Universidade Federal do Rio Grande do Sul

Instituto de Biociências

Programa de Pós-Graduação em Ecologia

Dissertação de Mestrado

Efeitos da estrutura de habitat e do espaço sobre a diversidade de mamíferos no

norte do Pantanal: uma abordagem de resolução fina

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Porto Alegre, Fevereiro de 2011

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre, Fevereiro de 2011

Em memória de Carlos Bastazini Neto

Agradecimentos

A elaboração desta dissertação só foi possível graças a um grande número de pessoas, que colaboraram de forma direta ou indireta, ao longo destes dois anos de mestrado e dos anos precedentes, durante a graduação. Assim sendo agradeço:

Em primeiro lugar, a minha família: minha mãe Fátima, meus irmãos Marcus e Demetrius, minha vó Isilda, e em especial meu falecido pai Carlos. Embora geograficamente distantes, vocês estiveram sempre comigo ao longo destes anos. A ajuda de vocês sempre foi essencial, mesmo não havendo palavra para agradecê-los, gostaria de dizer muito obrigado!

A Xênya, pelo companheirismo, carinho e amizade.

Aos meus orientadores, Andreas Kindel e Luiz Flamarion B. Oliveia, pelas oportunidades proporcionadas, as conversas, ensinamentos e pela amizade construída ao longo destes anos.

Aos meus amigos e colegas, que me ajudaram durante o trabalho de campo, sempre demonstrando carinho, amizade e solicitude, aguentando sol e chuva, longas viagens à cavalo, ataques de carrapatos, abelhas, lambe-olho, caga-fogo, formiga-de-novateiros, etc. E, pelas intemperanças (pra não dizer chiliques) em campo... Por isso sou extremamente grato à ajuda de vocês: Cecilia Siliansky de Andreazzi, Igor Pfeifer Coelho, José Cordeiro Luis Passos, Paula Braga Fagundes, e em especial à Alan Bolzan e Xênya Bernardes Garcia da Luz.

Aos professores Sandra M. Hartz, Demétrio L. Guadagnin e Leandro da S. Duarte por aceitarem o convite para participarem da banca.

A Xênya Bernardes Garcia da Luz e Rafael A. Dias pela leitura critica do manuscrito e pelas sugestões que ajudaram a melhorar a forma e o conteúdo do manuscrito.

Aos meus colegas e amigos do LEPEC, LEFF e do PPG-Ecologia, pelo carinho e amizade.

A CAPES pela concessão da bolsa de mestrado.

Ao Serviço Social do Comércio, em nome do Sr. Leopoldo G. Brandão, pelo financiamento do projeto.

Resumo

Compreender os mecanismos que causam variações espaço-temporais na diversidade biológica é uma das principais atribuições da ecologia. A teoria clássica de nicho prediz que o gradiente ambiental e sua complexidade mediam processos cruciais na estruturação das assembléias locais, permitindo a coexistência das espécies. A associação entre fatores espaciais e ambientais e diversidade inventário e diversidade diferenciação de mamíferos Neotropicais, tem sido usualmente investigada por estudos de resolução grosseira. Assim, o efeito do gradiente ambiental em resolução fina, ainda é praticamente desconhecido. Neste trabalho, eu investiguei os efeitos de processos ambientais, espaciais e ambientais espacialmente estruturados sobre a diversidade α e β de mamíferos, em uma área de aproximadamente de 1.100,42 km^2 no norte do Pantanal, a maior área úmida contínua do planeta. Utilizei um método de análise espacial chamado Análise de Coordenadas Principais de Matrizes Vizinhas e modelos lineares para descrever as contribuições desses processos. Os resultados demostram que fatores ambientais e espaciais, em conjunto, são mais importantes do que os efeitos independentes de cada fator, tanto para a diversidade α quanto para a β. O modelo completo explicou 18% da variação na diversidade α e 41% da variação na diversidade β. A diversidade β estimada foi negativamente relacionada com a diversidade α estimada. A diversidade β observada foi positivamente relacionada com a variação da estrutura de habitas entre sítios, embora o modelo tenha explicado uma porcentagem pequena da variação total. Os dados sugerem que embora os grandes mamíferos neotropicais sejam considerados espécies generalistas, eles não ocorrem de forma homogênea ao longo do gradiente, criado pelo mosaico da paisagem pantaneira, e que o papel da variação de nicho espacial é fundamental para manter a riqueza específica em nível regional.

Palavras-chave: partição da diversidade, nicho ecológico, micro-habitat, savanas e campos alagáveis, modelos espacialmente explícitos, armadilha fotográfica.

Abstract

Comprehending the mechanism that causes spatial-temporal variation in biological diversity is at the core of ecological inquiry. Classical niche theory states that environmental gradient and complexity mediate crucial processes that structure local assemblages, allowing species to co-exist. The association between spatial and environmental factors and mammalian inventory or differentiation diversity in the Neotropics, has been usually investigated by coarse grain studies, thus the effect of fine grain effects on mammalian diversity still largely unappreciated. In this paper, I investigated the effects of environmental, spatial, and spatially structured environmental processes on mammalian α- and β-diversity in an area of approximately 1,100.42 km^2 in the northern Pantanal, the largest continuous wetland on Earth. I used a spatial analysis method called Principal Coordinates of Neighbor Matrices analysis and linear models to depict the contributions of these processes. The results show that environmental and spatial factors, jointly, are more important than the independent effects of each factor for both, α- and β-diversity. The full model accounted for 18% of the variation in α-diversity and 41% of the variation in β-diversity. Estimated β-diversity decreased with estimated α-diversity. Observed β-diversity increased with site distinctness, although the model had a poor fit and explained a small amount of the total variance. My data suggests that although most large Neotropical mammals are broadly distributed and considered plastic species, they do not occur homogeneously across the landscape, and that the role of spatial niche is critical to maintain species richness at the landscape level.

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Introdução geral

Nicho Ecológico e a partição da diversidade biológica em componentes espaciais

Compreender os mecanismos que causam e mantêm a variação espaço-temporal da diversidade biológica é uma das principais atribuições da ecologia (Scheiner e Willig 2008). Os ecólogos têm desenvolvido e aplicado diferentes abordagens, a fim de identificar e explicar estes mecanismos (Cornell e Lawton 1992). Estas abordagens podem ser classificadas através de um continuum, segundo a importância das interações ecológicas na estruturação da comunidade (Cornell e Lawton 1992). Porém, por questões de simplicidade, estas abordagens têm sido separadas em duas classes de modelos, que representariam os extremos deste continuum: a primeira classe de modelos assume que as comunidades biológicas são estruturadas por processos determinísticos, baseados na concepção de nicho ecológico (Hutchinson 1957; MacArthur e Levins 1967; Leibold 1995; Chase e Leibold 2003), a segunda assume que o papel das interações entre as espécies é desprezível, e que a deriva ecológica, através de processos estocásticos, estruturaria as comunidades, os chamados modelos neutros (Caswell 1976; Hubbell 1997). Esta dicotomia conceitual entre as teorias baseada em nicho e neutralidade, ficou conhecida como o Paradoxo de MacArthur (Schoener 1989). Este paradoxo surgiu do fato de que, apesar de R. H. MacArthur ter sido um dos proponentes no desenvolvimento da teoria de nicho, seus estudos biogeográficos, geralmente baseavam-se na premissa de que as diferença de nicho entre as espécies, eram inexistentes ou desprezíveis, e que a estruturação das comunidades biológicas se davam por processos estocásticos. Assim, processos como extinção e colonização eram meramente resultados de distribuições probabilísticas (Chase e Leibold 2003; Chase e Bengtsson 2010).

O conceito de nicho ecológico desempenha um papel fundamental e sintetizador em ecologia (Vandermeer 1972; Leibold 1995; Chase e Leibold 2003). Desde a sua primeira definição, cunhada no início do século XX por R. H. Johnson (Schoener 2009), o conceito de nicho tem se revelado como uma das ferramentas mais poderosas para compreender e integrar fenômenos ecológicos e evolutivos entre os diferentes níveis de organização biológica (Leibold 1995; Chase e Leibold 2003), sendo usado com sucesso na identificação de processos determinísticos de manutenção de padrões espaciais em ecologia (e.g., MacArhtur et al. 1966; Chase e Leibold 2003; Levine e HilleRisLambers 2009, Harrison et al. 2010). Embora os modelos neutros sejam compatíveis com a evidência de padrões estocásticos e de contingência, eles são incapazes de explicar a relação ubíqua entre os gradientes ambientais e composição das comunidades biológicas e atributos funcionais de espécies (Harrison et al. 2010).

Há muito tempo, ecólogos reconhecem que a diversidade de espécies poderia ser particionada em diferentes componentes espaciais (Melo et al. 2009). Embora o conceito de diversidade de espécies em si, e o conceito de decomposição da diversidade em componentes espaciais só tenham surgido na segunda metade do século XX (Magurran 2004), uma rápida leitura através dos escritos de Darwin (1959; em especial os caps. 12 e 13) e de Wallace (1855, 1876), podem facilmente nos convencer que eles concebiam a existência da diversidade biológica dentro de unidades espaciais e da diversidade entre unidades espaciais. Porém, foi o contínuo trabalho de Whittaker, nas décadas de 60 e 70 (1960, 1972, 1977), que atraiu a atenção de ecólogos, biogeógrafos e biólogos da conservação para esta questão em especial.

A partição da diversidade tem sido empregada de forma "operacional", e os livros textos em geral, tratam as famosas escalas alfa, beta e gama, de forma um pouco abstrata. Porém, a partição de diversidade de Whittaker está profundamente enraizada

na teoria ecológica, e dois marcos teóricos, em especial, serviram de influência para o trabalho de gradientes de comunidades de Whittaker, e consequentemente a concepção da partição da diversidade: O primeiro marco teórico foi o surgimento do paradigma Gleasoniano de gradientes em comunidades biológicas (i.e, a visão de que as comunidades formam um contínuo ao longo do gradiente ambiental) em contrapartida ao paradigma Clementsiano (i.e, comunidades são vistas como uma espécie de "super-organismo" discreto). Apesar dos livros texto demonstrarem o embate destes dois paradigmas no início do século passado, esta discussão conceitual perdurou por décadas, e a substituição do paradigma Clementsiano pelo Gleasoniano, só foi possível graças ao trabalho de gradientes ambientais de Whittaker (Westman e Peet 1982), O segundo marco teórico, e talvez o mais importante, foi o desenvolvimento da teoria de nicho na segunda metade do século XX, em especial, os trabalhos de Hutchinson (1957) e MacArthur e Levins (1967). Os trabalhos destes autores romperam a visão de nicho, como ela foi concebida no início do século XX por R. H Johnson, R. Grinell e C. S. Elton. A partir dos trabalhos de Hutchinson (1957) e MacArthur e Levins (1967), o conceito de nicho ecológico ganhou um formalismo matemático, diferente dos primeiros modelos, mas a diferença mais importante dos modelos de nicho de Hutchinson (1957) e MacArthur e Levins (1967), é que, a partir do trabalho destes autores, o nicho deixa de ser algo inerente ao ambiente e passa a ser um atributo inerente às populações. Na visão clássica Hutchisoniana, o nicho ecológico é visto como um hipervolume multi-dimensional, onde as dimensões são as condições ambientais que definem o intervalo em que uma população pode persistir (Hutchinson 1957, ver também Schoener 2009; Chase e Leibold 2003). Whittaker (1972) acreditava que a riqueza específica era uma função direta da complexidade do hipervolume Hucthisoniano, e que o processo evolutivo favoreceria a diferenciação nas posições

ocupadas pelas espécies neste hiperespaço do nicho, e consequentemente, ao longo do gradiente ambiental (Whittaker 1972). Dentro desta perspectiva, o gradiente e a complexidade ambiental mediariam processos cruciais, nos quais as comunidades locais se estruturariam, através dos efeitos de fatores demográficos e de comunidades, tais como sobrevivência, forrageamento, predação e competição (Gibb e Parr 2010). Portanto, para compreender e explicar a distribuição das espécies ao longo de gradientes ambientais, no qual o nicho define a probabilidade de persistência de uma população ao longo do gradiente, Whittaker (1960, 1972, ver revisão em Magurran 2004) propôs que a diversidade biológica poderia ser dividida em componentes distintos: diversidade-ponto (dentro da amostra), diversidade-padrão (entre amostras), α (dentro do habitat) β (entre habitats), γ (na paisagem), δ (entre paisagens) e diversidade ε (na província biogeográfica). Embora a dependência de escala desses conceitos tenha sido criticada (Jurasinski et al. 2009), eles podem ser sintetizados em dois conceitos simples: a diversidade-inventário (ponto, α, γ e ε) e a diversidade-diferenciação (padrão, β e δ; Magurran 2004). Apesar da escala de interesse, estas quantidades se tornaram fundamentais para a compreensão de fenômenos ecológicos e para o desenvolvimento de programas de conservação.

O efeito de fatores ambientais e espaciais sobre a diversidade inventário e diversidade diferenciação de mamíferos neotropicais tem sido investigado por estudos que variam em sua extensão espacial, mas que, normalmente, se baseiam em uma resolução grosseira (Vásquez et al. 2006; Diniz-Filho et al 2008 a, b; Melo et al 2009; Padial et al. 2010). Assim, a implicação dos efeitos destes fatores em escala fina ainda é pouco compreendida.

Considerações sobre o Pantanal

O Pantanal é considerado a maior área úmida contínua do Planeta (Swarts 2000a, b, Zeilhofer 2006). Algumas estimativas apontam que o Pantanal possa ocupar uma área de até 210.000 km² (Swarts 2000b), distribuída pelo Brasil, Bolívia e Paraguai (Swarts 2000a). Classificado como um bioma de Campos e Savanas Alagáveis (Olson et al. 2001), a região apresenta um mosaico único de habitats diversificados, em resposta às mudanças geológicas que ocorrem desde o Quaternário, diferenças pronunciadas no regime anual de chuvas e de inundação e a ocupação e uso da terra (Swarts 2000a, Pott et al. 2004; Harris et al. 2005a; Alho 2008; Oliveira et al in press.). Esta heterogeneidade também é resultante do encontro de quatro províncias biogeográficas Cerrado, Amazônica, Chaquenha e Atlântica (Alho 2008).

Além de uma paisagem diversificada, o Pantanal abriga uma biota rica em espécies e algumas das maiores populações conhecidas de mamíferos neotropicais ameaçados de extinção (Harris et al. 2005a; Mamede e Alho 2006; Alho 2008). A região é comumente descrita como "um santuário de vida selvagem, sem paralelos, e de beleza espetacular" (Swarts 2000b, pag.1), que atrai pesquisadores e turistas do mundo todo. Porém, apesar de sua importância socioambiental, o futuro do Pantanal está em risco. Mudanças recentes no sistema de produção agropastoril, expansão da fronteira agrícola e das áreas urbanas estão modificando a paisagem da região (Starts 2000a; Silva e Girard 2004; Harris et al. 2005a,b; Junk e Cunha 2005, Oliveira et al. In press). Aproximadamente 95% da área do Pantanal pertence à iniciativa privada (Seidl et al. 2001) e algumas estimativas indicam que aproximadamente 45% da vegetação da Bacia do Alto Paraguai já foi suprimida (Harris et al. 2005b). Grandes projetos de aproveitamento hidroelétrico e o projeto de construção da Hidrovia Paraná - Paraguai irá modificar e comprometer a intrincada dinâmica das águas, característica da região,

comprometendo assim sua paisagem e biota (Swarts 2000a; Silva e Girard 2004; Harris et al. 2005a; Junk e Cunha 2005).

Quando se fala em gestão ambiental, o Pantanal é comumente comparado ao Everglades americano (Wade et al. 1993; Wade 1996; Barnett 2000; Seidl 2001). A comparação é normalmente realizada com a finalidade de se encontrar similaridades em aspectos hidrológicos, ecológicos e socioeconômicos entres estas duas importantes áreas úmidas e também, na esperança de que os gestores públicos sul-americanos percebam que ainda há tempo de se evitar a tragédia ambiental e econômica ocorrida na região dos Everglades, devido à má gestão dos recursos naturais. Comparar os Everglades com o Pantanal também demonstra outro fato importante: o Pantanal é uma região pouco estudada (ver também Swarts 2000a, b). Uma pesquisa no banco de dados do ISI Web of Knowledge revela que o número de estudos publicados sobre o *Everglades (n =* 1.961) é três vezes maior que o número de estudos publicados sobre o Pantanal (n = 623) (pesquisa realizada em 10/02/2011). Baseando-se em uma amostragem aleatória de 20 estudos de cada área, é possível observar que boa parte dos estudos publicados sobre o Pantanal versa sobre atividades econômicas (Figura 1), em especial a atividade pecuária (Figura 1), enquanto que boa parte dos estudos realizados sobre os Everglades tratam de assuntos ligados às ciências naturais (Figura 1). Este desconhecimento científico é outro fator limitante para o desenvolvimento de iniciativas de conservação eficientes na região.
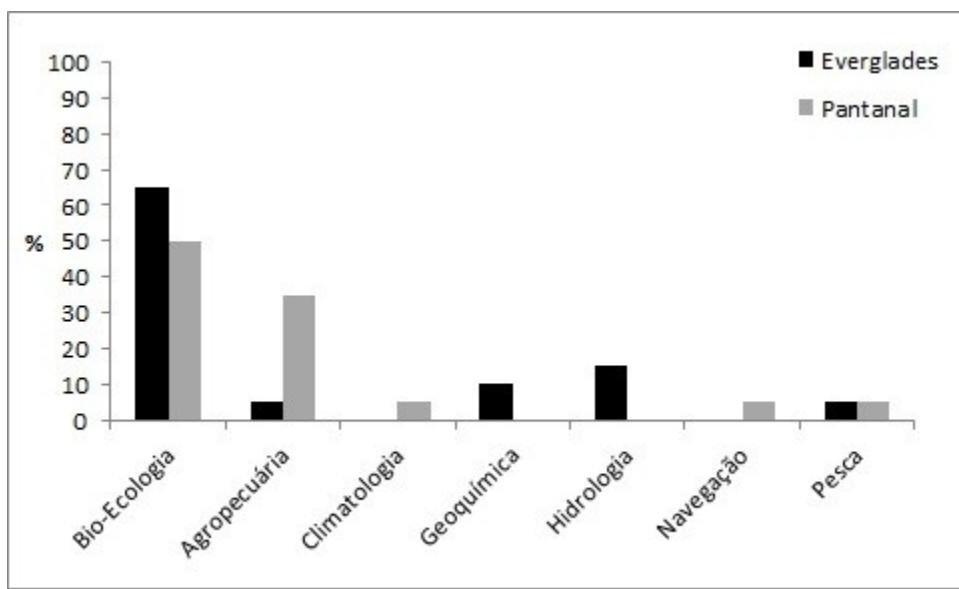
Figura 1. Comparação entre estudos realizados no Pantanal, América do Sul e nos Everglades, EUA. Comparação construída a partir 20 estudos sorteados de cada área, a partir da base de dados disponíveis na ISI Web of Knowledge (acesso em 10/02/2011).

Um último aspecto a ser considerado é que o Pantanal oferece um desafio a mais para biólogos da conservação e gestores ambientais: o Pantanal é um sistema dinâmico, relativamente recente e em formação (Eberhard 2000). Mudanças naturais na paisagem como alterações nos cursos dos rios e a expansão florestal sobre campos e savanas podem ser facilmente observadas de um ano para o outro (Eberhard 2000). Assim, a conservação do Pantanal exige que as iniciativas de conservação, sejam elas públicas ou privadas, esclareçam e assumam seus objetivos e suas escolhas entre conservar estado ou processo. O manejo de grandes mamíferos (sejam eles autóctones ou alóctones) pode ter um papel importante neste processo de tomada de decisão, em especial na dinâmica de tensão campo-floresta. A experiência demonstra que os mamíferos desempenham um papel central no funcionamento dos ecossistemas (Laws 1970; Estes et al. 1989; Brown e Heske 1990; McNaughton et al. 1988; Estes et al. 1998; Smith et al. 2003; Danell et

al. 2006; Dobson et al. 2006; Schipper et al. 2008), e muitos estudos indicam que os grandes mamíferos podem ser importantes tanto no processo de expansão de áreas florestais, agindo como dispersores de sementes (e.g., Fragoso 1997; Fragoso e Huffman 2000), quanto na manutenção de áreas abertas (e.g., Laws 1970; McNaughton et al. 1988; Danell et al. 2006). Assim, o conhecimento acerca da ecologia deste táxon, pode ser fundamental para o desenvolvimento de estratégias de conservação na região.

Embora o Pantanal abrigue algumas das maiores populações de mamíferos neotropicais do planeta (Trolle 2003; Harris et al. 2005a; Mamede e Alho 2006; Alho 2008), o conhecimento sobre este táxon na região ainda é incipiente (Brito et al 2009). Os estudos sobre mamíferos realizados na região têm focado principalmente em questões populacionais de mamíferos cinegéticos (e.g., Alho 1987; Mourão e Tomas. 2000; Tomas et al. 2001a, 2001b; Trolle et al. 2008) e de carnívoros (e.g., Schaller e Crashaw Jr. 1980; Trolle e Kéry 2003; Trolle et al. 2007), e no conflito entre a atividade pecuária e grandes carnívoros (e.g., Dalponte 2002, Zimmermann e Walpole 2005). Poucos estudos têm focado as questões em nível de comunidade (Mamede e Alho 2006; Diniz-Filho et al. 2008a; Desbiez et al. 2009, 2010). Até mesmo levantamentos básicos de espécies são raros (Trolle 2003).

Neste contexto, esta dissertação objetiva contribuir para a compreensão dos processos ecológicos, que mantém a variação da diversidade inventário e diversidade diferenciação de mamíferos no norte do Pantanal. Este trabalho se diferencia de estudos publicados anteriormente, principalmente pela sua escala de resolução (i.e., tamanho da menor unidade de estudo *sensu* Gotelli e Ellison 2004); a maior parte dos trabalhos já publicados utilizam resoluções grosseiras para compreender a associação de mamíferos e fatores ambientais e/ou espaciais (Vásquez e Gaston 2006; Diniz-Filho et al. 2008a, b; Melo et al. 2009; Padial et al 2010). Eu utilizei uma abordagem de resolução fina,

modelando a variação dos componentes de diversidade em função da variação de fatores ambientais. Embora estudos baseados em resoluções grosseiras sejam essenciais para podermos compreender grandes padrões de diversidade, acredito que a abordagem empregada neste trabalho contribuirá para a compreensão dos efeitos da estrutura de habitat sobre a variação da diversidade. Este tipo de resolução espacial também nos permite conduzir experimentos de mensuração e de manipulação (Hurlbert 1984), em uma escala relevante para os organismos (Gotelli e Ellison 2004). Além disso, este tipo de abordagem é interessante do ponto de vista da gestão de unidades de conservação. Assim, os resultados apresentados, além de apresentarem importantes implicações teóricas, fornecerão subsídios para a o desenvolvimento de estratégias de conservação eficientes para a maior área úmida do planeta.

Drivers of mammalian diversity in the northern Pantanal: disentangling spatial and fine-scale environmental effects[1]

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Abstract

Comprehending the mechanisms that drive spatial variation in biological diversity is at the core of ecological inquiry. Classical niche theory states that environmental gradient and complexity mediate crucial processes that structure local assemblages, allowing species to co-exist. The association between spatial and environmental factors and mammalian inventory or differentiation diversity in the Neotropics has been usually investigated by coarse grain studies, thus the effect of fine grain environmental factors on mammalian diversity still largely unappreciated. In this paper, we investigated the effects of environmental, spatial, and spatially structured

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1   This manuscript follows the guidelines established by the periodic Biodiversity and Conservation.

environmental processes on mammalian α- and β-diversity in an area of approximately 1,100.42 km^2 in the northern Pantanal, the largest continuous wetland on Earth. We used a spatial analysis method called Principal Coordinates of Neighbor Matrices and linear models in order to depict the contributions of these processes. Our results show that environmental and spatial factors, jointly, are more important than the independent effects of each factor for both, α- and β-diversity. The full models accounted for 18% of the variation in α-diversity and 41% of the variation in β-diversity. Estimated β-diversity decreased with estimated α-diversity. Observed β-diversity increased with site distinctness, although the model had a poor fit and explained a small amount of the total variance. Our data suggests that although most large Neotropical mammals are broadly distributed and considered plastic species, they do not occur homogeneously across the landscape, and that the role of spatial niche is critical in order to maintain species richness at the landscape level.

Introduction

Comprehending the mechanisms that drives variation in biological diversity across space is at the core of ecological inquiry. Ecologists have developed deterministic and stochastic approaches, in order to identify and explain these mechanisms, which have been entangled in what is known as the "MacArthur's Paradox," (Schoener 1989) i.e., the conceptual dichotomy between niche-based (deterministic) and neutral-based (stochastic) approaches (Chase and Leibold 2003; Chase and Bengtsson 2010). The concept of ecological niche provides ecologists a theoretical framework, capable of integrating ecological and evolutionary phenomena across levels of biological organization (Leibold 1995; Chase and Leibold, 2003), and it has been successfully used to identify and test deterministic processes driving spatial patterns in community ecology (MacArhtur et al. 1966; Leibold 1995; Chase and Leibold 2003; Levine and HilleRisLambers 2009; Harrison et al. 2010; Arakaki and Tokeshi 2011). Neutral-based theories (Caswell 1976; Hubbell 1997) propose that species abundance oscillates in a random walk due to random mortality and stochastic, but spatially constrained dispersal (Tuomisto and Ruokolainen 2006). Although neutral models are compatible with evidence for stochastic pattern of community structure, they are unable to explain the ever-present relationship between environmental gradients and community composition and species traits (Harrison et al. 2010).

Early ecologists recognized that species diversity could be partitioned into different components (Melo et al. 2009). Although the concept of diversity partitioning and the species diversity itself, did not arise until the late 1950s (Magurran 2004), a quick reading through Darwin's (1859) and Wallace's (1855, 1876) writings can easily convince one that they did conceive the existence of diversity within and between spatial unities. But it was the continuous work of Whittaker in the 1960s and 1970s

(1960, 1972, 1977) that has driven our attention to the importance of diversity partitioning across spatial scales.

Although many researchers have embraced Whittaker's diversity components as an abstract and/or "operational" concept, his diversity partitioning idea is deeply embedded in niche theory. According to the traditional Hutchisonian view, the ecological niche is seen as a multi-dimensional hypervolume, where the dimensions are environmental conditions that define the range in which a population can persist (Hutchinson 1957, see reviews in Chase and Leibold 2003 and Schoener 2009). Whittaker (1972), influenced by the work of Hutchinson (1957), believed that species richness was a direct function of the complexity of the Hutchisonian hypervolume and that evolutionary processes would favor species evolution toward differences in niche requirement, and consequently toward different location of their hypervolumes in the niche hyperspace. Thereby, different species would occupy different positions along the environmental gradient (Whittaker 1972). Thus, according to niche-based view, environmental gradient and complexity mediates crucial processes that structure local assemblages through effects on demographic and community factors such as survival, foraging behavior, predation and competition (Gibb and Parr 2010). Therefore, in order to understand species distribution along environmental gradients, Whittaker (1960, 1972, 1977) ascertained that ecological diversity could be partitioned across different spatial scales. During his early work, Whittaker (1960) proposed three basic levels of diversity decomposition, that were further developed, until they reached the following arrangement: point-diversity (within sample), pattern-diversity (between samples), and his well-known levels: α- (within habitat) β- (between habitats), γ- (within landscape), δ- (between landscapes) and ε- diversity (within biogeographic province) (Whittaker 1972; Magurran 2004). Although some authors have correctly criticized the scale-

dependency of these concepts (Jurasinski et al. 2009), they may be simplified and synthesized in two simpler concepts: inventory diversity, (point-, α -, γ- and ε-diversity) and differentiation diversity (pattern-, β- and δ-diversity) (Whittaker 1972, see reviews in Whittaker et al. 2001 and Magurran 2004). Nonetheless, despite the scale of interest, these quantities have become fundamental, not only for our understanding of ecological phenomena, but also for the development of conservation strategies.

Mammals play a central role in ecosystem functioning (Laws 1970; Estes et al. 1989; Brown and Heske 1990; McNaughton et al. 1988; Estes et al. 1998; Smith et al. 2003; Danell et al. 2006; Dobson et al. 2006; Schipper et al. 2008), and it has been demonstrated that mammalian extinctions can have serious deleterious effects on biological communities and ecosystems (Estes et al. 1989; Brown and Heske 1990; Estes et al. 1998; Beger et al. 2001; Smith et al. 2003; Dobson et al. 2006). Thus, understanding the spatial and environmental factors driving mammalian diversity is essential to the development of successful conservation initiatives, directed not only to the protection of mammal species themselves, but also to the protection of entire ecosystems.

The association between spatial and environmental factors and mammalian inventory or differentiation diversity in the Neotropics, have been usually investigated by studies that varied in their spatial extent, but that were based on large grain resolution (Vásquez and Gaston 2006; Diniz-Filho et al. 2008a, b; Melo et al. 2009; Padial et al 2010). Our study differs from earlier studies, due to its grain size; we investigated the effects of habitat, spatial, and spatially structured habitat processes on mammalian diversity at the micro-habitat scale. Although studies based on large grains are essential in order to appreciate broad-scale patterns of species diversity, we believe that fine-grain analyses will bring new insights to our comprehension on how species

diversity responds to micro-habitat related biotic factors and how it is structured across space. Moreover, small grain studies allow ecologists to conduct mensurative or manipulative experiments (Hurlbert 1984) at scales that are relevant to organisms (Gotelli and Ellison 2004), where they actually pursuit environmental cues, which serve as indicators of habitat's fitness potential (Campbell et al. 2010).

The Pantanal is considered the largest continuous wetland on Earth (Swarts 2000, and references therein, Zeilhofer 2006). The region presents an unique mosaic of diverse habitats, in response to geological changes, which have occurred since the Quaternary, pronounced differences in annual rain and flooding regime, in addition to human land use (Pott and Pott 2004; Harris et al. 2005; Alho 2008). This heterogeneity also results from the confluence of four biogeographic provinces: Cerrado, Amazon, Chaco and Atlantic Forest (Alho 2008, Harris et al. 2005). The Pantanal harbors an extraordinarily rich biota and some of the largest populations of endangered Neotropical mammals (Trolle 2003; Harris et al. 2005; Mamede and Alho 2006; Alho 2008). Nonetheless, the mammalian fauna of the Pantanal is, surprisingly, relatively little studied (Brito et al. 2009). Most of the studies focus on population parameters of game species (e.g., Alho 1987; Mourão and Tomas 2000; Tomas et al. 2001a, 2001b; Trolle et al. 2008) and carnivores (e.g., Schaller and Crashaw Jr. 1980; Trolle and Kéry 2003; Trolle et al. 2007), and human - carnivore conflicts (e.g., Dalponte 2002, Zimmermann and Walpole 2005). Few researches have been conducted in order to understand community processes and patterns in mammalian assemblages inhabiting the Pantanal (but see for instance, Mamede and Alho 2006; Diniz-Filho et al. 2008A; Desbiez et al. 2009, 2010). Even basic mammalian surveys are lacking (Trolle 2003).

Our main goal was to evaluate the effects of environmental, spatial, and spatially structured environmental factors driving mammalian diversity variation in the northern

Pantanal. Although, according to the scheme proposed by Whittaker (1972, see review in Whittaker et al. 2001 and Magurran 2004), point- and pattern-diversity would be the most adequate terms to our scale of interest, we decide to use the terms α – and β-diversity, as it is widely disseminated in the literature and it has been used without the appropriate regard to the scale of interest (Gray 2000; Whittaker et al. 2001), being more compatible and comparable with the available literature, and because these concepts are more familiar to wildlife managers. Of course, we do not envision our replicates as closed assemblages, but rather they represent open sites and the species richness and composition observed in each site reveals how mammals occupy and use the environmental gradient. Our specific goals were: i) to partition the effect of spatial and environmental mechanisms driving variation in mammalian α – and β-diversity at the micro-habitat scale; ii) to test the relationship between α – and β-diversity; iii) to test how "site distinctness" affects variation in β-diversity. To our knowledge, this is the first work to investigate spatial and environmental drivers of inventory and differentiation mammalian diversity, at the micro-habitat scale in the Pantanal. Besides its obvious contribution for understanding ecological processes driving spatial variation in inventory and differentiation diversity, our results also provide guidance for the development of sound conservation strategies in the planet's largest, and yet poorly known, wetland.

Material and Methods

Study site

Our study was conducted at the Private Reserve of Natural Heritage SESC-Pantanal (PRNH SESC), Central West Brazil (16°45'S and 56°15'W; Figure 1).

Encompassing an area *ca*. 1,076 km^2 the PRNH SESC-Pantanal is the largest private owned conservation reserve in Brazil, covering a complex and heterogeneous landscape (de Luca et al. 2009, RAMSAR 2010).

The area has a flood period between December and April due to the rainfall regime in the region and in the headwaters of the Upper Paraguay Basin. The annual rainfall varies between 1,000 and 1,600 mm, concentrated in the summer (Hasenack et al. 2010). The remaining months are marked by a pronounced drought. The annual temperature in PRNH SESC ranges between 6.1 and 44ºC (Hofmann et al. 2010), winter being the warmest season (Hasenack et al. 2010; Hofmann et al. 2010).

Although approximately 40% of the PRNH SESC and its surroundings is covered by woody dominated savannas (de Luca 2009), the reserve is a good sample of the diverse Pantanal landscape, encompassing permanent and seasonal rivers, streams and floodplains, man built ponds, shrub-dominated wetlands, seasonally semi-deciduous forests and alluvial forests which extend along the two major rivers that tangent the reserve (Cuiabá river at the western boundary and São Lourenço river at the eastern boundary) (de Luca et al. 2009, RAMSAR 2010). Due to its importance to the conservation of biodiversity, the PRNH SESC-Pantanal is part of important national and international conservation initiatives and treaties, being recognized as an Important Bird Area (IBA MT10; de Luca et al. 2009), Brazilian Priority Area for Conservation (MMA 2007) and as a wetland of international importance (RAMSAR site 1,270) by the Ramsar Convention (RAMSAR 2010).
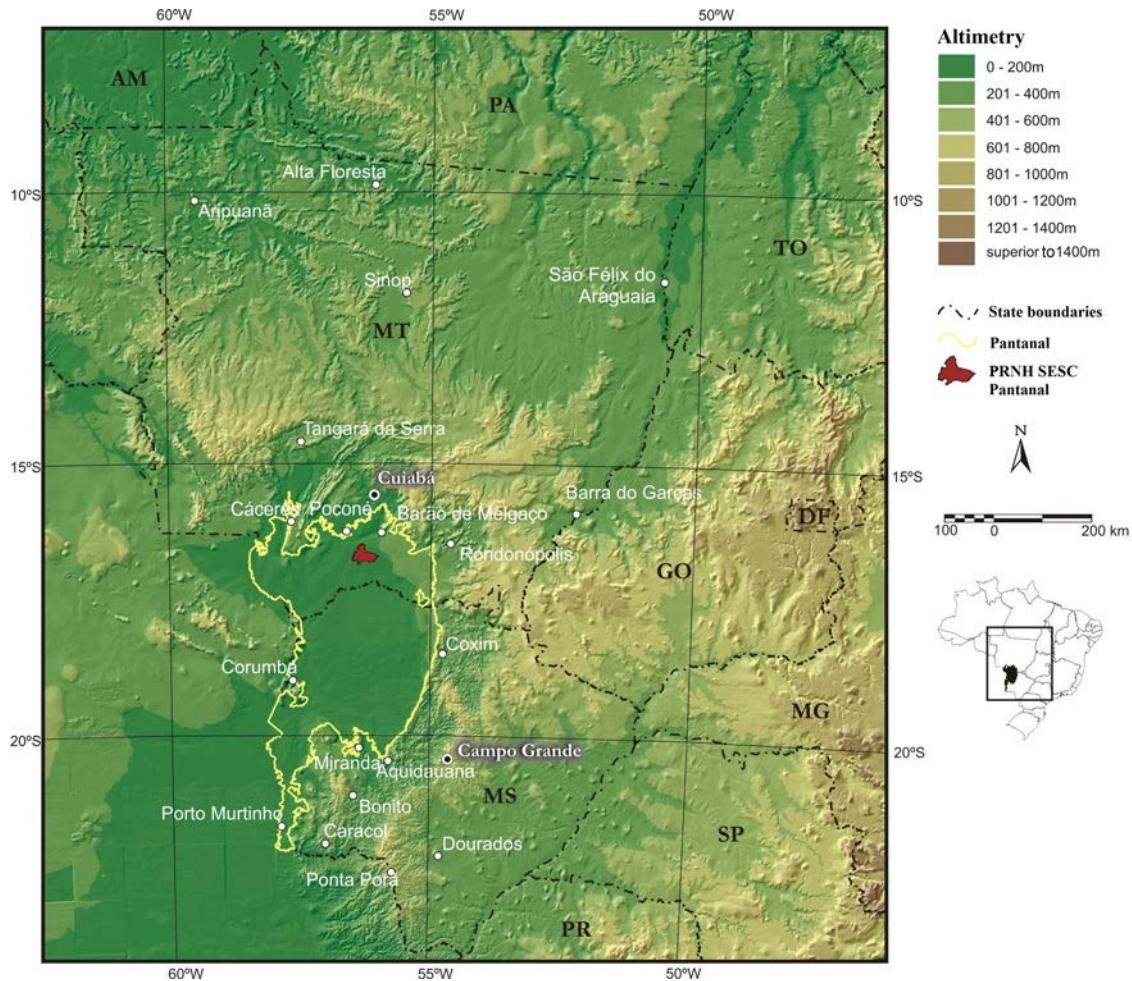
Figure 1. Map of the Brazilian Pantanal and the location of the PRNH SESC-Pantanal. Courtesy of G.S. Hofmann.

Experimental Design and Data Collection

We used a mensurative experiment approach (*sensu* Hurlbert 1984), where replicates were randomly distributed across the reserve. Each replicate consisted of a camera station located at the center of five vegetation quadrats (10 x 10m), arranged as a cross (Figure 2). Camera station allocation, and consequently, the center of innermost vegetation quadrat, was randomly assigned. The remaining four quadrats were placed 50m away (distance between the center points of each quadrat), along the four cardinal directions (Figure 2). In order to turn our study logistically possible, randomization of

sampling unities was restricted, based on two criteria: i) sampling stations should not be further than 2km from an access point (e.g., roads, trails, rivers, streams, fence lines, etc.); ii) each sampling unit should be placed at least 600m apart from one another. As we were unable to carry out a completely randomized design, we tested the spatial pattern of our replicates, using a nearest neighborhood analysis (Fortin and Dale 2005). This analysis revealed that the spatial pattern of our replicates follows a Poisson process ($Z = 0.81$; $p = 0.41$, $R = 1.04$), being randomly distributed across space.
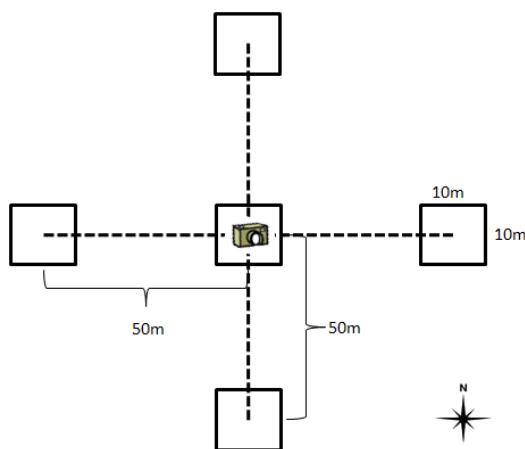
Figure 2. Lay-out of our replicates, used to sample mammalian diversity and vegetation structure. Five vegetation quadrats ($100m^2$) were arranged as a cross, centered at the camera station.

Mammalian survey

We conducted two camera-trap surveys between March 2010 and June 2010, during the ebb season (n = 80 trapping stations) and between August and September 2010, during the dry season, (n = 36). We sampled a total of 116 sites, forming an estimated convex polygon of 1,100.42 km^2 (Figure 3). We used 41 camera traps (PC90 High Output, Reconyx™, Inc. USA), which were rotated among all sites, in order to sample mammalian fauna. PC90HO is a full covert Infrared Night Vision (i.e., "flashless") camera trap, which operates on a passive infrared-triggered system (Swann

et al. 2011). Our original goal was to sample each site continuously for 21 days. Due to logistic constrains and batteries failures, our sampling effort in each camera station varied from 13 to 28 days, (x=21.20 ± SD=2.59), totaling a camera trapping effort of *ca.* 2,575 trapdays and 61,800 hours.
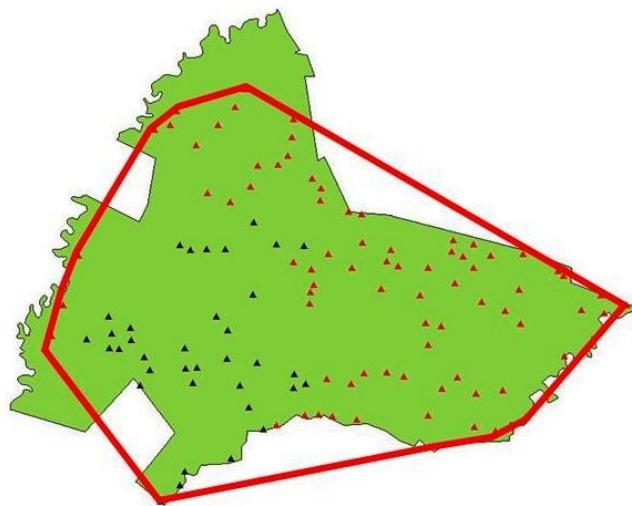
Figure 3. Schematic map showing camera trapping stations in the PRNH SESC-Pantanal, northern Pantanal, Brazil. Red triangles are the trap locations for the ebb season (n = 80), and blue triangles are the trap locations for the dry season (n = 36); Minimum convex polygon encompassing all sampling unities, covers an estimated area of 1,100.42 km^2.

We defined α-diversity as the observed species richness in each sampling unit. We removed from our analyses all small rodents that belonged to the families Cricetidae and Echimyidae. Non-identified mammals were also excluded from our analyses. Due to the difficulties and uncertainties related to the taxonomy of cervids classified in the genus *Mazama* (Duarte et al. 2008; Abril et al. 2010), we classified them in a single morphospecies, encompassing at least three species.

We modified the approach developed by Anderson et al. (2006) in order to estimate β-diversity. These authors proposed that β-diversity could be measured as the average dissimilarity from individual observation units to their group centroid in multivariate space. Although their approach was developed to compare β-diversity between regions or factors, we adopted their approach and used the distance of each sampling unit from the group centroid as our dependent variable, which measures the individual mean site dissimilarity from all remaining sites, or in other words, the discrepancy from its group expectancy. We computed Jaccard dissimilarity (d_j) as our resemblance measure, which is the complement to the well known Jaccard similarity coefficient (Legendre and Legendre 1998). Jaccard distance is an asymmetrical binary measure that compares each pair of sites, excluding double-zeros (Legendre and Legendre 1998) and may be interpreted directly as the probability that two species, one randomly drawn from each site, will not be shared (Anderson et al. 2006). Also, it has a clear correspondence to Whittaker's original concept of β-diversity (Anderson et al. 2006). We defined the multivariate space computing a Principal Coordinate Analysis (PcoA), and then calculated the distance of each site to the group centroid. Legendre et al. (2005) ascertained that measures related to β-diversity analyses, mainly belong to three different levels of "abstraction". Our approach fits their third level of abstraction, which they called: "*Variation in beta diversity among groups of sites*" i.e., how and why beta diversity varies among sites.

Environmental drivers

We counted and measured the circumference (to the nearest 0.5cm) of all trunks and stems of woody plants with circumference at-breast-height (CBH) ≥ 5cm, classifying them in three groups: palm trees (Arecaceae; Stevens 2001), represented by

five genera (*Acrocomia*, *Allagoptera*, *Copernicia*, *Bactris* and *Scheelea*); bamboo (subfamily Bambusoidae; Stevens 2001), represented by a single genus (*Guadua*); and all the remaining flowering plants. Palms were measured at the ground surface height. Then, we estimated basal area and density (Duringan 2003) in each quadrat for all woody plants within these three groups. The reason why we separated these three groups lays on the fact that we expected that palms would have significant positive effect on α- and β- diversity, due to its well known importance as a feeding resource to many mammal species (Andreazzi et al. 2009, and references therein), and that bamboo basal area and density would have a negative effect on diversity, either directly as bamboo stands may function as a "barrier" for animal movement, and indirectly, as they might affect growth and development of plants used as feeding resource.

Canopy and understory heights were estimated using an inclinometer (Carl Zeiss^{TM}).

We measured canopy closure i.e., the "proportion of the sky hemisphere obscured by vegetation when viewed from the center of each plot", as defined by Jennings et al. (1999) taking a photograph at the center of each quadrat, with a 180º fish eye lens (Nikon^{TM} FC-E8) coupled to a digital camera, leveled at 1.5 meters (Jennings et al. 1999). Canopy closure was estimated using the software Gap Analyzer (Frazer et al. 1999).

We estimated horizontal foliar obstruction using a vegetation profile board (25 x 25 cm) placed 5 m away from the center of each quadrat, in four different heights (0.0, 0.5, 1.0, and 1.5 m), rotating the board along the four cardinal directions. Therefore, we obtained 16 estimates in each quadrat, and used the arithmetic mean of these readings to characterize the site. At each observation height the observer recorded the ocular

estimation of the amount of the profile board that is obscured by plant parts (Hays et al. 1981), to the nearest 5%. This approach is modified from Hays et al. (1981).

All independent variables are summarized in Table 1.

Table 1. Description of environmental features used as independent variables in our models.

Variable	Acronym	Unit	Description
Bamboo basal area	BBA	$m^2.ha^{-1}$	Area occupied by the cross-section of bamboo ramets (CBH ≥5cm) at breast height
Palm basal area	PBA	m2.ha-1	Area occupied by the cross-section of palm tree trunks and stems (CBH ≥5cm) at ground surface height
Vascular basal area[1]	VBA	$m^2.ha^{-1}$	Area occupied by the cross-section of tree trunks and stems (CBH ≥ 5cm) at breast height
Bamboo density	BD	ind.m-2	Number of individual bamboo ramets per unit area
Palm density	PD	ind.m-2	Number of individual palm trees per unit area
Vascular density[1]	VD	ind.m-2	Number of individual flowering plants (excluding bamboos and palms) per unit area
Canopy height	CH	m	Canopy height estimated using a inclinometer
Understory height	UH	m	Understory height estimated using a inclinometer
Canopy closure	CC	%	Proportion of the sky hemisphere obscured by vegetation photographed at the center of each quadrat
Horizontal obstruction	HO	%	Average proportion of the profile board when viewed from across a distance of 5m

[1]All vascular woody species excluding palms and bamboos; see "vegetation structure" for details.

Numerical and statistical analyses

As our exclusive interest was depicting the effects of environmental and spatial factors on diversity, our first analytical step was to evaluate the effect of temporal components (i.e., season and trapdays) upon α- and β-diversity. This procedure helped

us to decide our analytical approach and whether it would be necessary to control for possible temporal effects on our models. Thus, we tested the effect of season and trap days on each diversity component, using linear models (Legendre and Legendre 1998; Zar 1999). The results from all linear models were not significant (all p-values > 0.50, for 114 degrees of freedom), with the exception of the relationship between trapdays and β-diversity (R^2 = 0.049; $F_{1, 114}$ = 5.96; p = 0.02). Nonetheless, this relationship had a small magnitude effect (slope = -0.008), thus we ignored these two variables (season and trapdays) in our final spatial models.

We inspected non-orthogonality in our set of independent variables, constructing a partial correlation matrix with all environmental attributes. Partial correlation methods allowed us to compute the correlation coefficient between every pair of variables, while holding the value of each of the other variables constant, taking into account the interactions of any of the other variables on the pair being examined (Zar 1999). From our entire set of explanatory variables, only Bamboo basal area and Bamboo density were strongly correlated with one another (partial-r =0.99), thus we removed Bamboo basal area from our models. All other pair of variables presented partial correlation < 60% and were kept in our final models.

In order to investigate the role of space affecting mammalian diversity we employed an eigenvector-based filtering method (Griffith 2003) known as Principal Coordinate of Neighbor Matrices (PCNM; Borcard and Legendre 2002; Borcard et al. 2004; Dray et al. 2006). PCNM analysis consists on the eigenvalue decomposition of a truncated matrix of geographic distances among sampling sites that is obtained through PCoA (Borcard and Legendre 2002; Borcard et al. 2004; Dray et al. 2006). The truncation reinforces the contribution of short distance effects after the filtering process (Diniz-Filho et al. 2005). We set the truncation distance to 4221.53 m, based on a

minimum spanning tree criterion analysis (Fortin and Dale 2005). Thus, all distances larger than 4221.53 m were replaced by four times that value before the PCoA, and values smaller than 4221.53 m were kept as they were calculated. PCNM decomposes the spatial relationships among sampling sites into orthogonal eigenvectors (usually termed "spatial filters"), which reflect variation at each specific spatial scale. Only the spatial filters associated with positive eigenvalues are retained, and they express spatial structure in descending order, so the first axes reflect large-scale spatial structures, while subsequent axes express variation at gradually finer scales (Borcard et al. 2004, Benedetti-Cecchi et al. 2010). Nevertheless, not all spatial filters associated with positive eigenvalues are informative and a selection procedure must be carried out in order to select those that contain significant spatial autocorrelation (Benedetti-Cecchi et al. 2010). Many methods have been developed and applied in order to select spatial filters (see review in Griffith 2003). We followed the approach used by Diniz-Filho and Bini (2005), selecting filters that removed the largest amount of spatial autocorrelation in the residuals, minimizing residual spatial autocorrelation measured by Moran's I (Moran 1950). According to Diniz-Filho and Bini (2005), the autocorrelation in filters and in the regression residuals can be used as stopping rules to define which filters should be kept in the modeling process. We set $I < 0.05$ as our threshold in order to select spatial filters. Thus, from all 39 PCNM eigenvectors associated with positive eigenvalues, generated from our data set, only a small number of eigenvectors were kept, after filter selection procedure and then used as explanatory variables in further analyses. Further details on PCNM can be seen in Borcard & Legendre (2002), Dray et al. (2006), Griffth and Peres-Neto (2006), Benedetti-Cecchi et al. (2010), and especially Borcard et al. 2004, whom present a good review and a step-by step guide.

We used partial Ordinary Least Squares (OLS) multiple regression models (Legendre and Legendre 1998; Zar 1999) in order to evaluate the independent role of environmental, spatial and spatially structured environmental factors on diversity components (Legendre and Legendre 1998). Thus, our set of explanatory variables comprised two independent sub-sets: the first matrix containing those spatial filters selected based on the minimization of the residual Moran's I; and the second matrix containing nine environmental variables. Because the explanatory environmental variables were not measured in the same scale, we standardized them to unit variance, in order to bring their means to zero and their variance to one (Legendre and Legendre 1998).

We repeated the process used to define β-diversity (i.e., computing site distance to the centroid of a metric ordination), using a dissimilarity matrix based on the Euclidean distance computed upon the standardized values of all environmental variables. We then, used a simple OLS linear model, and tested the relationship between "site distinctness "and β-diversity.

All numerical and statistical analysis were performed in R environment (R Development Core Team 2009), excepting PCNM and Multiple Regression Models, which were computed in the Spatial Analysis in Macroecology software, v. 4.0 (Rangel et al. 2010). In order to compute partial correlation coefficients we used the Corpcor R package (Schaefer et al. 2010); multivariate dispersion from the group centroid was implemented using the Vegan package (Oksanen et al. 2008).

Results

α-diversity

Mean α-diversity was 4.9 (SD = ± 2.20). Pooling all sites together, we recorded 29 taxa belonging to nine orders (Appendix I and Plate I).

The full model, containing vegetation structure and spatial filters, explained 18% of the total variance in α-diversity (Table 2). Environmental and spatial processes explained nearly, the same amount of variation, although environmental structure alone was not statistically significant (Table 2). Spatially structured environment explained <1%. As predicted, α-diversity decreased with Bamboo density (Table 2). In fact, it was the only environmental variable to have an exclusive effect on α-diversity that could not be captured by the other variables (Table 2). Contrary to our initial expectations, neither palm density nor palm basal area affected significantly the spatial variation in mammalian richness, in the presence of other variables (Table 2).

From all 39 positive spatial filters, only one was selected based on the minimization of residual Moran's I (Table 2). This spatial filter exhibited a short cline marked by a strong positive spatial autocorrelation in small-distance classes (< 5 km) and a negative spatial autocorrelation at the 10 km class.

PCNM removed most of the spatial autocorrelation in α-diversity as shown in the residuals correlogram in Figure 4a. The correlogram shows a long-distance cline, characterized by positive Moran's I coefficients for the fine-scale classes (<10 km) coupled with negative long-distance Moran's I (>35 km) (Figure 4a) The observed α-diversity correlogram demonstrates that, not accounting for autocorrelation, α-diversity modeling would present strong negative autocorrelation in long-distance classes (Figure 4a).

β-diversity

The full model, explained 41% of the total variance in β -diversity (Table 2), with habitat structure explaining nearly 64% of the total amount of explained variation (Table 2). Bamboo density and Horizontal obstruction were important environmental features causing variation in mammalian β–diversity (Table 2). They both had significant effects on β–diversity (Table 2). All other partial regression coefficients were not statistically significant (Table 2).

From all 39 positive spatial filters, only three were selected (Table 2) based on the minimization of residual Moran's I (Table 2). Two of these filters (spatial filter 3 and 6) captured strong positive spatial autocorrelation in the first distance classes (< 5 km) and a negative spatial autocorrelation at the 10 km class. Spatial filter 5, captured a strong positive spatial autocorrelation at small distances (<10km) and some positive spatial autocorrelation at long-distance classes. The final correlogram shows the same pattern exhibited for α-diversity; a long-distance cline, characterized by positive Moran's I coefficients for the 1st distance class (<10 km) coupled with negative long-distance Moran's I (between 40-50km) (Figure 4b). Although PCNM was effective removing most of the spatial autocorrelation structure in the regression residuals of this fitted model, negative long-distance autocorrelation still remained (Figure 4b).

Table 2. Summary statistics of Ordinary Least Squares partial-regression models, for α-diversity and β-diversity regressed against environmental factors and spatial filters in the northern Pantanal, Brazil. V.I.F: Variance Inflation Factor

	Coefficient	p-value	V.I.F	Proportion of explained variantion
α-diversity				
Full model		0.021**		0.18
Intercept	4.90	<0.001***		
Environment		0.28		0.09[p]
BD	-0.38	0.081*	1.24	
CC	0.14	0.75	4.8	
CH	-0.17	0.67	4.03	
HO	0.11	0.71	2.37	
PBA	0.04	0.9	2.06	
PD	0.09	0.74	2.18	
UH	0.52	0.16	3.55	
VBA	-0.13	0.57	1.40	
VD	0.01	0.96	1.66	
Space		0.002***		0.08[p]
Spatial Filter 6	6.9	0.002***	1.06	
Spatially structured environment				0.003
β-diversity				
Full model		<0.001***		0.41
Intercept	0.56	0.00***		
Environment		<0.001***		0.26[p]
BD	0.02	0.02**	1.26	
CC	-0.03	0.11	4.81	
CH	-0.01	0.46	4.37	
HO	-0.04	0.003***	2.55	
PBA	-0.01	0.62	2.06	
PD	-0.01	0.56	2.22	
UH	-0.01	0.2	3.57	
VBA	0.01	0.47	1.49	
VD	-0.01	0.18	1.72	
Space		<.001***		0.15[p]
Spatial Filter 3	0.26	0.003***	1.08	
Spatial Filter 5	-0.3	0.002***	1.22	
Spacial Filter 6	-0.21	0.01	1.07	
Spatially structured environment				0

***p ≤ 0.01; **p ≤ 0.05; *p ≤ 0.10

[p] Partial regression coefficients

a)   b)
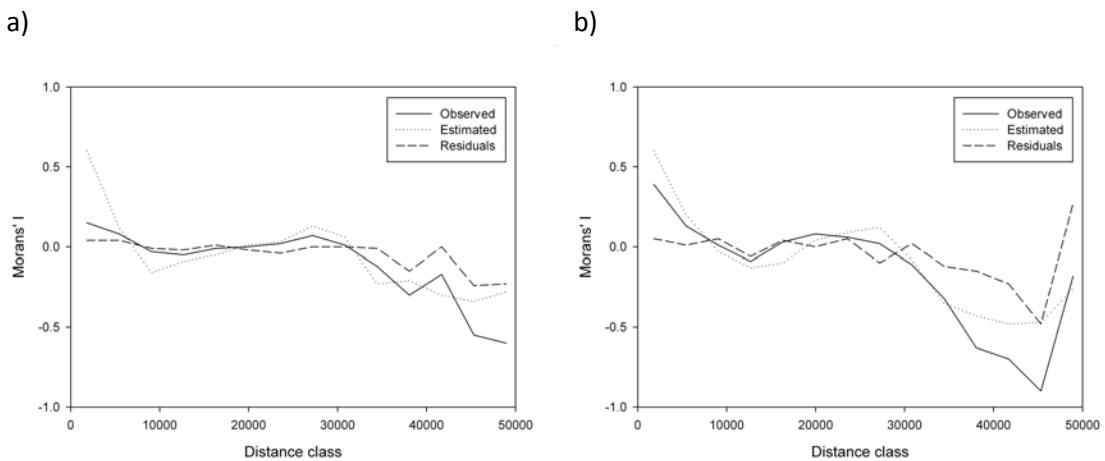
Figure 4. Moran' I correlograms for mammalian diversity components in the northern Pantanal. a) α-diversity; b) β-diversity.

Estimated β-diversity decreased with estimated α-diversity, which explained nearly 50% of the total variance in β-diversity ($R^2 = 0.49$; $F_{1, 114}= 111.495$; $p < 0.001$; Figure 5).
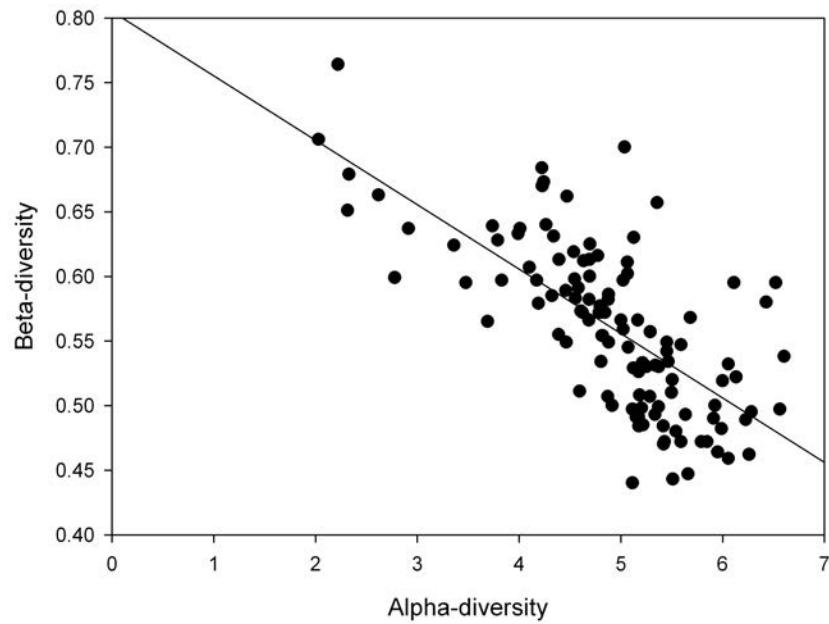
Figure 5. Relationship between estimated β-diversity and estimated α-diversity in the northern Pantanal, Brazil.

Observed β-diversity also increased with site distinctness, although the fitted model had a poor fit and explained a small amount of the total variance ($R^2 = 0.04$; $F_{1,114} = 4.59$; $p = 0.03$; Figure 6).
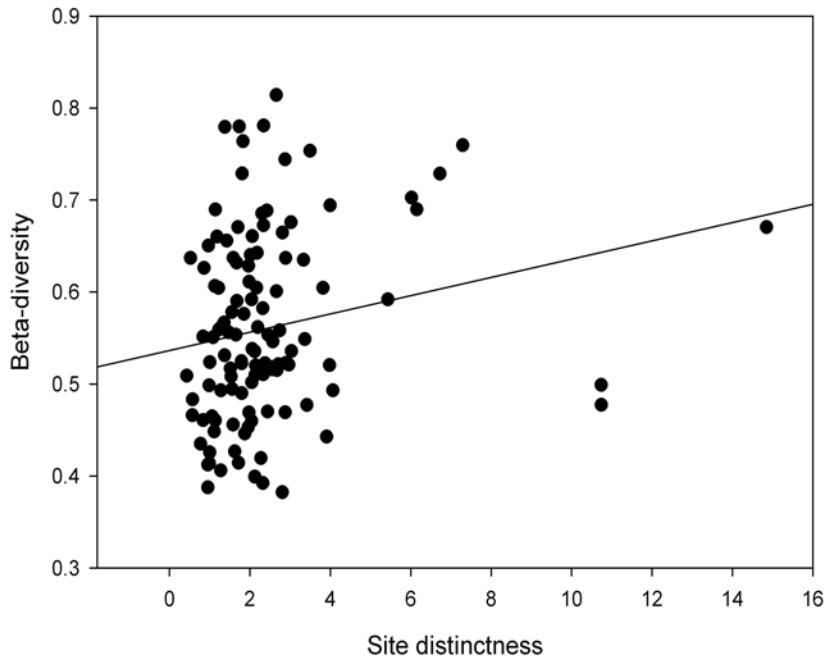
Figure 6. Relationship between observed β-diversity and site distinctness in the northern Pantanal, Brazil.

Discussion

Our results demonstrate the role of micro-habitat complexity driving mammalian diversity variation in the northern Pantanal. Although our models explained a small amount of variation in α-diversity (Table 2), they explained over 40% of the variation in β-diversity (Table 2). Accordingly, even though our explanatory variables could not explain most of the variation in the number of species occupying and/or using each site, they could successfully explain the variation in mammalian turn-over across space. Environmental factors alone accounted for over 60% of the total amount of explained

variation in species turn-over. Understanding patterns in biological diversity is a matter of scale (Whitaker et al. 2001; Willis and Whittaker 2002), and as pointed out by Diniz-Filho et al. (2008b), the explanatory power of environmental factors in fine-scale analyses are usually, much lower than broad-scale analyses (such as continental scales). These authors also recognize that spatial variation in α-diversity in fine-scale studies, tend to become much more complex and may become erratic, and are probably driven by more complex interactions of past and current ecological and evolutionary processes.

As pointed out (in the Introduction), although many researchers have embraced Whittaker's diversity components as merely as an "operational" concept, his diversity decomposition arose as consequence of the achievements of theoretical ecology in the 50s and 60s, especially the concepts of ecological niche developed by Hutchinson (1957) and MacArthur and Levins (1967). Whittaker (1972) believed that niche hyperspace, as proposed by Hutchinson, could become increasingly complex through evolutionary time, so additional species could fit into the community in niche hypervolumes different from those of other species. Thus, in his view, species richness was a direct response to this ever-increasing complexity. Whittaker (1972) also recognized that the array of habitat gradients across the landscape could also be conceived as a multidimensional hyperspace, and that species would evolve toward occupation of different positions in this hyperspace (β-niche). Our data shows that β-diversity rises, with environmental dissimilarity among sites, demonstrating the importance of β-niche along the environmental gradient.

β-diversity is determined through a complex array of processes relating to the interaction of species traits and characteristics of the landscape over time (MacKnight et al. 2007). But recent evidences have suggested that β-diversity can also arise as a result of stochastic processes (Cottenie 2005). An obviously and inherent implication of

using medium and large sized mammals as our model taxon in a fine-scale approach, is that our sites experience expressive changes in occupancy state, due to the high mobility of these species. In a comprehensive meta-analysis, Cottenie (2005) found that at small spatial scales, species sorting and neutral models acted together as important drivers in metacommunity dynamics across different taxa. The species sorting model (Chase and Leibold 2003) reinforces the ideas of Whittaker (1972), and emphasizes the role of spatial niche distribution across space, and that species co-existence is favored by environmental gradient (Chase and Leibold 2003; Leibold et al. 2004; Cottenie 2005). Thus our results seem to support this notion that micro-habitat quality and stochastic movement, jointly affect local assemblage structure.

Ecologists frequently investigate the relationship between α- and γ-diversity (Gering and Christ 2002). This paper presents an important theoretical contribution by modeling the relationship between α- and β-diversity. This relationship is essential to understand the relationship between scale and biodiversity, and local and regional processes and the factors that limit the richness of ecological communities. β -diversity decreased with fitted α-diversity, suggesting that species occur in a nested subset pattern rather than in a gradient replacement across the landscape. The nested subset hypothesis (Patterson 1986, 1987) states that the species comprising a depauperate fauna should constitute a proper subset of those in richer faunas, and that a set of such faunas, arranged by species richness, should present a nested series. This relationship also highlights the importance of animal movement across sites.

Both, α- and β-diversity were affected by broad-scale spatial structure. A common feature in our models was a strong long-distance cline, characterized by positive Moran's I coefficients at small distances and negative long-distance Moran's I. This pattern has been also reported by coarse scale studies (Diniz-Filho 2005).

Few studies have assessed the role of environmental and/or spatial factors on the diversity of Neotropical mammals, especially differentiation diversity (McKnight et al. 2007; Melo et al. 2009). These studies have used large grains in order to identify these factors. Although these studies are essential to understand broad-scale patterns in biological diversity, we believe, however, that small grain studies are especially useful as they quantify the importance of environmental factors at scales relevant to organism, where they actually interact and exploit resources and optimized their fitness, pursuing crucial habitat cues. Moreover, small grain studies are especially useful to reserve managers, that usually (and perhaps unfortunately) cope with the task of taking management decisions in reserves which are seen as "independent", small spatial unit set apart from the remaining landscape.

Our results also identified important environmental variables capable to explain diversity patterns. Bamboo density was the only variable significant in both, α- and β-diversity, models (Table 2). Bamboo ramets occur in high density and in nearly monospecific patches across the region. Studies have demonstrated that bamboo can negatively affect forest establishment, recruitment and growth, being an important biological driver of forest dynamics (e.g., Young 1991; Oliveira-Filho et al. 1994). As our data show, bamboo density affects negatively mammalian α-diversity. Regulating plant establishment and survival, bamboo stands may affect fauna indirectly, limiting resource availability. Nevertheless, Bamboo density and Horizontal foliar obstruction had significant effects on β-diversity (Table 2), which means that mammals occupying and /or using closed micro-habitats tend to be different from those using open micro-habitat. Nonetheless, this relationship may arise from the fact that large mammals can function as habitat engineers creating open sites. It is well known that large mammals act as an important regulating force of forest dynamics, affecting negatively plant

recruitment and survival, through feeding (browsing and grazing) and trampling (Laws 1970; McNaughton et al. 1988; Danell et al. 2006). Thus, site openness may be a habitat feature both influencing and influenced by large mammals.

Diversity decomposition, although an old idea, still very miscomprehended and debated (see review in Whitaker et al. 2001; Tuomisto 2010a, b). Nonetheless, it is at the foremost frontier of ecological thinking as it is tightly linked to the concept of metacommunities (Chase and Bengtsson 2010), which has recently attracted much attention from ecologists. Moreover, diversity partition may offer insights and basic guidelines for biodiversity conservation. Alpha diversity has attracted much attention from theoretical and applied ecologist and practitioners, as stressed by O'Brien et al (2011, p. 233): "…major policy initiatives at the international, national, and regional levels have committed entire government programs to attaining measurable targets of this variable in the conservation of biodiversity". Nonetheless, Legendre et al. (2005), correctly ascertained that understanding the processes that originate and maintain β-diversity is indispensable to conservation practices, such as reserve design as it may help to decide reserve allocation, size and ecosystem representation. Thus, it is critical that conservation agencies start to monitor spatial turnover in species richness in order to develop sound conservation planning.

Our results suggest that although most large Neotropical mammals are broadly distributed and are considered plastic species, they do not occur homogeneously across the landscape. Furthermore, the role of spatial variation in habitat structure may be critical in order to keep species co-existence at the regional level. Thus conservation initiatives that aim to optimize the number of mammal species at the regional level, in the northern Pantanal, must incorporate the management and maintenance of β-niches across the landscape.

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Appendix I. Mammal species recorded by camera trapping during the ebb and the dry season 2010 at the PRNH-SESC Pantanal, northern Pantanal. Phylogenetic order follows Wilson and Reeder (2005), with the exception of the so called "even-toed ungulates", which follows Price et al. (2005).

Order	Species	Vernacular name
Didelphimorphia		
	Didelphis albiventris	White-eared opossum
	Philander opossum	Gray four-eyed opossum
Cingulata		
	Dasypus novemcinctus	Nine-banded armadillo
	Euphractus sexcinctus	Hairy armadillo
	Priodontes maximus	Giant armadillo
Pilosa		
	Myrmecophaga tridactyla	Giant anteater
	Tamandua tetradactyla	Lesser anteater
Primates		
	Cebus cay	Azaras's capuchin
Rodentia		
	Cavia aperea	Brazilian guinea pig
	Hydrochoerus hydrochaeris	Capybara
	Dasyprocta azarae	Agouti
	Cuniculus paca	Paca
Lagomorpha		
	Sylvilagus brasiliensis	Tapeti
Carnivora		
	Leopardus pardalis	Ocelot
	Panthera onca	Jaguar
	Puma concolor	Puma
	Puma yagouaroundi	Jaguarundi
	Cerdocyon thous	Crab-eating fox
	Chrysocyon brachyurus	Maned wolf
	Eira barbara	Tayra
	Pteronura brasiliensis	Giant otter
	Nasua nasua	Coati
	Procyon cancrivorus	Crab-eating raccoon
Perissodactyla		
	Tapirus terrestris	Tapir
Cetartiodactyla		
	Sus scrofa	Feral pig
	Pecari tajacu	White-lipped peccary
	Tayassu pecari	Collared peccary
	Blastocerus dichotomus	Marsh deer

Ozotoceros bezoarticus	Pampa deer
Mazama spp.	Brocket deer

Plate I. Some mammal species recorded by camera trapping during the ebb and the dry season 2010 at the PRNH-SESC Pantanal, northern Pantanal. Phylogenetic order and nomenclature follows Wilson and Reeder (2005), with the exception of the so called "even-toed ungulates", which follows Price et al. (2005). a) *Didelphis albiventris* (Didelphimorphia); b) *Priodontes maximus* (Cingulata); c) *Myrmecophaga tridactyla* (Pilosa); d) *Cebus cay* (Primates); e) *Hydrochoerus hydrochaeris* (Rodentia); f) *Sylvilagus brasiliensis* (Lagomorpha); g) *Puma concolor* (Carnivora), h) *Tapirus terrestris* (Perissodactyla); i) *Blastocerus dichotomus* (Cetartiodactyla).

Conclusões e perspectivas futuras

Os resultados apresentados neste trabalho demonstram o papel da estrutura de habitat na variação da diversidade inventário e diversidade diferenciação, e a importância de se empregar modelos espacialmente explícitos. Embora o poder explanatório da estrutura de habitat, e estatisticamente não significativo, sobre a diversidade-inventário tenha sido baixo, ele explicou boa parte da variação da diversidade-diferenciação. Ambos os resultados parecem corroborar as evidências disponíveis na literatura: Baixo poder explanatório para modelos de diversidade-inventário em escala fina; efeitos significativos de processos ambientais sobre a diversidade-diferenciação.

Neste trabalho, eu representei o "ambiente" por um único modelo, que continha todas as variáveis ambientais. Processos de modelagem, dentro de uma abordagem de Teoria da Informação e Seleção Multi-modelos, permitirá testar a plausibilidade deste modelo, perante sub-modelos, contendo um número menor de variáveis. Este processo de modelagem, também permitirá a identificação das variáveis mais importantes na determinação da diversidade alfa e beta.

O desenho amostral empregado permitirá avaliação dos efeito das diferentes escala sobre os componentes de diversidade, através de análises aninhadas, considerando o efeito das média das cinco parcelas, conforme foi realizado no presente trabalho, e o efeito exclusivo da parcela central.

Inúmeros trabalhos tem demonstrado a relação entre diversidade alfa e gama. Este trabalho apresenta uma contribuição teórica importante, mostrando a relação entre a diversidade alfa e beta. Esta relação é essencial para se compreender a relação entre escala e diversidade biológica, e processos locais e regionais e o limite na riqueza de comunidades ecológicas. Projetos que envolvam a amostragem de múltiplos sítios e

métodos de análises que possam determinar um único valor estimado de beta diversidade por sítio, como apresentado neste trabalho, são essenciais para compreender esta relação. Meus resultados demonstram que, ao longo do gradiente ambiental, as espécies ocorrem em um padrão aninhado, talvez por limites impostos pelo *pool* regional de espécies. Nesta escala refinada, este padrão também pode surgir, pela variação na plasticidade das espécies no uso do gradiente ambiental.

Neste trabalho, demonstro que a distinção na composição é positivamente relacionada com a distinção estrutural de sítio, apesar do baixo ajuste. A remoção de alguns outliers, melhoraram significativamente o ajuste (resultado não demonstrado). Este resultado, juntamente com a modelagem da diversidade-diferenciação, tem implicações importantes em termos de conservação e indicam que a manutenção de beta-nichos são importantes para se manter a riqueza específica em nível regional, se o objetivo, for manter o *pool* regional de espécies (conservação de padrão ecológico)

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