.1 <sup>n</sup>	0.37	0.22 <sup>n</sup>	0.27 <sup>n</sup>	0.17 <sup>n</sup>		
[22] Mesofauna	0.18 <sup>n</sup>	0.1 <sup>n</sup>	0.12 <sup>n</sup>	0.16 <sup>n</sup>	0.21 <sup>n</sup>	0.06 <sup>n</sup>	0.04 <sup>n</sup>	0.16 <sup>n</sup>	0.11 <sup>n</sup>	0.2 <sup>n</sup>	0.13 <sup>n</sup>	0.22 <sup>n</sup>	0.16 <sup>n</sup>	0.1 <sup>n</sup>	0.25 <sup>n</sup>	0.13 <sup>n</sup>	0.15 <sup>n</sup>	0.13 <sup>n</sup>	0.64	0.18 <sup>n</sup>	0.24 <sup>n</sup>	
Mean	0.6	0.52	0.48	0.48	0.47	0.47	0.46	0.44	0.42	0.42	0.42	0.4	0.36	0.33	0.32	0.32	0.28	0.24	0.23	0.22	0.19	0.17
SD	0.23	0.22	0.2	0.2	0.16	0.21	0.21	0.19	0.16	0.16	0.15	0.16	0.13	0.15	0.09	0.16	0.11	0.1	0.13	0.06	0.07	0.12

<sup>n</sup> Non-significant values (p > 0.05)

**Table A2.** Mantel correlation results for species abundance data. Congruence among 22 community datasets was evaluated with Mantel's tests. The last two rows show the mean and standard deviation of congruence values obtained for each taxonomic group. Rows are ordered from the highest to the lowest mean value.

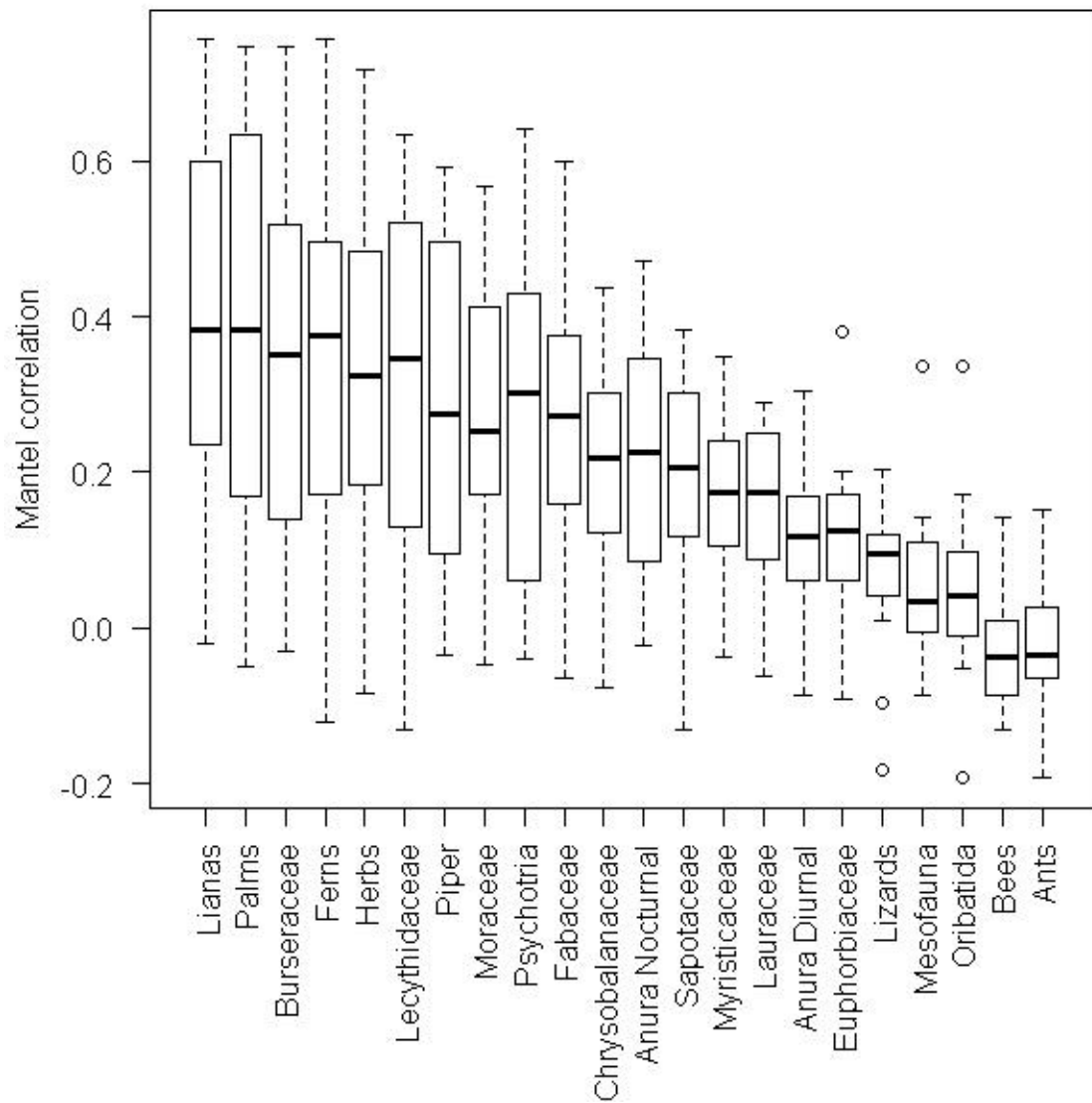
	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]	[17]	[18]	[19]	[20]	[21]	[22]
[1] Lianas																						
[2] Palms	0.69																					
[3] Burseraceae	0.67	0.75																				
[4] Ferns	0.76	0.67	0.56																			
[5] Herbs	0.66	0.72	0.57	0.63																		
[6] Lecythidaceae	0.61	0.63	0.52	0.6	0.52																	
[7] <i>Piper</i>	0.53	0.59	0.53	0.5	0.45	0.54																
[8] Moraceae	0.57	0.52	0.51	0.4	0.41	0.5	0.5															
[9] <i>Psychotria</i>	0.58	0.64	0.52	0.46	0.42	0.56	0.43	0.31														
[10] Fabaceae	0.6	0.53	0.45	0.37	0.48	0.45	0.31	0.36	0.33													
[11] Chrysobalanaceae	0.38	0.44	0.42	0.34	0.32	0.29	0.29	0.27	0.3	0.22												
[12] Anura_2	0.47	0.35	0.35	0.44	0.24	0.35	0.23	0.23	0.37	0.28	0.23											
[13] Sapotaceae	0.3	0.38	0.33	0.38	0.33	0.36	0.18	0.25	0.26	0.27	0.21	0.16										
[14] Myristicaceae	0.35	0.3	0.27	0.19	0.28	0.21	0.28	0.24	0.17	0.17	0.18	0.11	0.21									
[15] Lauraceae	0.24	0.29	0.27	0.26	0.25	0.28	0.26	0.19	0.22	0.16	0.17	0.1	0.2	0.12								
[16] Anura_1	0.3	0.17	0.14	0.24	0.25	0.2	0.1 <sup>n</sup>	0.09 <sup>n</sup>	0.13	0.26	0.02 <sup>n</sup>	0.16	0.12	0.11	0.09							
[17] Euphorbiaceae	0.38	0.17	0.18	0.07 <sup>n</sup>	0.18	0.13	0.2	0.17	0.06 <sup>n</sup>	0.17	0.12	0.05 <sup>n</sup>	0.11	0.13	0.07	0.03 <sup>n</sup>						
[18] Lizards	0.09 <sup>n</sup>	0.11 <sup>n</sup>	0.11 <sup>n</sup>	0.13 <sup>n</sup>	0.1 <sup>n</sup>	0.11 <sup>n</sup>	0.08 <sup>n</sup>	0.2	0.05 <sup>n</sup>	0.14	0.12	0.09 <sup>n</sup>	0.13	0.01 <sup>n</sup>	0.02 <sup>n</sup>	0.06 <sup>n</sup>	0.13					
[19] Mesofauna	0.08 <sup>n</sup>	0.11 <sup>n</sup>	0.06 <sup>n</sup>	0.11 <sup>n</sup>	0.13	-0.01 <sup>n</sup>	0.03 <sup>n</sup>	0.08 <sup>n</sup>	-0.01 <sup>n</sup>	0.12	-0.01 <sup>n</sup>	0.02 <sup>n</sup>	0.03 <sup>n</sup>	-0.04 <sup>n</sup>	0.05 <sup>n</sup>	-0.04 <sup>n</sup>	-0.09 <sup>n</sup>	0.03 <sup>n</sup>				
[20] Oribatida	0.07 <sup>n</sup>	0.1 <sup>n</sup>	0.09 <sup>n</sup>	0.17	0.08 <sup>n</sup>	0.02 <sup>n</sup>	-0.02 <sup>n</sup>	0.04 <sup>n</sup>	0.03 <sup>n</sup>	0.12	-0.01 <sup>n</sup>	0.03 <sup>n</sup>	0.02 <sup>n</sup>	-0.02 <sup>n</sup>	0.13	0.14	-0.05 <sup>n</sup>	0.04 <sup>n</sup>	0.34			
[21] Bees	-0.02 <sup>n</sup>	0 <sup>n</sup>	-0.02 <sup>n</sup>	-0.12 <sup>n</sup>	-0.08 <sup>n</sup>	-0.13 <sup>n</sup>	-0.01 <sup>n</sup>	0.02 <sup>n</sup>	-0.04 <sup>n</sup>	-0.06 <sup>n</sup>	0.13 <sup>n</sup>	0.06 <sup>n</sup>	-0.13 <sup>n</sup>	0.01 <sup>n</sup>	-0.06 <sup>n</sup>	-0.09 <sup>n</sup>	-0.09 <sup>n</sup>	-0.1 <sup>n</sup>	0.14 <sup>n</sup>	-0.04 <sup>n</sup>		
[22] Ants	0.15	-0.05 <sup>n</sup>	-0.03 <sup>n</sup>	-0.11 <sup>n</sup>	-0.02 <sup>n</sup>	-0.06 <sup>n</sup>	-0.04 <sup>n</sup>	-0.05 <sup>n</sup>	0.03 <sup>n</sup>	-0.07 <sup>n</sup>	-0.08 <sup>n</sup>	-0.02 <sup>n</sup>	-0.02 <sup>n</sup>	0.07 <sup>n</sup>	-0.06 <sup>n</sup>	-0.07 <sup>n</sup>	0.12	-0.18 <sup>n</sup>	0.03 <sup>n</sup>	-0.19 <sup>n</sup>	0.14 <sup>n</sup>	
Mean	0.4	0.39	0.32	0.34	0.27	0.33	0.34	0.28	0.28	0.28	0.19	0.21	0.11	0.16	-0.02	0.11	0.2	0.15	0.05	0.07	-0.02	0.06
SD	0.24	0.26	0.24	0.24	0.18	0.22	0.23	0.21	0.21	0.18	0.14	0.15	0.11	0.11	0.09	0.11	0.14	0.11	0.1	0.08	0.08	0.09

<sup>n</sup> Non-significant values ( $p > 0.05$ )

**Table A3.** Congruence among Lianas at different taxonomic and numeric resolutions and the other datasets (species abundance). Congruence was evaluated using Mantel correlations. The mean congruence was high for all combinations of taxonomic resolution.

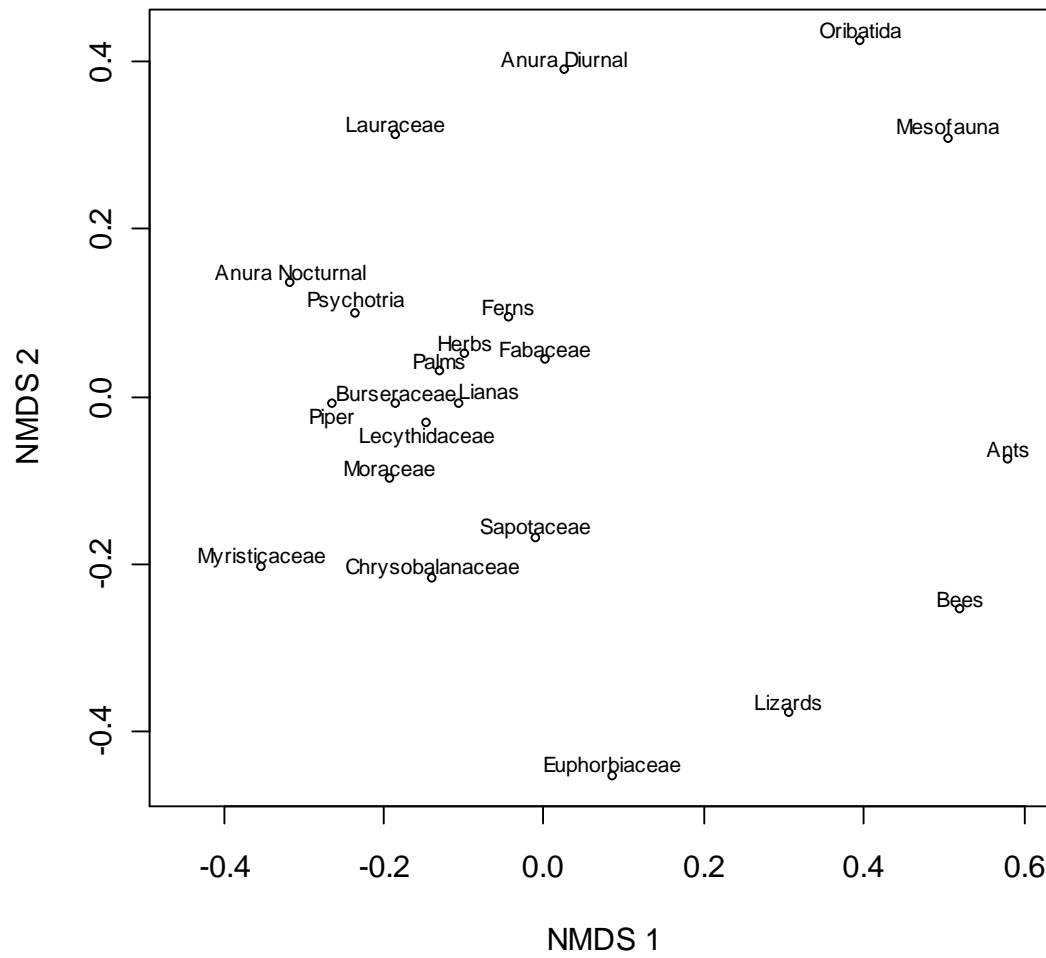
		Lianas			
		Species		Genera	
		Abundance	Ocurrence	Abundance	Ocurrence
Species abundance	Palms	0.69	0.72	0.70	0.57
	Burseraceae	0.67	0.69	0.67	0.51
	Ferns	0.76	0.73	0.65	0.49
	Herbs	0.66	0.68	0.66	0.59
	Lecythidaceae	0.61	0.62	0.52	0.38
	<i>Piper</i>	0.53	0.57	0.53	0.41
	Moraceae	0.57	0.60	0.57	0.46
	<i>Psychotria</i>	0.58	0.59	0.56	0.37
	Fabaceae	0.60	0.59	0.55	0.42
	Chrysobalanaceae	0.38	0.38	0.40	0.31
	Anura Nocturnal	0.47	0.49	0.41	0.26
	Sapotaceae	0.30	0.30	0.27	0.19
	Myristicaceae	0.35	0.34	0.35	0.33
	Lauraceae	0.24	0.23	0.21	0.15
	Anura Diurnal	0.30	0.30	0.34	0.30
	Euphorbiaceae	0.38	0.33	0.32	0.23
	Lizards	0.09 <sup>n</sup>	0.07 <sup>n</sup>	0.07 <sup>n</sup>	0.03 <sup>n</sup>
	Mesofauna	0.08 <sup>n</sup>	0.06 <sup>n</sup>	0.13 <sup>n</sup>	0.15 <sup>n</sup>
	Oribatida	0.07 <sup>n</sup>	0.06 <sup>n</sup>	0.09 <sup>n</sup>	0.07 <sup>n</sup>
	Bees	-0.02 <sup>n</sup>	0.01 <sup>n</sup>	0.02 <sup>n</sup>	0.06 <sup>n</sup>
Ants	0.15	0.11 <sup>n</sup>	0.13 <sup>n</sup>	0.16 <sup>n</sup>	
Mean	0.40	0.40	0.39	0.31	
SD	0.24	0.25	0.22	0.17	

<sup>n</sup> Non significant values ( $p > 0.05$ ).

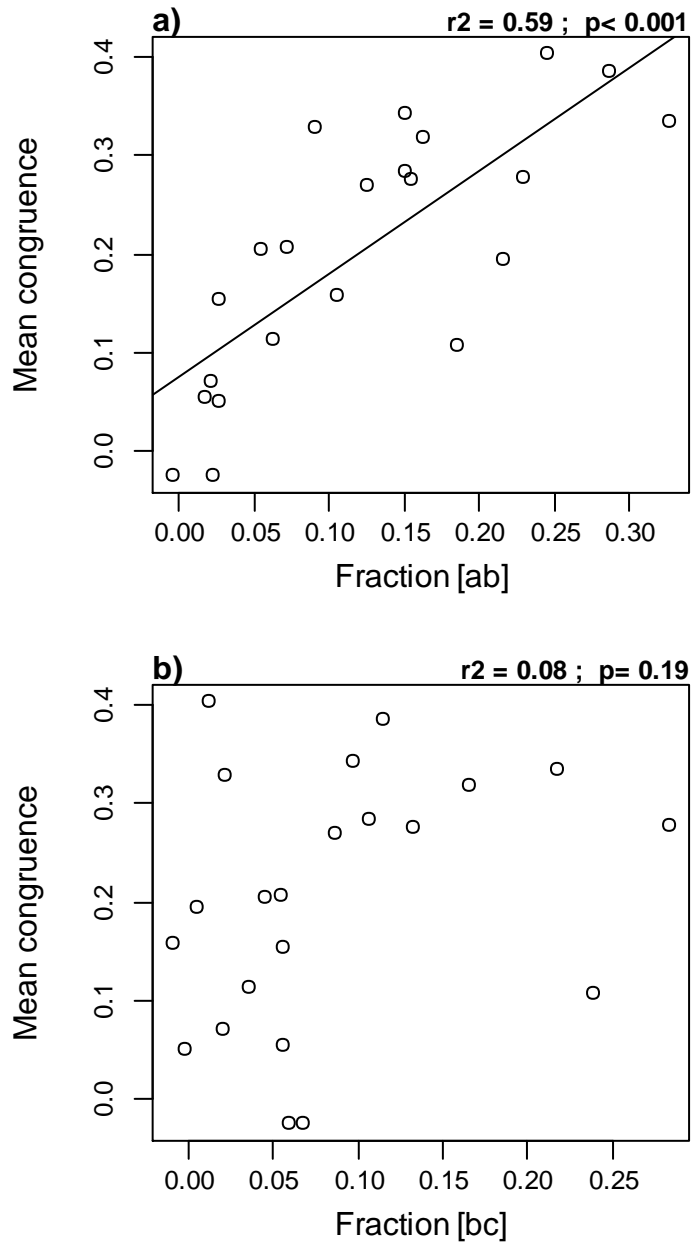


**Figure A1.** Mantel results for species abundance data (5000 permutations). Congruence among 22 community datasets was evaluated with Mantel correlations. This figure was constructed using the values presented in Table A2.





**Figure A2.** An ordination plot from second-stage NMDS obtained from the matrix of congruence (evaluated with the Mantel tests – see Table A1) among 22 community datasets. Stress = 19.11.



**Figure A3.** Relationship between the mean level of congruence values (Mantel) calculated for each group with the environmental [ab] and with spatial [bc] fractions derived from the partial RDA analyses. [ab] and [bc] represent the adjusted  $R^2$  resulting from RDAs between the biological matrices and the environmental predictor matrix and between the biological matrices and the spatial predictor matrix, respectively.

## Síntese

Acreditamos que o capítulo um irá facilitar bastante a fase inicial de pesquisadores novatos na área de ecologia espacial. Os conceitos e problemas discutidos no capítulo 1, bem como as referências citadas, podem nortear bem o aprendizado da ecologia espacial. Nos capítulos subsequentes, acreditamos que as principais mensagens são de que os autovetores espaciais não são tão flexíveis em criar variáveis espaciais que representam diversas escalas espaciais como se imaginava (Capítulo 2). As abordagens de dados brutos e de matrizes de distância são usadas para responder diferentes questões, entretanto, caso sejam utilizadas da forma errada, as conclusões provavelmente serão as mesmas, minimizando os problemas gerados pelo seu uso errôneo (Capítulo 3). No Capítulo 4 mostramos que os padrões de distribuição de diversos grupos são concordantes, indicando que o uso de grupos substitutos é uma boa forma para reduzir custos em estudos de monitoramento e criação de planos de manejo. Neste capítulo também é possível verificar que em escalas menores, como a extensão da reserva Ducke, os grupos de invertebrados não são boas ferramentas para biomonitoramento e criação de planos de manejo, pois nesta escala sua distribuição parece com uma distribuição aleatória. Ou seja, qualquer decisão tomada com base em invertebrados será tão eficiente quanto outra. Entretanto, o forte padrão ambiental e espacial observado para plantas nesta escala, bem como a concordância entre a maioria dos grupos, indica que os grupos de plantas podem ser boas ferramentas para serem utilizadas em estudos de biomonitoramento e em tomadas de decisões nestas escalas.

Em geral, observamos que a maioria dos grupos analisados neste trabalho apresentou um padrão ambiental mais forte que o padrão espacial. Isso indica que na escala dos dados analisados, variando de aproximadamente dez a aproximadamente 120 km, as principais características afetando os organismos são relacionadas ao ambiente. Pode ser que acima dessa extensão a capacidade de dispersão das espécies pode ter um efeito maior na diferenciação das comunidades e conseqüentemente os padrões espaciais sejam mais fortes e evidentes. Porém, apesar do baixo efeito espacial, nós salientamos que sempre é importante avaliar os efeitos espaciais em estudos ecológicos, pois dados estruturados espacialmente podem levar a erros tipo 1 e conseqüentemente a conclusões errôneas sobre os conjuntos de dados.

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## AULA DE QUALIFICAÇÃO

### PARECER

Aluno(a): VICTOR LEMES LANDEIRO  
 Curso: ECOLOGIA  
 Nível: DOUTORADO  
 Orientador(a): WILLIAM ERNEST MAGNUSSON

#### Título

"Relações espaciais da biodiversidade em florestas tropicais: em que o tratamento da autocorrelação espacial pode ajudar no entendimento e modelagem da distribuição de espécies e da diversidade beta?"

#### BANCA JULGADORA:

#### TITULARES:

Bruce Nelson (INPA)  
 Thiago Izzo (PDBFF)  
 Antônio Manzi (INPA)  
 Henrique Nascimento (INPA)

#### SUPLENTE:

Gonçalo Ferraz (PDBFF)  
 Philip Fearnside (INPA)

EXAMINADORES	PARECER	ASSINATURA
✓ Bruce Nelson (INPA)	(X) Aprovado ( ) Reprovado	<i>Bruce Nelson</i>
✓ Thiago Izzo (PDBFF)	(X) Aprovado ( ) Reprovado	<i>Thiago Izzo</i>
✓ Antônio Manzi (LBA/INPA)	(X) Aprovado ( ) Reprovado	<i>Antônio Manzi</i>
✗ Henrique Nascimento (PDBFF)	( ) Aprovado ( ) Reprovado	
✓ Gonçalo Ferraz (PDBFF)	(X) Aprovado ( ) Reprovado	<i>Gonçalo Ferraz</i>
✗ Philip Fearnside (INPA)	( ) Aprovado ( ) Reprovado	

Manaus(AM), 31 de outubro de 2008

OBS: *Dois recomendações para evitar perda de tempo:*  
 1. *Definir muito melhor o enfoque biológico geral*  
 2. *Definir melhor o trabalho para a forma de artigos que serão produzidos com o doutorado*

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**Avaliação de tese de doutorado**

Título: Relações espaciais e ambientais da biodiversidade em florestas tropicais

Aluno: Victor Lemes Landeiro

Orientador: William Magnusson

Co-orientador: Luis Mauricio Bini

**Avaliador: José Alexandre Felizola Diniz Filho**

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	<b>Muito bom</b>	<b>Bom</b>	<b>Necessita revisão</b>	<b>Reprovado</b>
Relevância do estudo	( X )	( )	( )	( )
Revisão bibliográfica	( X )	( )	( )	( )
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Metodologia	( X )	( )	( )	( )
Resultados	( X )	( )	( )	( )
Discussão e conclusões	( X )	( )	( )	( )
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*José Alexandre Felizola Diniz Filho*

Gotânia, GO, 28 de setembro de 2011, \_\_\_\_\_

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## Avaliação de tese de doutorado

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Avaliador: TADEU DE SIQUEIRA BARROS

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Bio Claro, 28/09/2011, Tadeu Siqueira  
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Título: Relações espaciais e ambientais da biodiversidade em florestas tropicais

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Orientador: William Magnusson

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**Avaliador: Thiago F. Rangel**

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Relevância do estudo	( X )	( )	( )	( )
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\_\_\_\_\_  
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### Referee evaluation sheet for PhD thesis

Title: Spatial and environmental relationships of biodiversity in tropical forests

Candidate: Victor Lemes Landeiro

Supervisor: William Magnusson

Co-supervisor: Luis Mauricio Bini

Examiner: Marie-Josée Fortin

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(X)	( )	( )	( )	( )
Literature review	( )	(X)	( )	( )	( )
Sampling design	( )	(X)	( )	( )	( )
Methods/procedures	(X)	( )	( )	( )	( )
Results	(X)	( )	( )	( )	( )
Discussion/conclusions	(X)	( )	( )	( )	( )
Writing style and composition	(X)	( )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	(X)	( )	( )	( )	( )

#### FINAL EVALUATION

Approved without or minimal changes

Approved with changes (no need for re-evaluation by this reviewer)

Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

Not acceptable (This product is incompatible with the minimum requirements for this academic level)

Toronto  
Place

October 5<sup>th</sup> 2011  
Date

*Marie-Josée Fortin*  
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Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to [pgecologia@gmail.com](mailto:pgecologia@gmail.com) and [claudiakeller23@gmail.com](mailto:claudiakeller23@gmail.com) or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

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### Avaliação de tese de doutorado

Título: Relações espaciais e ambientais da biodiversidade em florestas tropicais

Aluno: Victor Lemes Landeiro

Orientador: William Magnusson

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Montreal

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Aos 21 dias do mês de novembro do ano de 2011, às 09:00 horas, na sala de aula do Programa de Pós-Graduação em Ecologia - PPG ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia, o(a) Prof(a). Dr(a). **Elizabeth Franklin**, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). **Neusa Hamada**, do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o(a) Prof(a). Dr(a) José Luis Campana Camargo, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). Sheyla Couceiro, da Universidade Nilton Lins, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública da **TESE DE DOUTORADO** de **VICTOR LEMES LANDEIRO**, intitulada "Relações espaciais e ambientais da biodiversidade em florestas tropicais", orientada pelo(a) Prof(a). Dr(a). William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia e co-orientada pelo(a) Prof(a). Dr(a). Luis Maurício Bini, da Universidade Federal de Goiás.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

- APROVADO(A)       REPROVADO(A)  
 POR UNANIMIDADE       POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Bruce Walker Nelson

Prof(a).Dr(a). Elizabeth Franklin

Prof(a).Dr(a). Neusa Hamada

Coordenação PPG-ECO/INPA