INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA DE ÁGUA DOCE E PESCA INTERIOR - PPGBADPI

EFEITO DE FATORES AMBIENTAIS E ESPACIAIS NA DINÂMICA LIMNOLÓGICA E NA ESTRUTURA DE COMUNIDADES DE PEIXES EM UMA PLANÍCIE SAZONALMENTE ALAGÁVEL

IZAIAS MÉDICE FERNANDES

Manaus, Amazonas

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Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título em Ciências Biológicas, área de concentração em Biologia de Água Doce e Pesca Interior.

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PPGBADPI/INPA
Programa de Pós-Graduação em
Biologia de Água Doce e Pesca Interior

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INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

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Aos vinte e quatro dias do mês Maio de 2013, às 14 horas, no Auditório do PPG BADPI/Campus II-INPA, reuniu-se a Banca Julgadora da **DEFESA PÚBLICA DE DOUTORADO**, composta pelos seguintes membros titulares: Dr. Luis Mauricio Bini, Dr. Sidinei Magela Thomaz, Dr. William Ernest Magnusson, Dra. Flávia Regina Capellotto Costa e a Dra. Cláudia Pereira de Deus; tendo como membros suplentes: Dr. Carlos Eduardo de Carvalho Freitas e o Dr. Pedro Ivo Simões, a fim de proceder a arguição pública da **TESE** do estudante **IZAIAS MÉDICE FERNANDES**, intitulada: **EFEITO DE FATORES AMBIENTAIS E ESPACIAIS NA DINÂMICA LIMNOLÓGICA E NA ESTRUTURA DE COMUNIDADES DE PEIXES EM UMA PLANÍCIE SAZONALMENTE ALAGÁVEL.** O estudo foi conduzido sob orientação do Dr. Jansen Alfredo Sampaio Zuanon e coorientação do Dr. Jerry Magno Ferreira Penha.

Após a exposição da aula, dentro do tempo regulamentar, (o)a discente foi arguido(a) oralmente pelos membros da Banca Julgadora, tendo recebido o conceito final:

(X) **Aprovado**
( ) **Aprovado com "Distinção"**
( ) **Aprovado com "Distinção e Louvor"**
( ) **Reprovado**

Foi lavrada a ata e assinada pelos membros presentes da Banca Julgadora.

Dr. Luis Maurício Bini ____________________
Dr. Sidinei Magela Thomaz ____________________
Dr. William Ernest Magnusson W E Magnusson
Dra. Flávia Regina Capellotto Costa ____________________
Dra. Cláudia Pereira de Deus ____________________
Dr. Carlos Eduardo de C. Freitas ____________________
Dr. Pedro Ivo Simões ____________________

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PO. 514/2012 – INPA/MCTI-PR

F363 Fernandes, Izaias Médice

Efeito de fatores ambientais e espaciais na dinâmica limnológica e na estrutura de comunidades de peixes em uma planície sazonalmente alagável. --- Manaus: [s.n.], 2014.

xv, 122 f. : il.

Tese (Doutorado) --- INPA, Manaus, 2013.

Orientador : Jansen Alfredo Sampaio Zuanon.

Coorientador : Jerry Magno Ferreira Penha.

Área de concentração : Biologia de Água Doce e Pesca Interior.

1. Distribuição de espécies. 2. Comunidades de peixes. 3. Filtros ambientais. I. Título.

CDD 597.0929

Agradecimentos

Ao Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior e às coordenadoras Dr^{as}. Angela Varella e Sidinéia Amadio;

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pela bolsa de estudos, sem a qual seria impossível realizar cursar o doutorado;

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de estágio de Doutorado Sanduíche no Exterior (Processo BEX: 6140/11-4);

Ao Centro de Pesquisas do Pantanal, pelo apoio financeiro à realização da tese;

Ao meu orientador Jansen Zuanon, primeiro por ter aceitado ser meu orientador e por tudo que me ensinou durante esses quatro anos, e segundo por sempre mostrar aos seus alunos que mesmo que sejamos bons naquilo que fazemos, devemos sempre ter humildade e sermos compreensivos;

Ao meu coorientador Jerry Penha, a quem tenho grande respeito e admiração, pois foi quem me ensinou os primeiros passos dentro da pesquisa científica, e por me mostrar que se queremos ser bons pesquisadores, temos que estar sempre em busca de novos desafios;

Ao Prof. Dr. Milton Ribeiro (UNESP - Rio Claro) por me receber em seu laboratório e me mostrar a Ecologia de Paisagem, abordagem fundamental quando queremos entender os padrões de distribuição de espécies;

Ao Prof. Dr. Pedro Peres-Neto, por te me recebido em seu laboratório na Université du Québec à Montreal, pelas excelentes conversas que tivemos e pelas cervejas;

Aos meus amigos, Bruno, Chico Mario, Bruninho, Graziela, Carol, Zu, Dani, Sérgio, pelos bons momentos que passamos em Manaus.

Aos amigos do Projeto Igarapés: Helder, Rafa, Marla, Tiago Pires, Thiago Couto, Akemi, Gabriel e Gislene;

Ao meu grande amigo Julio, parceiro de planície de inundação, pelas conversas que tivemos sobre peixes, água, ecologia e política;

Aos meus amigos Pedro Podestá e Renato Henriques-Silva, a quem tive oportunidade de conhecer em Montreal;

Um agradecimento em especial para a Luzia Lourenço, minha companheira, amiga e eterna namorada, pelos bons momentos que passamos juntos, pelo apoio e compreensão.

Resumo

Planícies de inundação figuram entre os mais diversos e ameaçados sistemas naturais do mundo. Assim, compreender a dinâmicas espaço-temporal desses sistemas torna-se imprescindível afim de melhorar as práticas de manejo e conservação. Técnicas analíticas que permitem quantificar a contribuição de fatores local e regional têm permitido entender melhor como as comunidades locais são organizadas, assim como entender o papel da dispersão e colonização na montagem dessas comunidades. Apesar de muitos fatores ambientais locais contribuírem para explicar os padrões encontrados em comunidades locais, poucas são as informações da relação dessas variáveis com os locais onde elas foram medidas e qual a contribuição da paisagem, na qual elas estão inseridas. A influência de fatores locais (ambiente) e regionais (espacial) sobre a temperatura da água, oxigênio, condutividade e pH de uma área de 25km² de planície sazonalmente inundada do Pantanal foi avaliada durante o período de cheia 2006/2007. Fatores ambientais foram mais importantes no início e final da cheia, enquanto que fatores espaciais (regional) foram mais importantes do auge da cheia, quando todos os habitats aquáticos encontram-se conectados. A avaliação do efeito da conectividade, profundidade e cobertura vegetal em atributos da comunidade de peixes (biomassa, comprimento, densidade, diversidade e equitabilidade) utilizando dados de cinco períodos hidrológicos (2006, 2008, 2009, 2010 e 2011) demonstrou que a conectividade e a cobertura vegetal são fatores importantes para o tamanho, a biomassa e a diversidade de espécies de peixes acima de 50 mm, enquanto que a profundidade da coluna da água é importante para a diversidade de peixes de tamanho corporal abaixo de 50 mm que colonizam a planície sazonalmente alagada durante o período de cheia. Utilizando a abordagem de Elementos de Estrutura de Metacomunidades (EMS), a dinâmica espaço temporal das comunidades de peixes da planície sazonalmente inundada foi avaliada durante o período de cheia (janeiro a abril) de 2009. Os padrões encontrados mudaram ao longo da estação de cheia, com Nested e Quasi-Nested sendo encontrado no início da cheia (janeiro e fevereiro, respectivamente) quando o nível da água está subindo e os habitats aquáticos são menos conectados. Entretanto, esse padrão muda para Quasi-Clementsian nos dois meses seguintes, quando a planície encontra-se completamente inundada e os habitats estão mais conectados. O efeito de fatores ambientais, espacial e da conectividade foi avaliado utilizando o método de partição de variância e demonstrou que o efeito de fatores ambientais foi constante ao longo da cheia, porém a conectividade teve maior efeito no início da cheia enquanto fatores espacial tornam-se mais importantes a medida que o nível da água aumenta e a planície torna-se mais conectada.

Abstract

Environmental and spatial factors influencing the limnological dynamics and the fish community structure in a seasonal floodplain

Wetlands are among the most diverse and threatened natural systems worldwide. It is thus critical to understand their spatiotemporal dynamics in order to improve management and conservation practices regarding these habitats. Analytical frameworks that allow quantifying the relative contribution of local and regional factors have improved our understanding on how wetland fish communities are organized, however little is known regarding the limnological properties of temporary aquatic habitats. In the first chapter was evaluated the relative importance of these factors for water temperature, dissolved oxygen, conductivity and pH in the Pantanal floodplains during the wet seasons of the 2006/2007. Our results showed that local processes (e.g., depth and water temperature) were more important in the beginning of the rainy season whereas regional factors had a greater contribution during the flood peak, when all aquatic habitats were highly connected across the landscape. In a similar venue, was analyzed on the following chapter what was the most important factors accounting for several properties (biomass, standard length, density, diversity and evenness) of fish communities dwelling in the same habitats. Using data from these temporary aquatic habitats spanning five years (2006, 2008, 2009, 2010 and 2011), was reported that habitat connectivity and vegetation cover explained most of the variation in the diversity, biomass and standard length of large-bodied fishes (> 50 mm) while water depth was the most important factor accounting for the diversity of small-size fishes (< 50 mm). Finally, in the third chapter, was applied the Elements of Metacommunity Structure (EMS) framework in order to evaluate the spatiotemporal dynamics of these fish assemblages during four consecutive months of the 2009 rainy season. Significant changes in the distributional patterns along the season were detected. In the beginning of the flood, when habitat patches are less connected, the fish metacommunity structure followed a nested and a quasi-nested pattern (January and February, respectively). During the following two months, when the landscape is completely flooded and habitats are more connected, the fish distributional pattern changed for a quasi-Clementsian distribution. The relative contribution of environmental, spatial and connectivity factors was also evaluated, through variation partitioning analysis. This analysis showed that the environment explain a constant fraction of the variation in species distribution during the entire season, the connectivity factors are more important in the beginning of the wet season whereas spatial factors become significant only from the mid to the end of the rainy season.

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Introdução geral

Compreender o padrão de distribuição de espécies e os fatores responsáveis por esses padrões é o objetivo central da ecologia de comunidades. Por um longo tempo fatores ambientais locais foram considerados determinantes para entender a estrutura de comunidades locais, enquanto que fatores regionais, espaciais e processos históricos foram negligenciados (Ricklefs 1987, 2008; Cornnel & Lawton 1992; Kneitel & Chase 2004; Leibold et al. 2010). Enquanto em sistemas terrestres as características do solo e altitude são os principais fatores responsáveis pela distribuição de plantas (Zeilhofer & Schessl 1999; Ferris et al. 2000; Güsewell et al. 2012), em sistemas aquáticos, a temperatura da água, disponibilidade de oxigênio, condutividade e o pH são considerados os principais fatores químicos que limitam a distribuição de organismos aquáticos (Junk et al. 1983; Rahel 1984; Teixeira-de-Mello et al. 2009; Miranda 2010; Scarobotti et al. 2011; Landeiro et al. 2012).

Além de variáveis locais, fatores regionais como o tamanho do conjunto regional de espécies disponíveis para colonizar novos habitat (Súarez et al 2001; Chase 2003), bacia de drenagem (Hoeinghaus et al.2007; Pinto et al. 2009), conectividade ou isolamento (Kodric-Brown & Brown 1993; Taylor & Warren 2001; Peres-Neto & Cumming 2010) e a estrutura da paisagem são importantes para entender como comunidades locais são organizadas. Assim, existem evidências teóricas de que comunidades locais surge tanto como resultado das interações locais (intra e interespecíficos e entre espécies e ambiente) assim como de processos regionais como a dispersão (Leibold et al. 2004).

Técnicas que permitem quantificar a contribuição de fatores locais regionais (Bocard et al. 1992, Peres-Neto et al. 2006), têm permitido entender melhor como as comunidades são organizadas, assim como entender melhor o papel da dispersão e colonização (Pfister 1998; Nathan 2001) na montagem de comunidades locais. Entender o papel da dispersão tornou-se mais importante devido ao aumento da taxa de fragmentação da paisagem causado pelo avanço de atividades humanas e, conseqüentemente, a perda da diversidade biológica assim como do funcionamento dos ecossistemas (Dobson et al. 2006). A fragmentação da paisagem isola e reduz o fluxo genético entre populações antes conectadas o que pode levar populações a extinção local (Pulliam 1988; Taylor & Warren 2001). Estudos com diferentes organismos têm mostrado que a dispersão entre manchas de habitat e o grau de conectividade entre as manchas são os principais fatores responsável por modelar o padrão de distribuição das espécies (Kneitel & Miller 2003; Hodgson et al. 2009; Magle et al. 2009; Duggan et al. 2011; Hohausova et al. 2010). Assim, estruturas de paisagem que mantém a conectividade entre diferentes manchas de habitat permitem a persistência de populações mesmo em paisagem fragmentadas.

Conectividade da paisagem refere-se ao quanto a paisagem facilita ou impede o movimento entre manchas (Taylor et al. 1993). Conectividade pode ser medida de diferentes formas (Prugh 2009), porém os principais métodos utilizados são: estrutural e funcional. Enquanto conectividade funcional incorpora dados específicos sobre o movimento dos indivíduos dentro e fora da mancha focal ou ao longo de toda a paisagem estudada, conectividade estrutural mede o arranjo espacial de diferentes habitats ou manchas dentro da paisagem, e como a distribuição dessas manchas pode afetar a dispersão das espécies (Theolbald et al. 2011). Em ambientes terrestres, conectividade tem recebido mais atenção, quando comparado a ambientes aquáticos. Em ambientes terrestres a fragmentação dos habitats assim como a possibilidade de observar os indivíduos, talvez tenha permitido que mais avanços fossem alcançando nesses ambientes do que em ambientes aquáticos. Apesar de conectividade hidrológica ter sido negligenciada e ser pouca utilizada mesmo nos dias atuais (Fullerton et al. 2010) vários trabalhos têm utilizado a distância Euclidiana ou hidrológica, como substituta da medida de conectividade, e têm demonstrado que a distância pode explicar mudanças na estrutura de comunidade locais (Olden et al. 2001; Baber et al. 2002; Beisner et al. 2006; Landeiro et al. 2011). Ambientes aquáticos são considerados unidirecionais com relação ao fluxo e bidimensionais com relação à possibilidade de dispersão; entretanto, ambientes formados durante o período de cheia em planícies de inundação ou diferentes manchas de habitat em grandes rios, permitem que a dispersão ocorra em diferentes direções (multidirecional), da mesma forma como ocorre em ambientes terrestres. Assim, apenas a distância hidrológica entre manchas de habitat não é suficiente para medir a conectividade nesse tipo de ambiente.

Planícies de inundação são compostas por corpos de água permanentes assim como por habitats temporários criados pela a expansão destes e disponíveis apenas durante um período do ano ou ciclo hidrológico (Ward & Tockner 2001). Para utilizar esses habitats efêmeros, algumas espécies desenvolveram mecanismos que permitem à elas persistirem durante o período de tempo não favorável ou colonizar esses ambientes assim que eles são formados (Warner & Chesson 1985; Bayley 1995; Pake & Venable 1995). Entre os mecanismos, ovos resistentes a dissecação, dormência e adultos que podem resistir ao período de escassez de recursos e migração (Pake & Venable 1995; Brock et al 2003). Entretanto, alguns táxons são completamente extintos localmente e necessitam recolonizar esses ambientes quando eles tornam-se disponíveis (Lytle & Poff 2004).

Em sistemas de planície de inundação, as características como a presença de ambientes permanentes e temporários, dentro do mesmo sistema, permitem avaliar como a interação entre fatores ambientais (local) e dispersão (regional) pode afetar a composição de espécies em comunidades locais. O Ciclo natural de subida e descida da água, permite que habitat sejam sazonalmente criados durante o período de chuva e extintos durante o período de seca (Tockner et al. 2000) tornando as planícies ambientes altamente heterogêneos. Entre os diferentes táxons que exploram esses ambientes, os peixes tem demonstrado eficácia em explorar os ambientas sazonais (Henning et al. 2007, Zeug & Winemiller 2008) tanto em planície de inundação (Fernandes et al. 2010) como em poças temporárias em riachos (Pazin et al. 2006). Durante a inundação, as espécies deixam os corpos de água permanentes (e. g. rios, lagos e poças) e dispersão através da planície colonizando os habitats recém formados. Esta dispersão pode ser ativa, através do movimento voluntário de jovens e adultos, ou passiva, por meio do transporte de ovos e larvas (King et al. 2003). Dessa forma, a planície de inundação pode ser considerada como um cenário de experimentação natural onde a dinâmica hidrológica, a dispersão e colonização podem ser avaliadas anualmente, devido à dinâmica cíclica do sistema.

Referências

Baber, M. J., Childers, D. L., Babbitt, K. J., Anderson, D. H. 2002. Controls on fish distribution and abundance in temporary wetlands. Canadian Journal of Fisheries and Aquatic Sciences 59:1441-1450.

Bayley, P.B. 1995. Understanding large river-floodplain ecosystems. BioScience 45: 143–158

Beisner, B. E., Peres-Neto, P. R., Lindström, E. S. Barnett, A. and Longhi M. L. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87:2985-2991.

Borcard, D., Legendre, P., Drapeau. P. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Brock M. A., Nielsen D. N., Shiel R. J., Green J. D., Langley J.D. 2003. Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. Freshwater Biology 48:1207–1218.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498

Cornell, H. V., Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61:1-12.

Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J.,...Xenopoulos, M. A. 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87(8):1915-1924.

Duggan, J. M., Schooley, R. L. and Heske, E. J. 2011. Modeling occupancy dynamics of a rare species, Franklin‘s ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecology 26:1477-1490.

Ferris, R., Piece, A.J., Humphrey, J.W., Broome, A.C., 2000. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. Forest Ecology and Management 136:35-51.

Fernandes, I. M., Machado, F. A., Penha, J. 2010. Spatial pattern of fish assemblage in a seasonal tropical wetland: effects of habitat, herbaceous plant biomass, water depth, and distance from species sources. Neotrophical Ichthyology 8:289-298.

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J., Sanderson, B.L. 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshwater Biology 55: 2215-2237.

Güsewella, S., Peter M., Birrer, S., 2012. Altitude modifies species richness–nutrient indicator value relationships in a country-wide survey of grassland vegetation. Ecological Indicators 20:134–142.

Henning, J. A., Gresswell, R. E., Fleming, I. A. 2007. Use of seasonal freshwater wetlands by fishes in a temperate river floodplain. Journal of Fish Biology 71: 476–492.

Hoeinghaus, D.J., Winemiller, K.O., Birnbaum, J.S. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34:324–338.

Hodgson, J. A., Moilanen, A., Thomas, C. D. 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90(6):1608-1619.

Hohausova, E., Lavoy, R.J. Allen, M.S. 2010. Fish dispersal in a seasonal wetland: influence of anthropogenic structures. Marine and Freshwater Research 61:682–694.

Kneitel, J.M., Chase, J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7:69–80.

Kneitel, J.M., Miller, T.E. 2003. Dispersal rates affect species composition in metacommunities of Sarracenia purpurea inquilines. American Naturalist 162:165–171.

King, A.J., Humphries, P., Lake, P.S. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences 60:773–786.

Kodric-Brown, A., Brown, J. H. 1993. Highly structured fish communities in Australian desert springs. Ecology 74:1847-1855.

Landeiro, V. L., Magnusson, W. E., Melo, A. S., Espírito-Santo, H. R., Bini, L. M. 2011. Spatial eigenfunction analyses in stream networks: do watercourse and overland distances produce different results? Freshwater Biology 56(6):1184-1192.

Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.O.V., Magnusson, W.E., 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. Freshwater Biology 57:1554–1564.

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

Lytle, D. H., Poff, N. L. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19:94-100.

Junk, W.J., Soares, G.M., Carvalho, F.M. 1983. Distribution of fish species in a lake of the Amazon River floodplain near Manaus (lago Camaleao) with special reference to extreme oxygen conditions. Amazoniana 7: 397–431.

Leibold, M. A., Economo, E. P., Peres-Neto, P.R. 2010. Metacommunity phylogenetics: separating the roles of rnvironmental filters and historical biogeography. Ecology Letters 13: 1290-1299.

Magle S. B., Theobald, D.M., Crooks, K.R. 2009. A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landscape Ecology 24:267–280.

Miranda, L. E. 2011. Depth as an organizer of fish assemblages in floodplain lakes. Aquatic Sciences-Research Across Boundaries 73(2):211-221.

Nathan, R. 2001. The challenges of studying dispersal. Trends in Ecology & Evolution 16:481–483.

Olden, J. D., Jackson, D. A., Peres-Neto. P. R. 2001. Spatial isolation and fish communities in drainage lakes. Oecologia 127:572-585.

Pake, C. E., Venable, D. L. 1995. Is coexistence in Sonoran desert annuals mediated by temporal variability in reproductive success. Ecology 76:246–261.

Pazin, V. F. V., Magnusson, W. E. Zuanon, J., Mendonca, F. P. 2006. Fish assemblages in temporary ponds adjacent to 'terra-firme' streams in Central Amazonia. Freshwater Biology 51:1025-1037.

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

Pinto, B .C. T., Araujo, F. G., Rodrigues, V. D., Hughes, R. M. 2009. Local and ecoregion effects on fish assemblage structure in tributaries of the Rio Paraíba do Sul, Brazil. Freshwater Biology 54:2600–2615.

Pfister, C.A. 1998. Extinction, colonization and species occupancy in tidepool fishes. Oecologia 114: 118–126.

Prugh L. R. 2009. An evaluation of patch connectivity measures. Ecological Applications 19:1300–1310.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661

Rahel, F.J.1984 Factors structuring fish assemblage along a Bog lake successional gradient. Ecology 65(4):1276–1289.

Ricklefs, R. 1987. Community diversity relative roles of local and regional processes. Science 355:167-171.

Ricklefs, R. E. 2008. Disintegration of the ecological community. The American Naturalist 172(6):741-750.

Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81:3074–3086.

Scarabotti, P. A., López, J. A., Pouilly, M. 2011. Flood pulse and the dynamics of fish assemblage structure from neotropical floodplain lakes. Ecology Freshwater Fish 20: 605–618.

Súarez, Y. R., Petrere-Jr. M., Catella. A. C. 2001. Factors determining the structure of fish comunities in Pantanal lagoons (MS, Brazil). Fisheries Management and Ecology, 8: 173-186.

Taylor, P. D., Fahring, L., Henein K., Merriam, G. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571-573.

Taylor, C. M.,Warren, Jr. M. L. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. Ecology 82:2320–2330.

Teixeira-de-Mello, F., Meerhoff, M., Pekcan-Hekim, Z., Jeppesen, E. 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. Freshwater Biology 54:1202– 1215.

Theobald, D. M., Crooks, K. R., Norman, J. B. 2011. Assessing effects of land use on landscape connectivity: loss and fragmentation os western US forests. Ecological Applications 21:2445-2458.

Tockner, K., Malard, F., Ward, J.V. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861–2883.

Ward, J.V., Tockner, K. 2001. Biodiversity: towards a unifying theme for river ecology. Freshwater Biology 46:807–819.

Warner, R. R., Chesson, P. L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 12: 769–787.

Zeilhofer, P., Schessl, M. 2000. Relationship between vegetation and environmental conditions in the northern Pantanal of Mato Grosso, Brazil. Journal of Biogeography 27:159-168.

Zeug, S.C., Winemiller, K.O. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89:1733–1743.

Objetivo geral

Avaliar como fatores locais e regionais influenciam a dinâmica limnológica de ambientais sazonais, assim como entender qual o papel da conectividade, da estrutura da paisagem e de fatores locais e regionais na variação espaço-temporal das comunidades de peixes que ocupam esses ambientes.

Objetivos específicos

Avaliar o efeito de fatores locais (ambiental) e regional (espacial) na dinâmica limnológica de uma área de planície sazonalmente inundada;

Avaliar o efeito da conectividade e da cobertura vegetal em atributos da comunidade de peixes em uma área de planície sazonalmente inundada;

Avaliar variações espaço-temporal na estrutura da metacomunidade de peixes em uma área de planície sazonalmente inundada.

CAPÍTULO I

Fernandes, I.M., Ribeiro, M., Penha, J. Fantin-Cruz, I. Solino-Carvalho, L. Silveira R. & Zuanon J. What really matters in limnological dynamics of wetlands temporal habitats: environmental or spatial factors? A ser submetido para publicação no periódico *Ecological Indicators*

Abstract

We assessed the variation patterns of the temperature, oxygen, conductivity and pH in a seasonally inundated area of the of Brazilian Pantanal floodplain. These variables were chosen because most published studies have shown they are the principal environmental (limnological) factors responsible for species distribution in aquatic systems and neither study have yet assessed the effect of the local and regional factors on them. Thus, the objective of this paper is to understand which factors govern spatiotemporal variation in water conditions in the floodplain. In order to do this, we used a dataset built on data collected in nine (minimal) to 27 (maximum) plots distributed in an area of 25 km² in three sampling occasions throughout one rainy season. Results indicate that both environmental and spatial factors were important to explain the observed variation in limnological characteristics of the floodplain, but their relative importance change along the rainy season. Spatial factors were more important on high water period, whereas environmental factors were more pronounced on the beginning and end of the flooding season. There is an increase in connectivity during the peak of the high water period, making the habitats more similar and decreasing the limnological heterogeneity, which make spatial effects more important. These changes in the factors that govern environmental characteristics of seasonally inundated habitats may help to explain the heterogeneity in aquatic species distribution along time in the species-rich tropical floodplains.

Keywords: Spatial variability, temporal variability, wetland, limnology.

1. Introduction

Knowledge about the relation between environmental factors and species distribution is important to understand how local communities are structured (Tilman, 1982; Chase and Leibold, 2003), and how they can be managed. While in terrestrial systems soil characteristics and altitude are among the main factors explaining plant distribution (Zeilhofer and Schessl, 1999; Ferris et al., 2000; Güsewell et al., 2012), in aquatic systems, water temperature, dissolved oxygen, conductivity and pH are considered the main factors related to species distribution (Rahel, 1984; Junk et al., 1983; Teixeira-de-Mello et al., 2009; Landeiro et al., 2012; Miranda, 2010; Scarobotti et al., 2011). Despite that recognized importance to explain species distribution in aquatic systems, few studies have dealt with the factors that govern spatio-temporal heterogeneity in these variables (Douglas Shields et al., 2011) and how aquatic organisms respond to these changes (Thomaz et al., 2007).

In permanent aquatic ecosystems, drought periods represent a critical phase to biological communities, characterized by habitat reduction, high mortality rates, and loss of connectivity among habitat patches (Bond et al., 2008). During this period, local factors are predominant and each aquatic habitat may show different chemical and biological features (Rodriguez and Lewis, 1997), whereas in wet season the water level increases and aquatic habitat tends to be much more connected with each other, increasing their physical, chemical and biological similarity (Thomaz et al., 2007). Thus, fine-scale processes or local environment factors are supposed to be more important on the beginning of inundation phase, when the connectivity is lower, whereas large-scale processes or spatial factors should become more important at the peak of the inundation period, when habitats are interconnected and individuals can disperse throughout the floodplain.

Wetlands are environments formed by seasonal accumulation of rainwater or by expansion of permanent waterbodies (Tockner et al., 2000) and provides habitats for a high diversity of organisms (Junk, 1973; Junk et al., 1989; Perelman et al., 2001; Baber et al., 2002, Kneitel and Miller 2003; Pazin et al., 2006; Williams, 2006; Fernandes et al., 2010; Girard et al., 2010). The alternation of the aquatic and terrestrial phases makes wetlands highly productive and cause pronounced seasonal oscillations in the chemical and physical characteristics, and, consequently, in species composition (Junk et al., 1989). During the drought season, terrestrial species are abundant while aquatic organisms are present only as egg banks or rhizomes in a muddy substrate. However, when the wet season starts, terrestrial species migrate or die, and aquatic species becomes dominant (Penha et al., 1999).

The interaction among altitude, soil type, flooding duration and magnitude (Zeilhofer and Schessl, 1999) result in a high habitat heterogeneity, which is reflected on an also high landscape diversity at both fine and large scales in wetlands (Tockner et al., 2000; Siziba et al., 2011). Landscape chacatreristics have been used with success to explain terrestrial species distribution (Magle et al., 2009; Duggan et al., 2011; Burges et al., 2012), and similar effects (coupled with the effects of limnological factors) have been found in relation to the distribution and abundance of aquatic species (Douglas Shields et al., 2011; Dembkowski and Miranda, 2012).

Due to its cyclical nature, wetlands are less stable and changes in its limnological characteristics are most pronounced than permanent waterbodies. Thereby, these systems can be used as natural experiments to assess the relative role of environmental and spatial factors governing changes in limnological variables, and its possible effects on the biota. Thus, this paper aimed to assess how water temperature, oxygen, conductivity and pH change temporally and spatially during a whole rainy season, and what are the relative contributions of environmental and spatial factors for these changes. We hypothesize that water temperature and dissolved oxygen are mainly affected by local environmental factors such as vegetal cover and water depth, whereas conductivity and pH should be influenced mostly by soil characteristics (i.e. clay, sand, silt and organic matter content) and inundation time (hydroperiod). In this way, we expect that the effects of environmental variables decrease and of spatial factors increase from the begging to the peak of the flooding phase, , then reversing the pattern during the drying phase, when local environmental factors become again more important and similar to the pattern observed in the beginning of the wet season.

2. Material and Methods

2.1. Study area

The Pantanal represent the biggest wetland of the world (160.000 km²), localized in the central portion of South America. Similar to other wetlands around the world, the Brazilian Pantanal is severely threatened by habitat alteration, flow and flood control, species invasions, and pollution (Tockner and Stanford, 2002; Junk and Nunes da Cunha, 2005; Junk et al., 2006). Nevertheless, a large part of the Pantanal still maintains pristine conditions (Harris et al., 2005) and allowing understanding the natural dynamics of its limnological characteristics. During the rainy season an area of about 110.000 km² may be temporarily inundated, which is reduced to about 2% of the total, when the water becomes restricted to permanent water bodies, such as rivers, lakes, secondary channels and ponds (Hamilton et al., 2006).

Aiming to understand the relationships among land use, inundation dynamics, biological diversity and species distribution, the Pantanal Long-Term Sampling Sites (PLTSS) was implanted on Cuiabá River floodplain in 2005 (56º 21' W, 56º 18' E, 16º 19' N, 16º 22' S). The PLTSS consists of 30 plots of 250 m length x 1m width systematically distributed throughout 25 km². The plots follow the topographical land level (i.e., have the same altitude and water depth throughout its extension), and are distributed with a minimum distance of 1 km from each other (for more information on the PLTSS see Fernandes et al., 2010; Signor and Pinho, 2011).

The area where the PLTSS was installed is characterized by sandy soils of fluvio-lacustrine origin, slightly acid, with high aluminum content and lower fertility (Zeilhofer and Schessl, 1999). The flooding period occurs between December and May, and a drought phase occurs between June and November. The overall low topography and the seasonal inundation resulting from the overflow of permanent waterbodies plus local rainfall result in different landscape units (grasslands, wet forests and dry forests) (Nunes de Cunha and Junk, 2004). Grasslands and wet forests are invariably flooded during the rainy season, but dry forests are flooded only during atypically high inundation events (Junk and Nunes de Cunha, 2005), which did not occur during this study. During the drought period the floodplain consists of predominantly terrestrial environments and water can be find only in rivers, lakes and permanent ponds.

2.2. *Sampling procedures*

The plots were sampled at three different phases: (i) rising, at early inundation period (December 2006, 27 plots) , (ii) flood, when the water reaches its highest level and the floodplain was inundated for about 60 days (February 2007, 27 plots); and (iii) receding, when the floodplain was drying and few plots remained flooded (April 2007, 9 plots).

In each plot six permanent sampling units were selected at every 50 meters (from 0 m to 250 m). A set of environmental variables was measured at each sampling unit: water temperature (°C), oxygen (mg/l), pH and electrical conductivity (μS/c), using a YSI 556 multiparameter system, and water depth using a measuring tape fixed to a pole. The hydroperiod of the each plot was estimated by repeated recordings of the water level using a measuring tape fixed to a stake placed at the "zero" point of each plot, and visited weekly from December 2006 to July 2007. Thus, the time (number of days) since the begging of inundation was used as the hydroperiod length for each plot. Soil was characterized based in samples of the upper layer (20 cm), obtained at each sampling points where limnological variables were measured. The six soil samples were mixed and homogenized and analyzed in order to determine the percent contents of clay, sand, silt and organic matter.

Information on vegetation cover at the landscape scale was obtained from Google Earth^{TM} images and transformed into a raster grid, after manually defining the contour of each vegetation polygon. Based in the combined information of vegetation structure and inundation, six types of landscape units were identified: wet grassland, wet forest, wet pasture, wet grassland with pasture, dry forest and dry pasture. Despite these finer landscape classification, in this study the landscape was characterized in only two categories, forest and grassland, because while grasslands and pastures included principally grasses and aquatic macrophytes (submerged, emergent and floating), forests are composed by shrubs and trees without detectable plant undergrowth species. In order to assess if different landscape units affect the water quality (temperature, dissolved oxygen, conductivity and pH), the percent cover of the two vegetation cover types was measured inside a 5 m (B5), 10 m (B10), 25 m (B25), 50 m (B50), 100 m (B100), 150 m (B150), 300 m (B300) and 500 m (B500) buffer around each sampling unit using the rgdal (Keitt et al., 2011) and maptools (Lewin-koh et al., 2011) statistical packages, after preparing the image using the ArcGis 9.2 software (ESRI)). Thus, landscape cover was represented by a vegetal cover index which varies from 0 when only grassland is present to 1 when only forest is present.

2. 3. Data analysis

In order to evaluate if limnological characteristics (water temperature, oxygen, conductivity and pH) are spatially structured throughout the floodplain and temporally structured along the inundation period, analyzes were performed separately for each sampling occasion. Variables that did not attend the normality assumption were transformed using log (x+1) or square rooted. All variables were standardized using *z-scores* transformation (Legendre and Legendre, 1998). This standardization is achieved by subtracting each observation from the variable mean and dividing by its standard deviation. This procedure is necessary when the variables are expressed in different measurement units (Legendre and Legendre, 1998).

Because landscape and soil variables were nested and presented high correlation values, a principal components analysis (PCA) was applied to each environmental attribute (soil and landscape characteristics) in order to summarize the data into fewer and uncorrelated dimensions (Legendre and Legendre, 1998). The number of axes necessary to represent the variance of the data was defined using the broken stick model (Jackson et al., 1993). For landscape characteristics, the first axis was sufficient to represent all eight variables (Appendix B), whereas soil characteristics demanded the two first axes (the first (soil 1) summarizing the relationships among sand, clay and silt, and the second (soil 2) representing the soil's organic matter content (Appendix C). *Corfiv* function from AED package (Zuur, 2010) was used to evaluate the collinearity between explanatory variables (water temperature and depth, hydroperiod, soil 1, soil 2 and landscape). When some variables showed correlation values higher than 0.6 and VIF (variance inflation factors) higher than 3.0, one of them was chosen to represent the set (Zuur et al., 2009).

Although autocorrelation is a natural condition of some variables (Tobler, 1970; Fortin and Dale, 2005), it affects the independence of the samples and the amount of degrees of freedom, which is smaller than expected when the observations are independent (Legendre, 1993; Griffith and Peres-Neto, 2006; Peres-Neto and Legendre, 2010), increasing the chances of type I errors and making statistical tests less conservative (Legendre and Fortin, 1989; Diniz-Filho et al., 2003). This is especially important regarding spatial variables, and two different statistical procedures (spatial regression) can be utilized (Fortin et al., 2012): the space is included as a covariate predictor (Griffit and Peres-Neto, 2006; Dray et al., 2006); or the space is included in the error term (Pinheiro and Bates, 2000; Diniz-Filho et al., 2003; Zuur et al., 2009). We choose to work with the error term using Generalized Least Squares (GLS) models (Pinheiro and Bates, 2000) in order to deal with autocorrelation among environmental variables.

A model was built to each limnological variable (temperature, oxygen, conductivity and pH) without autocorrelation structure, and five models that take into account spatial autocorrelation structure using gls function from nlme package in R (Pinheiros et al., 2012). The autocorrelation was introduced into the model by defining the spatial correlation structures (Exponential, Gaussian, Linear, Rational Quadratic or Spherical) inside of the data (Zuur et al., 2009). The Akaike Information Criterion (AIC - Burnham and Anderson, 2002) with the small sample correction (AICc - Hurvich and Tsai, 1989) was used to select the best model. In addition to AICc value where the lower values indicate the the best models, and ΔAICc values were used to evaluable the acceptability of each model (ΔAICc < 2 = strong support in the data; ΔAICc>=2 and < 4 = little support in the data; ΔAICc > 4 = without support in the data) (Burnham and Anderson, 2002).

The relationships between response and explanatory variables were assessed through slope value (b), stander error, t-value and p-value of the best model. Moran's I statistic was used to assess residual's spatial autocorrelation (Legendre and Fortin, 1989; Legendre, 1993, Fortin and Dale, 2005) of the best model. This approach allows to assess the efficiency of the method in analyzing data that affected by spatial autocorrelation (Appendix J, k, L and M).

To assess the relative contributions of the environmental and spatial factors to explain temperature, oxygen, conductivity and pH variation in the floodplain, we used variation partition techniques (Peres-Neto et al., 2006). Environmental variables that showed significant relationship with response variables in GLS models were used as environmental predictors, whereas spatial predictors were constructed using Moran's Eigenvector Maps - MEM (see Dray et al., 2006 and De Bie et al., 2012 for more details). This procedure yielded 33 spatial predictors for the rising period, 39 for the flood period, and 7 for receding period; model select procedure (forward.sel function of the 'packfor' library by Dray et al., 2011) was used to retain only spatial predictors that showed relationship with response variables (Peres-Neto and Legendre, 2010). Variation partition decomposes the total variation of response variables into a purely environmental component [E], a component representing spatially structured environmental variation [E+S], a purely spatial component [S], and the residual fraction of variation not explained [R] by spatial or environmental factors (Peres-Neto and Legendre, 2010). All statistical calculations were carried out with the R software (R Development Core Team, 2012).

3. Results

3.1. Environmental characteristics of floodplain

The highest average value of oxygen was found in the flood period, and the lowest in the receding period. Conductivity showed an inverse pattern, with lowest average in the flood and higher values in rising and receding periods. Differently, pH showed a tendency to linear increasing throughout the inundation period. Other explanatory variables showed different patterns, with mean hydroperiod length increasing along the inundation, whereas mean temperature decreased. As could be expected, depth was highest in flood period and lower in the beginning and the end of the inundation season (Table 1). The soil samples showed high sand content (mean: 75%; range: 52 to 91%), low clay (12%; 3 - 31%), silt (12%; 4 - 21%) and organic matter (4.7%, 1.08 - 61.3%) content. The vegetal cover index ranged from 0 (only grassland present) to 1 (only forest present), however the mean value was 0.26 (B5), 0.27 (B10), 0.28 (B25), 0.31 (B50), 0.34 (B100), 0.37 (B150), 0.42 (B300) and 0.44 (B500).

Table 1 Physicochemical characteristics (mean (range)) of the water in the floodplain during rising, flooding and receding periods along inundation season.

Variables	Rising	Flood	Receding
Responses variables			
Temperature (°C)	33.4 (27.5 - 43.5)	32.4 (26.0 - 42.3)	27.9 (22.6 - 36.9)
Oxygen (mg/l)	5.0 (1.9 - 8.6)	6.19 (0.8 - 11.8)	3.1 (0.64 - 9.8)
Conductivity (μS/c)	17.3 (2.9 - 44.9)	9.0 (4.0 - 34.0)	17.9 (11.0 - 26.0)
pH	5.9 (2.93 - 6.85)	6.27 (5.5 - 7.1)	7.2 (6.3 - 8.3)
Explanatory variables			
Hydroperiod (days)	6.4 (1.0 -17.0)	64 (24 - 81)	134 (127 - 146)
Depth (cm)	17.4 (2.3 - 47)	25.2 (3.0 - 64.0)	17.5 (3.0 - 42.0)

There were no correlations between variables in the rising period, whereas in the flood period depth showed a significant negative correlation with temperature (r=-0.71; p<0.001) and a significant positive correlation with soil 1 (r=0.67; p<0.001). Thus, depth was removed from the models for the flood period. In the receding period, depth showed a positive correlation with hydroperiod (r=0.64; p<0.001), whereas altitude showed correlation with soil 2 (r=0.82; p<0.001). Thus, depth and altitude were also removed from the models for receding period. When temperature data were analyzed, altitude showed correlation with soil2 (r=0.82; p<0.001) and landscape (r=-0.61; p=0.001) and altitude was removed. The AICc values showed that the model with spatial autocorrelation structure was always better than the model without it (Appendix D).

3.2. Temperature

Temperature was negatively affected by water depth in all sampling periods; additionally, temperature also was affected by landscape in the rising period (Table 2 and Appendix F). In the rising period, lower temperature values were found in places with higher water depth and forest cover, whereas shallow water and grassland cover resulted in higher water temperature. During the flood and receding periods the landscape did not affect the limnological characteristics of the floodplain, and higher temperatures were found in shallow places while lower temperatures were registered in deeper sites, independent of the vegetation cover type.

Table 2 Coefficients of multiple regression analyzes (b±SE) and associated t-values for water temperature in relation to environmental variables using spatial generalized least square (GLS) models. The spatial structure was introduced into the model with a Linear term for rising period, a Ratio Quadratic term for flood period, and Gaussian term for receding period.

Variables	Rising		Flood		Receding	
	b±SE	t-value	b±SE	t-value	b±SE	t-value
Altitude	0.161±0.123	1.312	0.197±0.129	1.524	---	---
Hydroperiod	0.087±0.123	0.708	-0.027±0.111	-0.241	0.387±0.356	1.087
Depth	-0.317±0.072	-4.413**	-0.267±0.075	-3.569**	-0.467±0.134	-3.483**
Soil 1	0.031±0.208	0.149	-0.100±0.171	-0.583	-0.466±0.679	-0.687
Soil 2	-0.070±0.191	-0.366	0.001±0.174	0.007	-0.240±0.267	-0.899
Landscape	0.376±0.176	2.143*	0.292±0.159	1.840	-0.580±0.348	-1.669

* $p<0.05$; ** $p<0.01$; --- variable removed from the model because of collinearity with others variables.

In the rising period, 12% of the temperature variation were explained by purely environmental factors (depth and landscape), 13% by purely spatial (MEM: 22, 4, 1, 8, 5, 12, 7 and 8), and 25% were explained by environmental factors spatially structured. Environmental heterogeneity decreased during the flood period, with 14% of the variation explained by purely environmental factors (depth), 24% by purely spatial (MEM: 6, 21, 5, 7, 9, 10, 16, 4, 14, 19, 17, 1, 24 and 8) and 35% by spatially structured environmental factors. Environmental heterogeneity increased again at the end of the flooding season, with decreasing importance of purely spatial

(6%; MEM: 3) and spatially structured environmental factors (1%), and increasing effects of purely environmental factors (23%; depth) (Fig. 1; Appendix N).

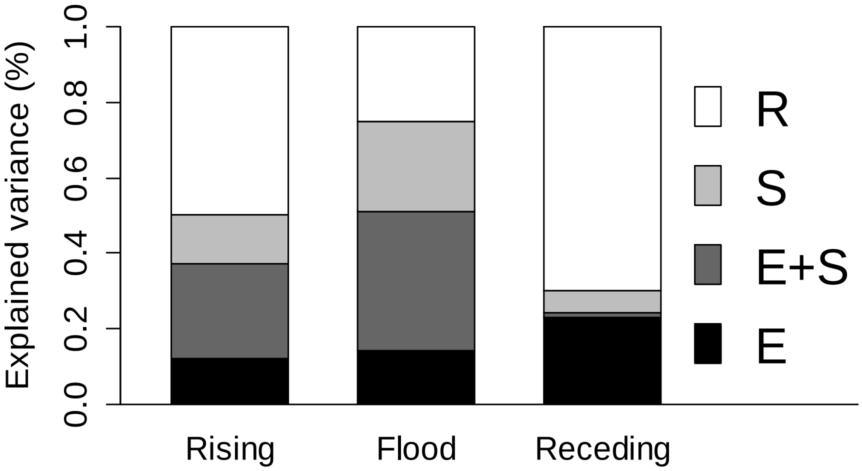


Fig. 1. Variation partition for temperature showing the contribution of the purely environmental component [E], purely spatial component [S], spatially structured environmental variation [E+S], and the residual fraction of variation [R] not explained neither by spatial nor environmental factors.

3.3. Oxygen

Dissolved oxygen content had a positive relationship with temperature during the three sampling periods. Landscape did not affect the oxygen content in the rising period, but in the flood and receding periods this variable became important. Thus, higher oxygen values were found in places with grassland cover, higher water temperature and lower water depth, whereas lower oxygen values were found in places with forest cover, lower temperature and higher water depth water in the flood and receding periods. Differently, in the beginning of the inundation (rising period) higher oxygen values were found at deeper places but with warmer water.

Table 3 Coefficients of multiple regression analyzes (b±SE) and associated t-values for oxygen in relation to environmental variables using generalized least square (GLS) models. Spatial structure was introduced into the model with a Spherical term for rising, a Gaussian term for flood, and a Ratio Quadratic term for receding period.

Variables	Rising		Flood		Receding	
	b±SE	t-value	b±SE	t-value	b±SE	t-value

Altitude	0.099±0.085	1.160	0.043±0.112	0.388	---	---
Hydroperiod	-0.085±0.096	-0.888	0.109±0.111	0.977	-0.181±0.217	-0.836
Depth	0.392±0.113	3.458**	---	---	---	---
Temperature	0.458±0.132	3.460**	0.376±0.077	4.271**	0.767±0.138	5.570**
Soil 1	-0.247±0.147	-1.681	-0.198±0.175	-1.134	-0.286±0.443	-0.646
Soil 2	-0.078±0.129	-0.607	0.210±0.176	1.189	0.791±0.245	3.220
Landscape	0.233±0.200	1.163	0.499±0.174	2.853**	1.949±0.440	4.425**

* $p<0.05$; ** $p<0.01$; --- variable removed from the model because of collinearity with others variables.

In the rising period, oxygen had 11% of variation explained by environmental factors (depth and temperature), whereas purely spatial (MEM: 4 and 17) factors explained 4%, and 1% was explained by spatially structured environmental factors. When the floodplain becomes largely connected in the flood period, the component explained by purely environmental (temperature and landscape) factors decreased, explaining only 5% of the variation; purely spatial factors effects (MEM: 7, 5, 21, 6, 26, 4, 14, 18, 8, 20 and 9) increased to 39%, and spatially structured environmental factors accounted for 20%. In the end of the flooding season, when the floodplain is drying and less connected (receding period), the environmental factors (temperature and landscape) explained 43% of the variation in oxygen content of the water, purely spatial factors (MEM: 3 and 4) explained 16%, and spatially structured environmental factors accounted for only 4% of the oxygen variation (Fig. 2; Appendix N).

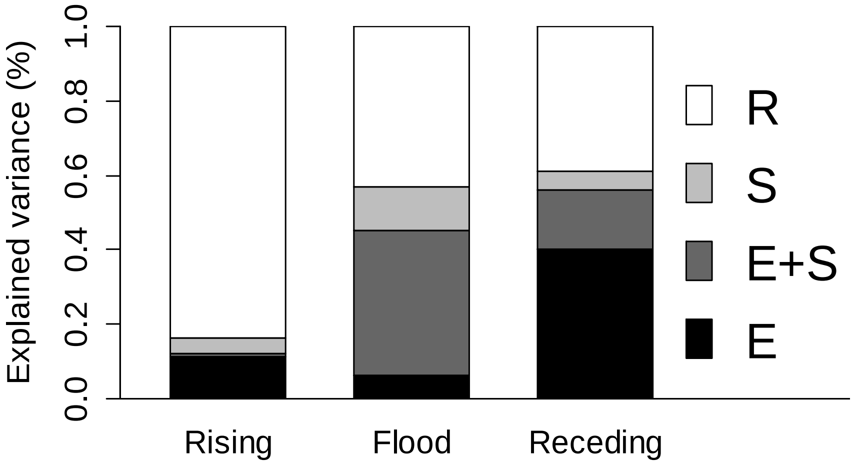


Fig. 2. Variation partition for oxygen showing the contribution of the purely environmental component [E], purely spatial component [S], spatially structured environmental variation [E+S], and the residual fraction of variation not explained [R] neither by spatial nor environmental factors.

3.4. Conductivity

The conductivity was negative affected by the altitude in the rising period, and by the temperature in the two first sampling periods (rising and flood). However, the effect of the temperature changed throughout the flooding season, being positive in the rising period and becoming negative in the flood period. In other words, while higher conductivity values were found in places whit warmer water in the rising period, the contrary was observed in flood period (Table 4; Appendix H).

Table 4 Coefficients of multiple regression analyzes (b±SE) and associated t-values for water conductivity in relation to environmental variables using spatial generalized least square (GLS) models. Spatial structure was introduced into the model with a Gaussian term for rising and food periods and a Spherical term for receding period.

Variable	Rising		Flood		Receding	
	b±SE	t-value	b±SE	t-value	b±SE	t-value
Altitude	-0.580±0194	-2.986**	0.130±0.168	0.774	---	---
Hydroperiod	0.121±0.141	0.862	-0.165±0.168	-0.977	0.174±0.437	0.399
Depth	0.013±0.089	0.150	---	---	---	---
Temperature	0.225±0.100	2.246*	-0.257±0.123	-2.094*	-0.235±0.155	-1.522
Soil 1	0.356±0.230	1.545	0.037±0.256	0.145	-0.607±0.833	-0.729
Soil 2	0.117±0.205	0.570	-0.289±0.265	-1.092	0.048±0.333	0.144
Landscape	0.055±0.214	0.258	0.205±0.249	0.822	-0.251±0.418	-0.601

* $p<0.05$; ** $p<0.01$; --- variable removed from the model because of collinearity with others variables.

In the rising period, environment factors (altitude and temperature) explained 24% of the conductivity variation, and purely spatial factors (MEM: 10, 20, 9, 13, 11, 3, 26 and 2) accounted for 45%. This pattern changed in the flood period when the importance of environmental factors (mainly temperature) decreased, explaining only 2%, whereas purely spatial factors (MEM: 14, 9, 11, 2, 12, 5, 13, 28, 16 and 16) explained 58% of the conductivity variation. In the receding period, at the end of the flooding season, environmental factors were not important (0%) and purely spatial factors (MEM: 4) accounted for 15% of the conductivity variation (Fig. 3; Appendix N).

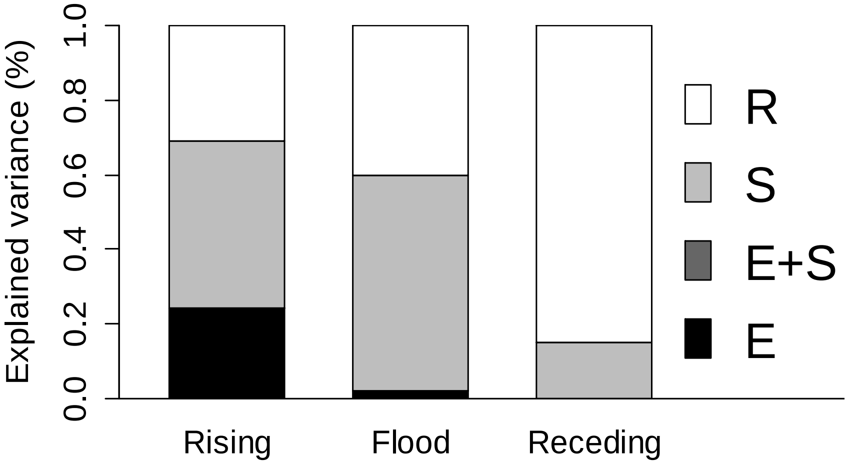


Fig. 3. Variation partition for conductivity showing the contribution of purely environmental component [E], purely spatial component [S], component representing spatially structured environmental variation [E+S], and the residual fraction of variation not explained [R] neither by spatial nor environmental factors.

3.5. pH

Water temperature affected pH values in all sampling periods, with a positive correlation in the rising and flood periods, but turning negative in the receding period (Table 5; Appendix I).

Table 5 Coefficients of multiple regression analyzes (b±SE) and associated t-values for pH in relation to environmental variables using spatial generalized least square (GLS) models. The spatial structure was introduced into the model with a Gaussian term for rising and flood periods, and an Exponential term for receding period.

Variable	Rising		Flood		Receding	
	b±SE	t-value	b±SE	t-value	b±SE	t-value

Altitude	-0.119±0.109	-1.095	-0.036±0.193	-0.187	---	---
Hydroperiod	0.090±0.108	0.831	0.012±0.159	0.078	-0.276±0.242	-1.137
Depth	0.016±0.087	0.182	---	---	---	---
Temperature	0.255±0.100	2.527*	0.410±0.150	2.731**	-0.343±0.131	-2.608*
Soil 1	0.111±0.176	0.631	-0.055±0.261	-0.210	-0.302±0.479	-0.631
Soil 2	0.060±0.162	0.369	0.260±0.257	1.014	-0.001±0.181	-0.004
Landscape	0.317±0.186	1.698	0.108±0.296	0.364	-0.490±0.284	-1.727

* $p<0.05$; ** $p<0.01$; --- variable removed from the model because of collinearity with others variables.

The contribution of purely environmental factors (notably temperature) for pH increased along the inundation season, accounting for 1%, 7% and 12% for rising, flood and receding periods, respectively. The contrary occurred with purely spatial factors, which explained 38% (MEM: 30, 19, 3, 8, 9, 2 and 4) of the variation at the beginning of the inundation (rising), then decreasing to 25% (MEM: 18, 26, 7, 34, 3, 6 and 20) in the flood period, to 0% (zero) in the receding (Fig. 4; Appendix N). Contrary to the other studied variables, pH showed a stronger effects of spatial factors in beginning of the inundation season than in the flood period, when the floodplain was extensively connected.

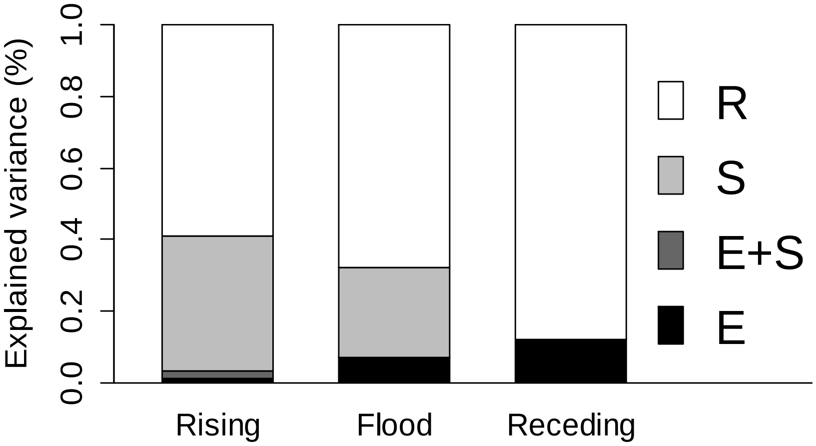


Fig. 4. Variation partition for pH showing the contribution of the purely environmental component [E], purely spatial component [S], component representing spatially structured environmental variation [E+S], and the residual fraction of variation not explained [R] neither by spatial nor environmental factors.

4. Discussion

Temperature was affected by water depth in all sampling periods, and by landscape characteristics in the rising period. Temperature was important for oxygen and pH in all sampling periods, and for conductivity in rising and flood periods. Landscape showed effects on the oxygen concentration in the flood and receding periods, whereas altitude affected conductivity at the beginning of the inundation season. The contribution of the environmental factors increased throughout the inundation season for oxygen, temperature and pH, whereas for conductivity the pattern was inverted. Purely spatial factors presented a larger contribution in flood period for all variables analyzed. When comparisons were done between rising and receding periods, the contribution of purely spatial factors was higher for temperature and conductivity in the rising period, and for pH in the receding period; oxygen concentration was similarly affected in both sampling periods.

4.1. Temperature

A negative effect of depth in water temperature has been observed for other systems, such as rivers, lakes and wetlands (Douglas Shields et al., 2011). This relationship can be explained simply by the fact that more water volume implies more energy necessary to warm up the water. Water temperature has a strong relationship with the amount of solar irradiation that reach the surface and evaporative cooling (Erez et al., 1990), thereby information about factors such as cloudiness, vegetal cover and wind velocity are fundamental to understand spatial and temporal variation in water temperature. Unfortunately, we have not information about cloudiness degree or wind velocity, but we found a negative effect of landscape in water temperature. In places where plant canopy is more closed (forest), less solar irradiation reach the water surface, thus lowering water temperature (Reeder, 2011; Chimney et al., 2006), whereas places with grassland cover, which receives a higher amount of direct solar irradiation, had warmer water.

4.2. Oxygen

Contrary to studies in lakes, rivers and streams, where oxygen consumption increases with temperature resulting in a negative relationship between them (Boyd et al., 1978, Kersting, 1981; Guashi et al., 1998; Loperfido et al., 2009; He et al., 2011), we found a positive relationship between temperature and oxygen in the seasonally flooded environment of the

Pantanal. A negative relationship between temperature and oxygen occurs because in high water temperature there is loss of oxygen due to both saturation decrease as well as by increased consumption resulting from higher decomposition rates (Driever et al., 2005; Chimney et al., 2006). The positive relationship found in this study may be due to two interconnected factors. First, because our study had been conducted in a highly vegetated shallow floodplain, the net primary productivity can be high enough to maintain high oxygen levels, despite to increase in temperature; second, the decomposition and respiration rates are not high enough to cause a depletion in the oxygen content (Penha et al., 1999).

Another factor that may give support for this explanation is the high water transparency caused by sedimentation of the suspended particles due to the reduced (to absent) water flow (Girard et al., 2010) and nutrient uptake from the water column by periphyton (Cronk and Mitsh, 1994). A high water transparency associated with low water depth permit that the solar irradiation reaches to the bottom, and light does not constitute a limiting factor for photosynthesis. Thus, in shallow temporary wetlands, a high primary productivity is maintained by phytoplankton, periphyton and submerged macrophytes (Cronk and Mitsh, 1994), and although an oxygen loss due to saturation may occur, the high productivity maintains high oxygen levels even under high water temperatures.

Such as in our study the negative effects of the vegetal cover for oxygen are also known (Dale and Gillespie, 1976; Driever et al., 2005; Reeder, 2011). Places with vegetal cover do not permit that solar irradiation solar reaches the water, inhibiting the growth of the aquatic plants that coupled with abundant litter in decomposition process decrease the oxygen available. Girard et al. (2010) showed that temporary aquatic habitats in the Brazilian Pantanal with arboreal cover have small water velocity than open-water areas or places with grassland cover. Furthermore, the presence of dense vegetation prevents wind action on the water surface, reducing the mixing of the water column and limiting the intake of oxygen from the atmosphere.

4.3. Conductivity

The negative relationship between altitude and conductivity in the beginning of the inundation season can be due to the nutrients and organic matter loading, through runoff, to lower altitude places (depressions) in the floodplain. In the rising period, all nutrients and organic matter (plant litter) accumulated during the drought season start decomposing and the increase in water temperature can accelerate the decomposition rate (Fierer et al., 2005; Davidson and Janssens, 2006) causing the release of metabolites and increasing the conductivity values in places with higher water temperature (Reddy, 1981). During the peak of the flooding season, this relationship becomes negative. Likely on this period, a great part of the organic matter was already decomposed (Chimney et al., 2006), accompanied by an increase in dissolved nutrient removal due to plant, phytoplankton, and periphyton growth (Penha et al., 1999). Consistent with this pattern, the oxygen also increased with temperature, indicating that the primary productivity can be higher in warmer places. So, the increase in primary productivity is coupled with nutrients utilization by plant life, resulting in lower water conductivity and higher transparency values.

4.4. pH

The observed relation between pH and temperature was not unexpected, and it can be explained by one indirect relationship with primary productivity. Variation in pH due to the balance between photosynthesis and respiration is well documented in freshwater ecosystems (Guashi et al., 1998; Wetzel, 2001; Chimney et al., 2006; Hauer and Hill, 2007), thereby a positive relationship between oxygen and pH was also observed (Reddy, 1981; Frodge et al., 1990). During de photosynthesis process, carbon dioxide (CO_2) is removed from the water, increasing the pH, but the contrary occur in the absence of photosynthesis or in places where decomposition or respiration rates are predominant (Chimney et al., 2006) and more carbon dioxide is released to the water (Erez et al., 1990), lowering the pH. But, why this relation is inverted in the end of the inundation season? In this period the water volume and inundated area are reduced, and water was found only in low altitude places. Thus, we believe that when the floodplain is drying, all the organic matter is carried to a small area, increasing the amount of CO_2 due to increased decomposition and respiration processes, resulting in lower pH values.

4.5. The relative contribution of environmental and spatial factors

Most of the published studies dealing with freshwater aquatic organisms point out water temperature, dissolved oxygen, conductivity and pH as the main environmental predictors responsible by community structure (Oberdorff et al., 1995, Olden et al., 2001; Gray et al., 2012). However, those studies did not indicate how fine, intermediate and broad scale factors affect those variables and what mechanisms govern the spatiotemporal changes in environmental conditions of aquatic habitats. As far as we know, this study innovates in dealing simultaneously with environmental and spatial factors in the search for the mechanisms responsible for temporal changes in water temperature, oxygen, conductivity and pH in a natural and complex wetlands system.

Environmental factors were more important in determining changes in temperature and oxygen at the beginning and end of the inundation season, and for conductivity in the rising and for pH in the receding phases. In the beginning of the inundation season, the floodplain habitats are strongly disconnected and the temporary habitats present unique physicochemical characteristics; at the end of the inundation season the floodplain is drying up and becoming progressively less connected, increasing the influence of local factors (Thomaz et al., 2007, Layman et al., 2010). Environmental factors (depth, landscape and water temperature) were always more important in determining changes in water temperature and dissolved oxygen than spatial factors; however, the significant role of spatial predictors (Appendix N) at intermediate and broad scales indicates that water temperature and oxygen content result not only of the local characteristics, but also of the balance between oxygen production and consumption in wider spatial scales. The spatial predictors modeled by MEM accounted for 45% and 38% of the variation in conductivity and pH at the beginning of the inundation season. These predictors may represent different spatial scales, but are mainly influenced by broad-scale factors (Bocard et al., 2004; Peres-Neto and Legendre, 2010; De Bie et al., 2012). This means that the local availability of nutrients and soil characteristics can be spatially structured (Bruland & Richardson, 2004; Iqbal et al., 2005), and, together with decomposition and photosynthesis processes, interplay to compose the fine, intermediated and broad scale eigenvectors (Bardgett et al., 2001). In the end of the inundation season, spatial predictors did not significantly affect pH, and predictors acting at intermediate scales may reflect the importance of the decomposition process for water conductivity in the floodplain.

Spatial factors represented the most important drivers for all limnological variables at the peak of the flooding season except for pH, which received a stronger contribution of spatial factors in the beginning of the inundation season (rising period). During the flood period all habitats are more connected with each other, and the floodplain’s environmental characteristics become more homogeneous (Thomaz et al., 2007). In this period the contribution of the local environmental factors are reduced, whereas spatially structured environmental factors increase in importance in determining changes in water temperature and oxygen, with a decreased influence of purely environmental factors (water temperature, depth and landscape). In this phase of the inundation season, spatial predictors accounting by intermediate and broad scale processes become more important. Different of the beginning and end of the inundation season, local characteristics play a minor role, and processes occurring in intermediate and broad scales (e.g. solar irradiation, decomposition and primary productivity) become more important. As observed in the begging and end of the inundation season, spatial predictors of the fine, intermediate and broad-scale processes were important for conductivity and pH, and we believe that soil characteristics and processes related with decomposition and primary productivity (Erez et al., 1990; Chimney et al., 2006), among others, should be the factors controlling conductivity and pH variation in temporary environments. So, hydrological connectivity at the peak of the floods permits energy to dissipate and organisms' dispersion, resulting in floodplain homogenization. Thus, water temperature and oxygen showed more influence of spatial factors in the flood period, while this influence seems to be constant throughout of the inundation season for conductivity and pH.

The variation explained by spatially structured environmental factors was high for water temperature in rising and receding periods, and for oxygen in the flood and receding periods. These results can represent two distinct situations. First, environmental predictors as well as water temperature and oxygen are spatially structured, and the component [E+S] represents the spatialized component of the environment that induced the observed correlation between water temperature and oxygen. Second, some important spatially structured variables may have been missed, and the component (E+S) represents the covariation between the measured and unmeasured environmental drivers (Peres-Neto and Legendre, 2010).

5. Conclusions

We demonstrated that the negative relationship between water temperature and dissolved oxygen can be change in a highly vegetated shallow floodplain with high water transparency. The relationship of the environmental variables with water temperature, dissolved oxygen, conductivity and pH changes throughout of the inundation season, demonstrating the need to include information about the direction of changes (rising, flood, and receding) in the analysis of the data from temporal habitats. The effect of the environmental factors was more important in the begging and end of the inundation season, while spatial factors were important in peak of the floods when the hydrological connectivity was higher.

Acknowledgements

We would like to thank the Pantanal Research Center for the financial support and the National Council for Scientific and Technological Development (CNPq) for Postgraduate scholarship as well as the Coordination for the Improvement of the Higher Level Personnel (CAPES) that provided sandwich scholarship for I. M. Fernandes (#BEX: 6140/11-4). JZ receives a productivity grant from CNPq (#307464/2009-1).

References

Baber, J.M., Childers, D.L., Babbitt, K.J., Anderson D.H., 2002. Controls on fish distribution and abundance in temporary wetlands. Can. J. Fish. Aquat. Sci. 59, 1441-1450.

Bardgett, R.D., Anderson, J.M., Behan-Pelletier, V., Brussaard, L., Coleman, D.C., Ettema, C, Moldenke, A, Schimel J.P. and Wall D.H., 2001. The influence of soil biodiversity on hydrological pathways and the transfer of materials between terrestrial and aquatic ecosystems. Ecosystems 4, 421–429.

Bond, N. R., Lake, P. S., & Arthington, A. H. (2008). The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia, 600(1), 3-16

Bruland, G. L., Richardson, C. J. (2004). A spatially explicit investigation of phosphorus sorption and related soil properties in two riparian wetlands. J. Environ. Qual 33(2), 785-794.

Burgess, S.C., Treml E.A., Marshal D.J., 2012. How do dispersal costs and habitat selection influence realized population connectivity? Ecology 93(6) 1378–1387.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Chase, J.M., Leibold, M.A., 2003. Ecological niches. Chicago, IL: University of Chicago Press.

Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. Proc. Natl. Acad. Sci.104,17430-17434.

Chimney, M.J., Wenkert, L., Pietro, K.C., 2006. Patterns of vertical stratification in a subtropical constructed wetland in south Florida (USA). Ecol. Eng. 27, 322–330.

Cronk, J.K., Mitsch, W.J. 1994. Periphyton productivity on artificial and natural surfaces in constructed freshwater wetlands under different hydrologic regimes. *Aquat. Bot.48*(3), 325-341

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Dale, H.M., Gillespie, T., 1976. The influence of floating vascular plants on the diurnal fluctuations of temperature near the water surface in early spring. *Hydrobiologia*, *49*(3), 245-256.

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., Declerck, S.A.J., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol. Lett. 15, 740–747.

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

Driever, S.M., van Nes, E.H., Roijackers, R.M.M., 2005. Growth limitation of *Lemna minor* due to high plant density. Aquat. Bot. 81, 245–251.

Dray, S. Legendre, P. Blanchet G., 2011. packfor: Forward Selection with permutation (Canoco p.46). R packfor: Forward Selection with permutation (Canoco p.46). R package version 0.0-8/r100. http://R-Forge.R-project.org/projects/sedar/.

Dembkowski D.J., Miranda L.E., 2012. Hierarchy in factors affecting fish biodiversity in floodplain lakes of the Mississippi Alluvial Valley. Environ. Biol. Fishes 93(3), 357-368.

Douglas Shields, F., Lizotte, R.E., Knight, S.S., 2011. Spatial and temporal water quality variability in aquatic habitats of a cultivated floodplain. River Res Applic. doi:10.1002/rra.1596.

Duggan, J.M., Schooley R.L., Heske, E.J., 2011. Modeling occupancy dynamics of a rare species, Franklin‘s ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecol. 26, 1477-1490.

Erez, J., Krom, M.D., Neuwirth, T., 1990. Daily oxygen variations in marine fish ponds, Elat, Israel. Aquaculture 84, 289–305.

Gray, D. K., Arnott, S. E., Shead, J. A., & Derry, A. M. (2012). The recovery of acid-damaged zooplankton communities in Canadian Lakes: the relative importance of abiotic, biotic and spatial variables. Freshw. Biol. 57(4), 741-758.

Fernandes, I. M., Machado, F. A., Penha, J., 2010. Spatial pattern of fish assemblage in a seasonal tropical wetland: effects of habitat, herbaceous plant biomass, water depth, and distance from species sources. Neotropical Ichthyol. 8, 289-298.

Ferris, R., Piece, A.J., Humphrey, J.W., Broome, A.C., 2000. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. F. Ecol. Manag. 136, 35-51.

Fortin, M.J., Dale, M.R.T., 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge.

Fierer, N., Craine, J.M., McLaughlan, K., Schimel, J.P., 2005. Litter quality and the
temperature sensitivity of decomposition. Ecology 86,320-326.

Fortin M.J., James, P.M.A., MacKenzie, A., Melles, S.J., Rayfield, B., 2012. Spatial statistics, spatial regression, and graph theory in ecology. Spatial Statistics 1: 100-109.

Frodge, J.D., Thomas, G.L., Pauley, G.B., 1990. Effects of canopy formation by floating and submergent aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. Aquat. Bot. 38, 231-248.

He, J., Chu, A., Ryan, M.C., Valeo, C., Zaitlin, B., 2011. Abiotic influences on dissolved oxygen in a riverine environment. Ecol. Eng. 37, 1804-1814.

Guasch, H., Armengol, J., Marti, E., Sabater, S., 1998. Diurnal variation in dissolved oxygen and carbon dioxide in two low-order streams. W. Res. 32, 1067-1074.

Girard, P. Fanti-Cruz, I., Loverde-Oliveira, S.M., Hamilton, S.H., 2010. Small-scale spatial variation of inundation dynamics in a floodplain of the Pantanal (Brazil). Hydrobiologia 638, 223-233.

Griffith, D.A., Peres-Neto, P.R., 2006. Spatial modelling in ecology: the flexibility of eigenfunction spatial analyses in exploiting relative location information. Ecology 87,2603–2613.

Güsewella, S., Peter M., Birrer, S., 2012. Altitude modifies species richness–nutrient indicator value relationships in a country-wide survey of grassland vegetation. Ecol. Ind. 20, 134–142.

Hauer, F.R., Hill, W.R., 2007. Temperature, light and oxygen. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology., 2nd ed. Academic Press, San Diego, pp.103–117.

Hamilton, S.K., Sippel, S.J. Melack, J.M., 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. Arch. Hydrobiol. 137,1–23.

Harris, M.B., Tomas, W., Mourão, G., da Silva, C.J., Guimarães, E., Sonoda, F., Fachim, E., 2005. Safeguarding the Pantanal wetlands: Threats and conservation initiatives. Conserv. Biol. 19, 714–720.

Iqbal, J., Thomasson, J. A., Jenkins, J. N., Owens, P. R., Whisler, F. D. 2005. Spatial variability analysis of soil physical properties of alluvial soils. S. Scien. Soc. of Amer. Journal 69(4), 1338-1350.

Jackson, D.A., 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. Ecology 74, 2204–2214.

Junk, W. J. 1973. Investigations on the Ecology and Production Biology of the 'Floating Meadows'(Paspalo-Echinochloetum) on the Middle Amazon. Part II: The Aquatic Fauna in the Root Zone of Floating Vegetation. Amazoniana 4,(I) 9-102.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. J. Fish. Aquat. Sci. 106, 110-127.

Junk, W.J., Soares, G.M., Carvalho, F.M., 1983. Distribution of fish species in a lake of the Amazon River floodplain near Manaus (lago Camaleao) with special reference to extreme oxygen conditions. Amazoniana 7, 397-431

Junk W.J., Nunes de Cunha, C., 2005. Pantanal: a large South American wetland at a crossroad. Ecol. Eng. 2 391–401.

Junk, W.J., Nunes da Cunha, C., Wantzen, K.M., Petermann, P., Strussmann, C., Marques, M.I., Adis, J., 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquat. Sci. 68, 278-309.

Kersting, K., 1981. Annual and diel oxygen and temperature regime of the Lakes Maarsseveen. Hydrobiol. Bull. 15, 10–28.

Kneitel, J.M.,Miller, T.E., 2003. Dispersal rates affect species composition in metacommunities of Sarracenia purpurea inquilines. Am. Nat. 162, 165–171.

Keitt, T.H., Bivand, R., Pebesma E., Rowlingson, B., 2012. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.7-12. http://CRAN.R-project.org/package=rgdal.

Layman, C. A., C. G. Montaña, and J. E. Allgeier. 2010. Linking fish colonization rates and water level change in littoral habitats of a Venezuelan floodplain river. Aquatic Ecology 44, 269-273.

Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.O.V., Magnusson, W.E., 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. Freshwater Biol. 57, 1554–1564.

Legendre, P., Fortin, M.J., 1989. Spatial pattern and ecological analysis. Vegetatio 80, 107–138.

Lewin-Koh, N.J., Bivand, R, Pebesma, E.J., Archer, E., Baddeley, A., 2012. maptools: tools for reading and handling spatial objects. R package version 0.8-16. http://CRAN.R-project.org/package = maptools.

Magle, S.B, Theobald, D.M., Crooks, K.R., 2009. A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landscape Ecol. 24, 267–280.

Oberdorff, T., J. F. Guégan & B. Hugueny, 1995. Global scale patterns in freshwater fish species diversity. Ecography 18: 345–352.

Olden N.L., 1984. Assessing the significance of a spatial correlogram. Geog. Anal. 16, 1-16.

Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2001. Spatial isolation and fish communities in drainage lakes. Oecologia **127**:572-585.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner H., 2012. vegan: Community Ecology Package. R package version 2.0-4.

Pazin, V.F.V., Magnusson, W.E., Zuanon, J., Mendonça, F. P., 2006. Fish assemblages in temporary ponds adjacent to ´terra firme´ streams in Central Amazonia. Freshwater Biol. 51, 1025-1037.

Penha, J.M.F., Da Silva, C.J., & Bianchini-Júnior, I. 1999. Productivity of the aquatic macrophyte Pontederia lanceolata Nvtt.(Pontederiaceae) on floodplains of the Pantanal Mato-grossense, Brazil. *W. Ecol. Manag. 7*(3), 155-163

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team., 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-102.

Perelman, S.B., Leon, J.C., Oesterheld, M., 2001. Cross-scale vegetation patterns of Flooding Pampa grasslands. J. Ecol. 89, 562–577.

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

Peres-Neto, P.R., Legendre, P., 2010. Estimating and controlling for spatial autocorrelation in the study of ecological communities. G. Ecol. . Biog. 19, 174-184.

Rahel, F.J., 1984 Factors structuring fish assemblage along a Bog lake successional gradient. Ecology 65(4), 1276–1289.

Reeder, B.C., 2011. Assessing constructed wetland functional success using diel changes in dissolved oxygen, pH, and temperature in submerged, emergent, and open-water habitats in the Beaver Creek wetlands complex, Kentucky (USA).Ecol. Eng. , 37, 1772–1778.

Reddy, K.R., 1981. Diel variations of certain physico-chemical parameters of water in selected aquatic systems. Hydrobiologia 85, 201–207.

Rodríguez, M. A. & M. L. Lewis. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco river. Ecol. Monogr. 67(1), 109-128.

R Development Core Team., 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Scarabotti, P.A., López, J.A., Pouilly, M., 2011. Flood pulse and the dynamics of fish assemblage structure from neotropical floodplain lakes. Ecol. Freshw. Fish. 20, 605–618.

Signor, C.A., Pinho, J.B., 2011. Spatial diversity patterns of birds in a vegetation mosaic of the Pantanal, Mato Grosso, Brazil. Zoologia 28, 725-738.

Siziba, N., Chimbari, M.J., Masundire, H., Mosepele, K., 2012. Spatial variations of microinvertebrates across different microhabitats of temporary floodplains of lower Okavango Delta, Botswana. African J. Ecol. 50, 43–52.

Zeilhofer, P., Schessl, M., 1999. Relationship between vegetation and environmental conditions in the northern Pantanal of Mato Grosso, Brazil. J. Biogeogr. 27, 159-168.

Teixeira-de-Mello, F., Meerhoff, M., Pekcan-Hekim, Z., Jeppesen, E., 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. Freshwater Biol. 54, 1202– 1215.

Tilman, D., 1982. Resource competition and community structure. Princeton, NJ: Princeton University Press.

Tobler, W.R., 1970. A computer movie simulating urban growth in the Detroit region. Econ. Geog. 46: 234–240.

Tockner, K., Malard, F., Ward, J.V., 2000. An extension of the flood pulse concept. Hydrol. Process. 14, 2861–2883

Tockner, K., Stanford, J.A., 2002. Riverine flood plains: present state and future trends. Environ. Conserv. 29,308–330.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R.

Zuur A.F., 2010. AED: Data files used in Mixed effects models and extensions in ecology with R. (2009). Zuur et al. (2009). R package version 1.0.

Yee, T.W., Mitchell, N.D., 1991. Generalized additive models in plant ecology. J. Veg. Sci. 2: 587–602.

Wetzel, R.G., 2001. Limnology, Lake and River Ecosystems, third ed. Academic Press, San Diego, CA, 1006 pp.

Williams, D.D., 2006. The Ecology of Temporary Waters. Oxford University Press. 348 pp.

CAPÍTULO II

Fernandes, I.M., Penha, J. & Zuanon J. Size-dependent response of tropical wetland fish communities to changes in vegetation cover and habitat connectivity. A ser submetido para publicação no periódico *Landscape Ecology*

Abstract

Floodplains are among the most diverse and productive natural systems in the world. However, the replacement of native vegetation by exotic grasses for livestock production, is causing landscape homogenization, habitat fragmentation and reducing connectivity among habitat patches. We assessed the effect of water depth, exotic and native vegetation cover and habitat connectivity on the abundance, species richness, body size and biomass of fish communities of a large seasonal wetland for five years. The kind of vegetation cover, exotic or native, did not affect the assemblages of small-sized fish (< 80 mm Standard Length as adults), which were mostly regulated by water depth and habitat connectivity. However, large-sized fish assemblages (SL>80 mm SL as adults) were affected by water depth, habitat connectivity and by the kind of vegetation cover. This shows the effect of habitat characteristics may be different to the fish species, as depends on fish size. In habitats mostly covered by exotic pastures, the total biomass of large-sized fish was lower, and it had a lower overall species richness. Also, these species were less abundant and individuals smaller than the species average in these patches. We concluded that habitat connectivity is very important for both small and large-sized fish species as abundance, species richness and biomass were higher in more connected patches. Additionally, the native flora, in particular wooded vegetation, positively affects somatic growth and community biomass of large and small-sized assemblages of fish in Pantanal. Thus, transformations in the landscape and changes in the dynamics of inundation may have negative consequences for the long-term persistence of fish communities in the Pantanal wetlands.

Key words: Temporary habitat; Effective distance; Landscape connectivity; Exotic species; Water depth; Cattle ranching impacts; Pantanal.

Introduction

Floodplains are among the most diverse and productive natural systems worldwide (Tockner et al. 2000). These systems are periodically inundated by the overflow of water from the main river, lateral channels and floodplain lakes, and also by direct precipitation and groundwater. Inundated lowlands form ephemeral aquatic habitats that are colonized by aquatic organisms from nearby permanent water bodies (Agostinho et al. 2001; Cucherousset et al. 2007;

Henning et al. 2007) and by individuals emerged from resting eggs, seeds or propagules left in the soil during the previous inundation (Heckman 1998; Shröder 2001; Brock et al. 2003; Pagotto et al. 2011). During the dry season, the precipitation is low and evapotranspiration is high, so these systems return to their terrestrial phase occupied by plants and animals that are not adapted to flooded conditions. At this time the aquatic organisms are forced to return to permanent waterbodies (Penha et al. 1998; Rebellato and Nunes da Cunha 2005; Jenkins and Boulton 2007; Junk et al. 2011). These characteristics makes the floodplain a very productive system and encouraged human populations to establish and grow along the margins of large rivers. As a consequence, anthropogenic pressure on these ecosystems has increased by the need to expand energy, agriculture and livestock production, which is causing habitat fragmentation, exotic species introduction and biodiversity loss (Samson and Knopf 1994; Steinman and Rosen 2000; Walters et al. 2006).

The introduction of exotic species is one of the main threats to biological diversity all over the world. It affects natural systems through the exclusion of native species, homogenization of the landscape, changes on fire regimes and fragmenting the habitat by decreasing the connectivity among habitat patches (Brooks et al. 2004; Hoffmann et al. 2004; Hejda et al. 2009; Alho et al. 2011; Junk and Nunes da Cunha 2012; Simberlof et al. 2013). More connected habitat are more likely to be occupied than less connected ones (MacArthur and Wilson 1967, Fahrig 2003), because the individuals can use suitable habitat patches as "stepping-stones" (Brown and Kodric-Brown 1977) to colonize nonocuppied habitats (Gilpin 1980; Loehle 2007). As a result, these colonisations increase the metapopulation persistence at the landscape scale. Besides the factors on regional scale, such as connectivity and landscape composition (e g. vegetation cover), factors performing locally, as biological interaction (e. g. predation by wading birds in shallow water and by fish in deep water) (Power 1984; Harvey and Stewart 1991; Englund and Krupa 2000) and habitat characteristics (e. g. water depth) can affect the communities distribution both spatially and temporally (Baber et al 2002; Steinman et al. 2003; Babbitt et al. 2009; Fernandes et al. 2010; Fernandes et al. 2013). The theoretical model proposed by Power (1987) showed that water depth affect biological interactions in stream. This model states that the terrestrial predators (mainly wading birds and mammals) force large-sized fish to occupy deep waters, and piscivorous fish in deep water force small-sized fish to move to shallow water (Harvey and Stewart 1991), both effects mediated by differences in food availability along the depth gradient.

Abundance and species richness has been used as satisfactory general descriptors of communities structure (Magurran 2004), whereas body size and biomass provide information about the system productivity in aquatic habitats. These information together have been used to guide fisheries management decisions. In river-floodplain systems, like the Pantanal, fish species highly depend on resources available on ephemeral habitat formed during the wet season (Agostinho et al. 2001; Cucherousset et al. 2007). So, the decrease of connectivity between permanent water bodies and temporary habitats can affect negatively the fish use of the floodplain and the fisheries productivity in following years (Sommer et al. 2001; Opperman et al. 2010). The Brazilian Pantanal, one of the biggest wetlands of the world, have being mainly threatened by landscape changes caused by livestock production and by flood control by dams (Zeilhofer and Moura 2009; Girard 2011). The change of the configuration of habitats in the landscape may result in reduction of connectivity between temporary and permanents aquatic habitats (Zhao et al. 2012) that may prevent their use by fish. To improve our understanding about how changes on landscape affect the dynamics of fish on wetland and to increase our ability to guide management, we evaluated how changes in water depth, native and exotic vegetation cover and connectivity affect the abundance, species richness, body size and biomass of fish assemblages. Based on other studies (Harvey and Stewart 1991; Kodric-Brown and Brown 1993; Englund and Krupa 2000; Taylor and Warren 2001; Casatti et al. 2009), we hypothesize that water depth and connectivity have a positive effect on these community attributes. Moreover, vegetation cover formed by exotic pastures should affect them negatively but native vegetation should affect positively.

Material and Methods

Study area

The Pantanal is a seasonally flooded wetland that ranges over an area of around 160.000 km². It is in the central region of South America between parallels 16º and 22º S and 55º and 58º W, which includes portions of Brazil, Paraguay and Bolivia. In the late 18th century to the early 19th centuries, livestock production became important in Brazilian territories (Silva et al. 2000). Until 1970, it was developed through extensive farming practices by using only natural grasslands to feed the cattle and extensive farming practices (Seidl et al. 2001). However, due to the low nutritive value of natural grasslands (carrying capacity = 0.81 individuals. ha^{-1}), farmers replaced the natural grasslands by an exotic African grass (*Urochloa humidicola* (Rendle) Morrone & Zuloaga, carrying capacity = 1.02 $individuals.ha^{-1}$) (Seidl et al. 2001; Junk et al. 2006), resulting in the lost of 17.5% of its original vegetation (Harris et al. 2005).

This study was performed in the Pantanal Long-Term Sampling Sites (PLTSS) located in the northern portion of the Brazilian Pantanal (Fig. 1). The PLTSS extents an area of 25 km^2 (56º 21' W, 56º 18' E, 16º 19' N, 16º 22' S) throughout three private properties where its main activity is livestock production. The PLTSS consists of a square grid containing 30 plots (250 m length x 1 m width) that follows the topographic gradient and are located 1 km apart from each other (for more details see Fernandes et al. 2010; Signor & Pinho 2011). In this region, the wet season lasts from December to June and the dry season from July to November. Situated about 10 km from Cuiabá River, the research site is characterized by a highly heterogeneous landscape with different types of vegetation cover (Fantin-Cruz et al. 2010). Within and nearby the PLTSS there are 25 small permanent ponds (mean: 0.1 ha and range: 0.01 - 0.36 ha) and one lake (222 ha), where fish use as refuges during the drought and that become source of colonization to the floodplain during the wet season (Fernandes, I. M. *unpublished data*).

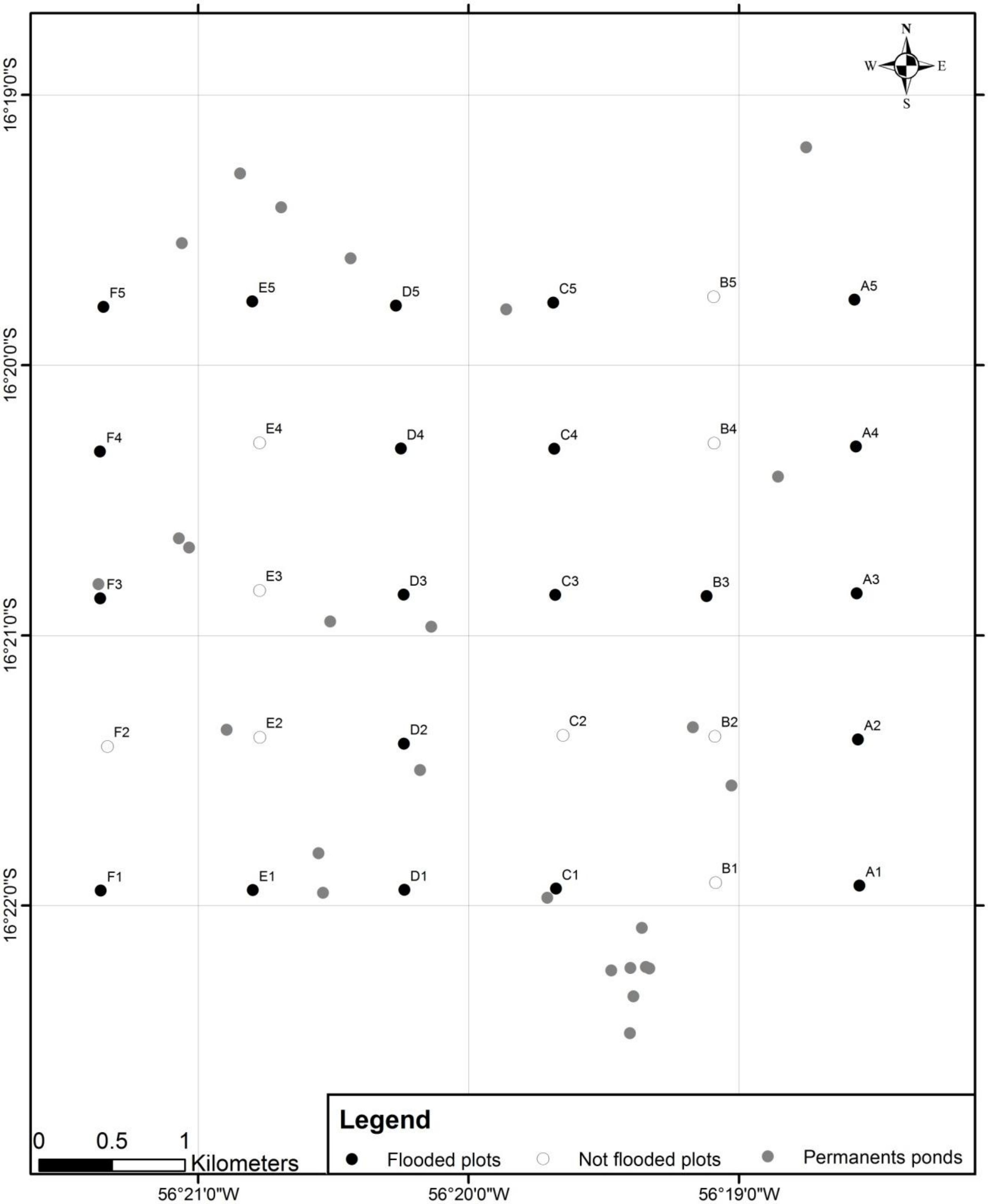


Fig. 1Map of the PLTSS grid in Pantanal wetland. Dark and white circles represent plots that were flooded and not flooded, respectively, in 2006, 2008, 2009, 2010 and 2011. Grey circles represent the permanent ponds inside and around the PLTSS.

Fish sampling

Fish were sampled between March and April of each year across all flooded plots (2006 - 22 plots, 2008 - 22 plots, 2009 - 21 plots, 2010 - 18 plots and 2011 - 22 plots). These are the months that flood peaks usually happens and most of the plots are flooded for at least two months (Fantin-Cruz et al. 2010). Fish were collected by two methods: throw traps and gill nets. A throw trap consists in a metal structure in form of a cube (1m³) that is covered by a 1.5 mm nylon mesh and was employed six times per plot (every 50 meters). The individuals enclosed by the trap were swept with a triangular fish trap that was used until no additional specimen was collected after 10 consecutive sweeps. Besides, seven gill nets (20.0 x 1.5 m) were distributed (mesh size of 12, 15, 18, 20, 25, 30 and 50 mm between opposing knots) along each plot. In 2006, the gillnets were set between 0700 and 0800 hours and removed between 1800 and 1900 on the same day, whereas in other years they were set between 1600 and 1700 hours and removed on the following day between 0800 and 0900 hours. The change from daytime exposition was necessary to sample the fish during the sunset and sunrise when they are more active. However, as a consequence of this change, catfish became more abundant than cichlids in the samples, though the dominance of the characids was maintained. Each method was used on a different day to minimize the effects of the disturbance in the fish assemblage. The combination of active and passive sampling methods allows to capture mobile and sedentary species, and individuals in a large size range (Weaver et al. 1993; Jackson and Harvey 1997; Lapointe et al. 2006). All individuals captured were euthanized with Eugenol, fixed in 10% formalin solution, preserved in 70% ethanol and identified to the species level. Finally, each individual was weighted and measured by standard length (SL) (details in Fernandes et al. 2010).

Environmental variables

For each plot, altitude were acquired from simple frequency geodetic Global Position System (GPS) that tracked for 10 minutes, or until the error was less than 50 mm. As each plot has the same topographic altitude from start to finish just one measure was enough to represent the entire plot (see details in Magnusson et al. 2005). The water depth of a plot was the average of six measurements taken at places where the throw trap was launched. The plots on higher altitudes that were dry were visited during the samplings to ensure they did not become inundated. A rectangular area of about 35 km² that includes the PLTSS area and its surroundings was extracted from Google Earth^{TM} images and transformed into a shapefile. Then, the vegetation patches were manually marked out in polygons. Vegetation cover on each polygon was later identified based on field information into five vegetation class: wet grassland, wet pasture, dry pasture, wet forest and dry forest. Grasslands include mostly native grasses species and aquatic macrophytes (submerged, emergent and floating), pastures are composed mainly of exotic African grass (Urochloa humidicola (Rendle) Morrone & Zuloaga), and forests are composed by shrubs and trees without detectable undergrowth plant species. Although we used an image of 2003, all the area was annually visited by two of us from 2004 to 2011 and neither natural nor human landscape changes were observed.

The percentage of each vegetation class was calculated from a 450 m circular buffer around the center of each plot. Because of the high correlation among the five vegetation class, we applied a principal components analysis (PCA with covariance matrix because variable scales are similar) to reduce the dimensionality of the data, after arcsine square root transformation. The two axes extracted using the broken stick model (Jackson et al. 1993) accounted for 89.3% of the variation in vegetation cover. We performed Pearson correlation matrices between PCA axes and the different vegetation class to identify which classes contributed more to axes formation. The first axis accounted for 58.7% and showed high positive correlation to wet grassland ($r = 0.65$; $p < 0.001$), dry forest ($r = 0.5$; $p = 0.004$) and wet forest ($r =0.50$; $p=0.02$) and negative correlation to dry pasture ($r = -0.56$; $p = 0.02$) and wet pasture ($r = -0.99$; $p < 0.001$). In sum, this first axis represented the gradient from exotic to natural vegetation cover. The second axis accounted for 30.5% and was positively correlated to wet forest ($r = 0.82$; $p < 0.001$) and negatively correlated to wet grassland ($r = -0.69$; $p = 0.001$) and dry forest ($r = -0.46$; $p=0.02$). The PCA2 axis mainly represented the variation gradient of vegetation cover from wet grassland to wet forest. These two PCA axes were used to represent vegetation cover in all subsequent analyses.

Connectivity metric

The landscape connectivity represent the extent to which the landscape facilitates or prevents movement of organisms among patches (Taylor et al. 1993). Connectivity can be measured in different ways (Prugh 2009), and have been commonly classified into two main classes, namely functional and structural. The functional connectivity incorporates data about individuals movements throughout the landscape, on the other hand, structural connectivity is measured by how the spatial arrangement of different habitat and potential barriers in the landscape may affect species dispersion (Theobald et al. 2011).

Here, we used the probability of connectivity index (PC), which is based on the habitat availability concept, probabilities of dispersal among patches and graph structure (Saura and Pascual-Hortal 2007). It measures the probability of two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) (Bodin and Saura 2010). As we are interested in local connectivity, we used a version of the probability of connectivity index based on patch (PC_{flux}) that permits to measure the local contribution of each patch to the global PC index (Foltête et al. 2014):

$$PC_{flux}(j)\,\frac{\sum_{i=1}^{n} aiajp_{ij}^{*}}{A^{2}}$$

where $\boldsymbol{n}$ is the number of habitat patches in the landscape, $\boldsymbol{ai}$ and $\boldsymbol{aj}$ are the volume of the patches $\boldsymbol{i}$ and $\boldsymbol{j}$ and $\boldsymbol{A}$ is the total landscape area (both habitat and non habitat); $\boldsymbol{p_{ij}^{*}}$ is the probability that an individual in patch $\boldsymbol{i}$ will disperse to patch $\boldsymbol{j}$. The dispersal probability $\boldsymbol{p_{ij}^{*}}$ was computed using a negative exponential function (Urban and Keitt 2001, Saura and Pascual-Hortal 2007): $p_{ij}^{*} = exp(-\alpha d_{ij})$; α was determined so that $p_{ij}^{*} = 0.05$ when d_{ij} is a maximum distance found, and d_{ij} is least-cost distance between patch $\boldsymbol{i}$ and patch $\boldsymbol{j}$. Thus, the parameter p_{ij}^{*} expresses a greater or lesser decrease in the probability of flux (p) with distance (d). Effective distance (least-cost distance) was calculated using data about vegetation cover, water level and altitude. We used the raster grid previously built to represent the vegetation cover data. The 30 plots' water depth and altitude data were interpolated to build the water level and elevation layers by means of ordinary kriging, with the assumption of a spherical model to build the semivariogram (Zimmerman et al. 1999). Since altitude and vegetation cover did not change along the study, just one layer was built to represent these variables in the analyzes, however, for water level, it was built one layer for each year. Effective distance was calculated including measures of factors that facilitate individual movement across the landscape (flooded areas such as wet forest, wet grassland and wet pasture) or restrict it (dry forest and dry pasture). Therefore, effective distance between two patches represents the minimum cumulative effort (least-cost distance) to move across the resistance layer (Theobald et al. 2011). To create the resistance layer, we assigned a resistance value cost of 1 to wet forest, 2 for wet grassland, 3 for wet pasture and 100 for dry forest and dry pasture. We chose 1 to wet forest because this vegetation class occur in areas of low altitude and are first inundated, so they may become important dispersion corridors and 2 to grassland because they are important habitat that occur in patches with lower hydroperiods (the number of days that a wetland holds water during the wet season), and shallower than wet forests (Fantin-Cruz et al. 2010). And wet pasture was set as 3 because these are patches where wet grassland and wet forest were replaced by exotic pasture. The value of 100 to dry forest and dry pasture was decided because these habitats are permanently dry and represent permanently impassable barriers to the fish. The water level and altitude layers were reclassified with resistance values ranging from 1 to 10, and higher resistance values were imposed for high elevation and shallower regions. After reclassification, the three layers were combined to build the resistance layer. Given its greater accuracy, vegetation data was given a higher weight (0.5) on the final resistance layer and water level and elevation, which were estimated by interpolation, were given lower weights (0.4 and 0.1 respectively) (see Adriensen et al. 2003 for more details about the methods). All the steps were performed in ArcGis (ESRI 2006). The least-cost layer was calculated among plots and permanent ponds using the “costDistance” function of the 'gdistance' package (Etten 2012) in the R 2.15.3 Statistical Software (R Development Core Team 2013). During the sampling period, changes occurred in water level but did not occur in vegetation cover and altitude. Therefore, the least-cost-distances changes among the years was solely due to the water level. The vegetation type cover and altitude only affects the spatial variability in the least-cost metric.

Data analysis

We separated small-sized and large-sized fish using literature information (Reis et al. 2003) of the maximum adult body size from each species (standard length). Small-sized fish (SL< 80 mm as adults) are numerically dominant taxa whereas large-sized fish (SL> 80 mm as adults) are less abundant but dominant in biomass in the samples. For each size class (i.e. small and large-sized fish) in each plot and year, we computed abundance as the number of individuals captured, and species richness as the total number of species. Body size was calculated by the average standard length of all individuals and fish biomass was calculated by the sum of the weight of all individuals.

The effects of water depth, native and exotic vegetation cover (represented by PCA1 and PCA2) and connectivity (PC_{flux}) on the fish community attributes (abundance, species richness, body size and fish biomass) were assessed with Generalized Additive Model for Location, Scale and Shape (GAMLSS, Rigby & Stasinopoulos 2005). The GAMLSS, a semi-parametric regression type model, was introduced by Rigby and Stasinopoulos (2005) to overcome some limitations of generalized linear models (GLM) and generalized additive models (GAM). This model can deal with normal and non-normal distributed data and include in the same model linear and nonlinear relationships between the response and predictor variables (Landi et al. 2014). The GAMLSS procedure was used with cubic spline smoothing function (cs) to assess the connectivity (PC_{flux}) effect about fish community attributes. This was necessary because the relationship among connectivity, abundance, species richness, body size and fish biomass was nonlinear. Year of sampling was fitted as random-effect and abundance, species richness, body size and biomass were fitted as fixed-effect variables. Abundance, species richness, body size, biomass, water depth and connectivity (PC_{flux}) were log transformed before analysis and were modeled following a normal distribution (Zuur et al 2009). GLMLSS were implemented using the gamlss library (Rigby & Stasinopoulos 2005). All analyzes were performed in the R 2.15.3 Statistical Software (R Development Core Team 2013).

Results

Environmental characteristics

The temporary aquatic habitats in the PLTSS were shallow throughout the study period. The lowest values of mean water depth and connectivity were found in 2010, when the inundation level was atypical (18.6 cm), while the highest values were found in 2008 (28.2 cm, Table 1). The vegetation cover was dominated by wet grassland (36.8%) and wet forest (30.2%) and had a lower but important contribution of wet pasture (14.7%), dry forest (14.1%) and dry pasture (4.1%).

Table 1 Variation in water depth and connectivity/isolation in PLTSS during the study period. PC is probability of connectivity index

Years	**Water depth (cm)**			**Connectivity**
	Min	Max	Mean±SD	PC
2006	6.0	52.0	18.7±12.0	0.00000079
2008	12.2	54.8	28.2±12.9	0.00000112
2009	5.5	47.7	17.7±12.4	0.00000100
2010	3.0	39.2	18.6±11.3	0.00000072
2011	10.8	47.8	23.1±11.4	0.00000095

Fish community

Throughout the 5 years of samplings, a total of 6813 individuals from 70 species were collected; about 62% (4220) were small-sized fishes (Mean body size = 15.08 mm and range: 3.4 - 70.3 mm of SL) and 38% (2593) were large-sized fishes (Mean body size = 93.20 mm and range: 8.0 - 371.3 mm of SL). Additional information such as captured species, individual numbers (abundance), mean body size and biomass are found in supplementary material (Appendix 1 and 2).

Abundance

There was an inverse relation between abundance of small-sized fish abundance and the amount of wet forest cover, and positive effect from the wet grassland cover (Table 2; Fig. 2a). Overall, more individuals were found in patches more connected (Table 2; Fig. 2b). The large-sized fish abundance was higher in deeper and more connected plots than in shallow and less connected (Table 3; Fig. 2c; Fig. 2d). Plots dominated by native vegetation cover (wet grassland, wet forest and dry forest) had more individuals than those with exotic grass (PCA1 effect; Table 3; Fig. 2e).

Table 2 Coefficients of the Generalized Additive Model for Location, Scale and Shape (b ± SE) and associated t-tests for small-sized fish community attributes in relation to environmental variables. The PCA1 represents the gradient from dry and wet pasture to wet grassland and wet and dry forest and the PCA2 represents the gradient from wet grassland to wet forest (see *Environmental variables*). Fish biomass is expressed in grams and body size in mm.

Variables	Water depth		PCA1		PCA2		Connectivity (PC_{flux})	
	b±SE	t	b±SE	t	b±SE	t	b±SE	t
Abundance	0.06±0.08	0.73	0.02±0.17	0.17	**-0.60±0.17**	**-3.49****	**0.62±0.08**	**7.39****
Species richness	**0.17±0.04**	**4.13****	-0.02±0.08	-0.29	-0.13±0.08	-1.50	**0.15±0.04**	**3.63****
Body size	**0.07±0.02**	**2.97****	0.01±0.05	0.31	**0.18±0.05**	**3.38****	**-0.08±0.02**	**-3.18****
Fish biomass	**0.25±0.09**	**2.65****	0.13±0.19	0.66	0.37±0.19	1.85	**0.26±0.09**	**2.73***

* p<0.05; ** p<0.01.

Table 3 Coefficients of the Generalized Additive Model for Location, Scale and Shape (b±SE) and associated t-tests for large-sized fish community attributes in relation to environmental variables. The PCA1 represents the gradient from dry and wet pasture to wet grassland and wet and dry forest and the PCA2 represents the gradient from wet grassland to wet forest. Fish biomass is expressed in grams and body size in mm.

Variables	Water depth		PCA1		PCA2		Connectivity (PC_{flux})	
	b±SE	t	b±SE	t	b±SE	t	b±SE	t
Abundance	**0.37±0.06**	**5.33****	**0.39±0.14**	**2.81***	-0.04±0.13	-0.29	**0.29±0.07**	**4.26***
Species richness	**0.24±0.03**	**6.61****	**0.22±0.07**	**2.95****	0.09±0.07	1.27	**0.14±0.03**	**3.97****
Body size	**0.10±0.26**	**3.77****	**0.18±0.05**	**3.28****	**0.13±0.05**	**2.54****	0.008±0.02	0.31
Fish biomass	**0.73±0.11**	**6.30****	**1.02±0.23**	**4.28****	**0.50±0.23**	**2.14****	**0.41±0.11**	**3.53****

* p<0.05; ** p<0.01.

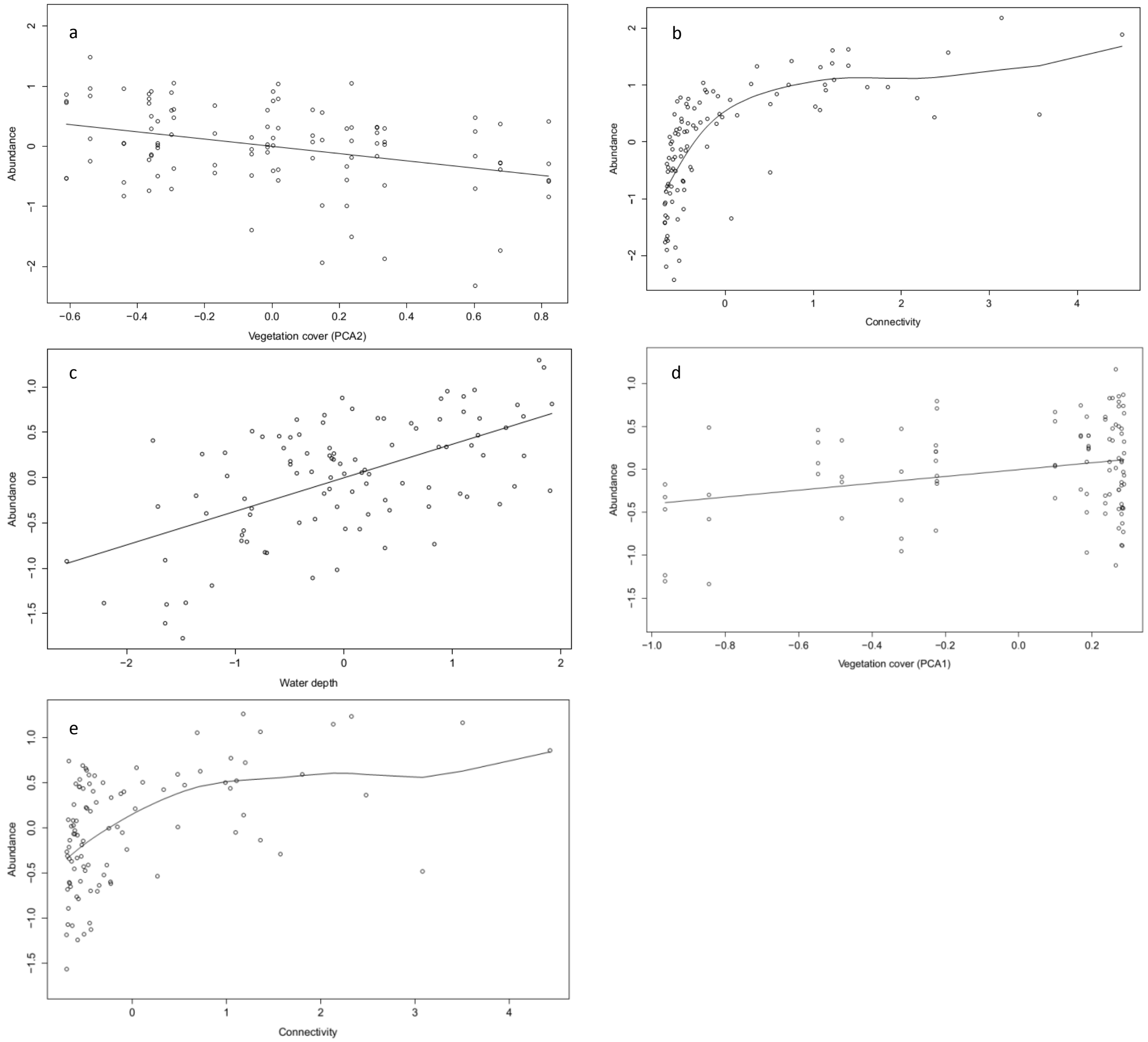


Fig. 2 Relationships between abundance of small-sized fish species and vegetation cover (a) and connectivity (b), and relationships between abundance of large-sized fish and water depth (c), vegetation cover (d) and connectivity (e). The PCA1 represents the gradient from exotic to natural vegetation cover and the PCA2 is the gradient from wet grassland to wet forest.

Species richness

Spatial variation in species richness of small-sized fish showed a positive relationship to water depth and connectivity (Fig. 3a; Fig. 3b), but vegetation cover (Table 2) was not important to explain variation in this community attribute. On the other hand, in addition of being positively related to water depth (Table 2; Fig. 3c), and to connectivity (Table 3; Fig. 3d) the species richness of large-sized fish had also a positive effect of the gradient from exotic pasture to native vegetation cover (PCA1 effect; Table 3; Fig. 3e). But it was not significantly related to gradient from wet grassland to wet forest (PCA2 effect; Table 3).

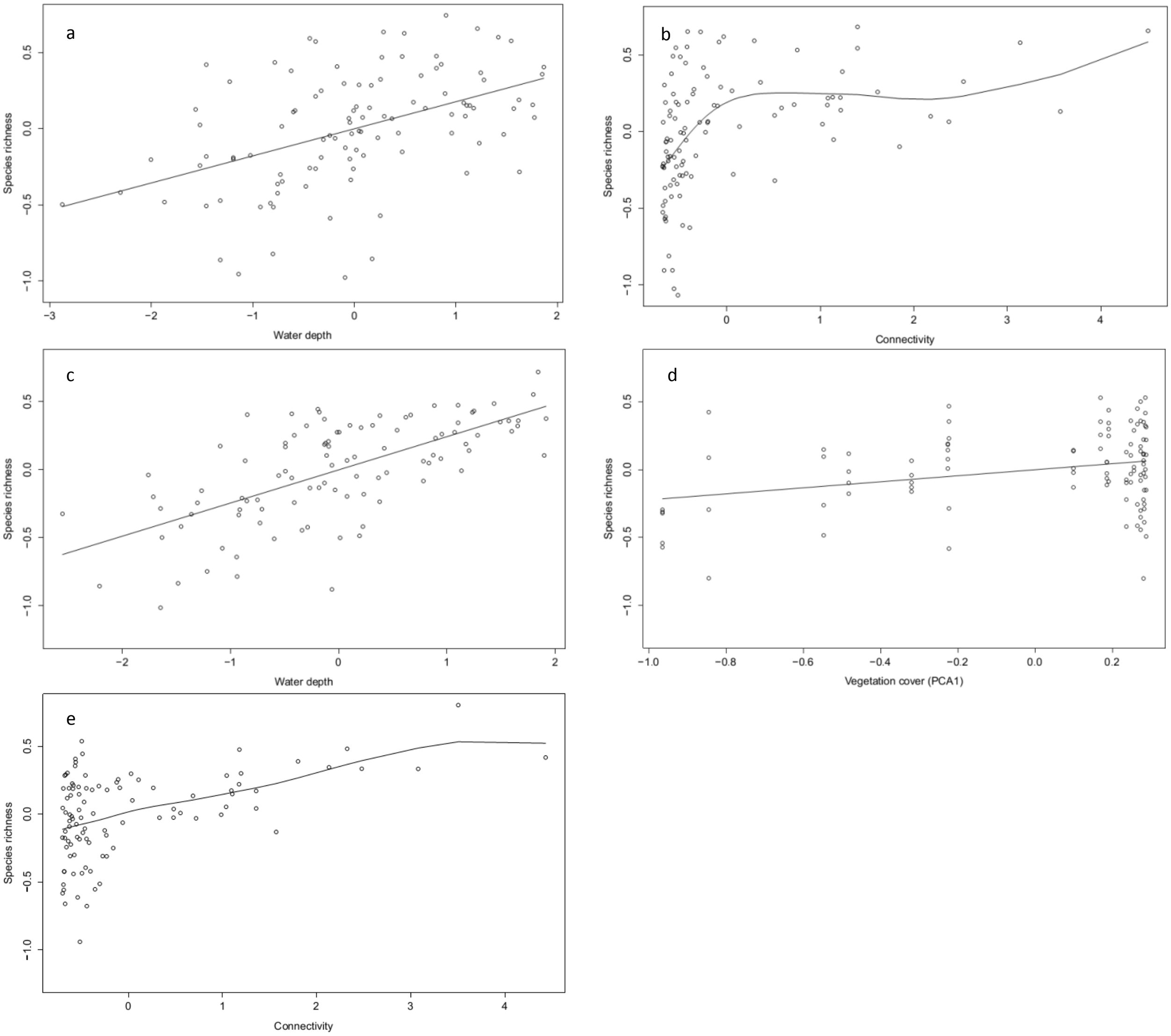
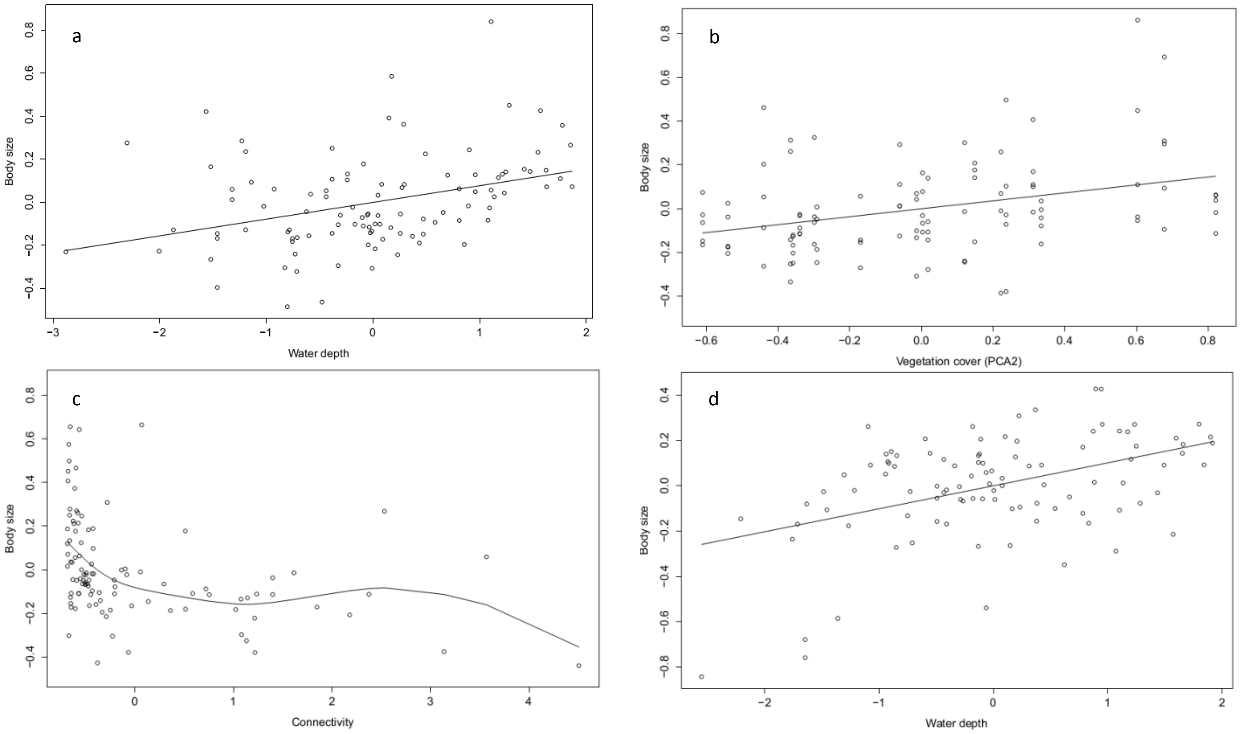


Fig. 3 Relationships between species richness of small-sized fish and water depth (a) and connectivity (b), and relationships between species richness of large-sized fish and water depth (c), vegetation cover (d) and connectivity (e). The PCA1 represents the gradient of dominance from exotic to natural vegetation cover and the PCA2 is the gradient of dominance from wet grassland to wet forest.

Body size

The body size of small-sized fishes showed a positive relationship with the gradient from wet grassland to wet forest (PCA2 effect; Table 2; Fig 4a) and a negative relationship with connectivity (Table 2; Fig. 4b). Water depth and the gradient from exotic to native vegetation cover did not affected this attribute (Table 2). To large-sized fish, body size was higher in the deepest plots (Table 3; Fig 4c) covered by wet grassland and forest, however plots surrounded by exotic vegetation were composed of fish with lower standard length (PCA1 effect; Table 3; Fig. 4d). Finally, body size increased from wet grassland to wet forest (PCA2 effect; Table 3; Fig 4e) but connectivity was not important to the explained variation of the body size of large sized-fish (Table 3).



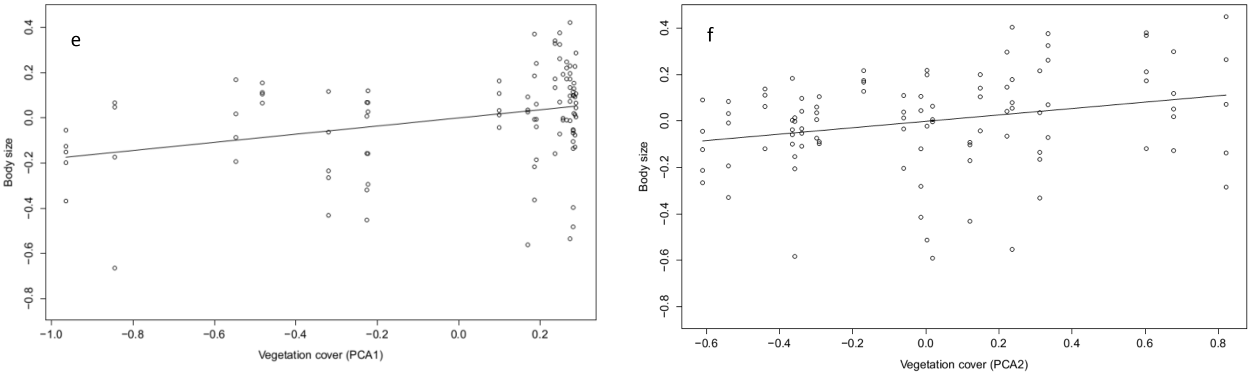


Fig. 4 Relationships between body size of small-sized fish and water depth (a), vegetation cover (b) and connectivity (c), and relationships between body size of large-sized fish and water depth (d) and vegetation cover (e and f). The PCA1 represents the gradient of dominance from exotic to natural vegetation cover and the PCA2 is the gradient of dominance from wet grassland to wet forest.

Fish biomass

Biomass of small-sized and large-sized fishes were positively related by water depth and connectivity (small-size fishes: Table 2, Fig. 5a, b; large-size fishes: Table 3; Fig. 5c,d). Although vegetation cover was not important for small-sized fishes (table 2), spatial variation in biomass of large-sized fishes was affected by this variable (Table 3). Similar to the observed for body size, variation on the gradient from exotic to natural vegetation (PCA1 effect; Table 3; Fig. 5e) and from wet grassland to wet forest (PCA2 effect; Table 3; Fig. 5f) were important to explain the large-size fish biomass. Thus, plots surrounded by a greater percentage of wet forests showed higher biomass of large-sized fishes than plots surrounded by wet grassland, and plots dominated by exotic vegetation were dominants had lower biomass than plots with natural vegetation.

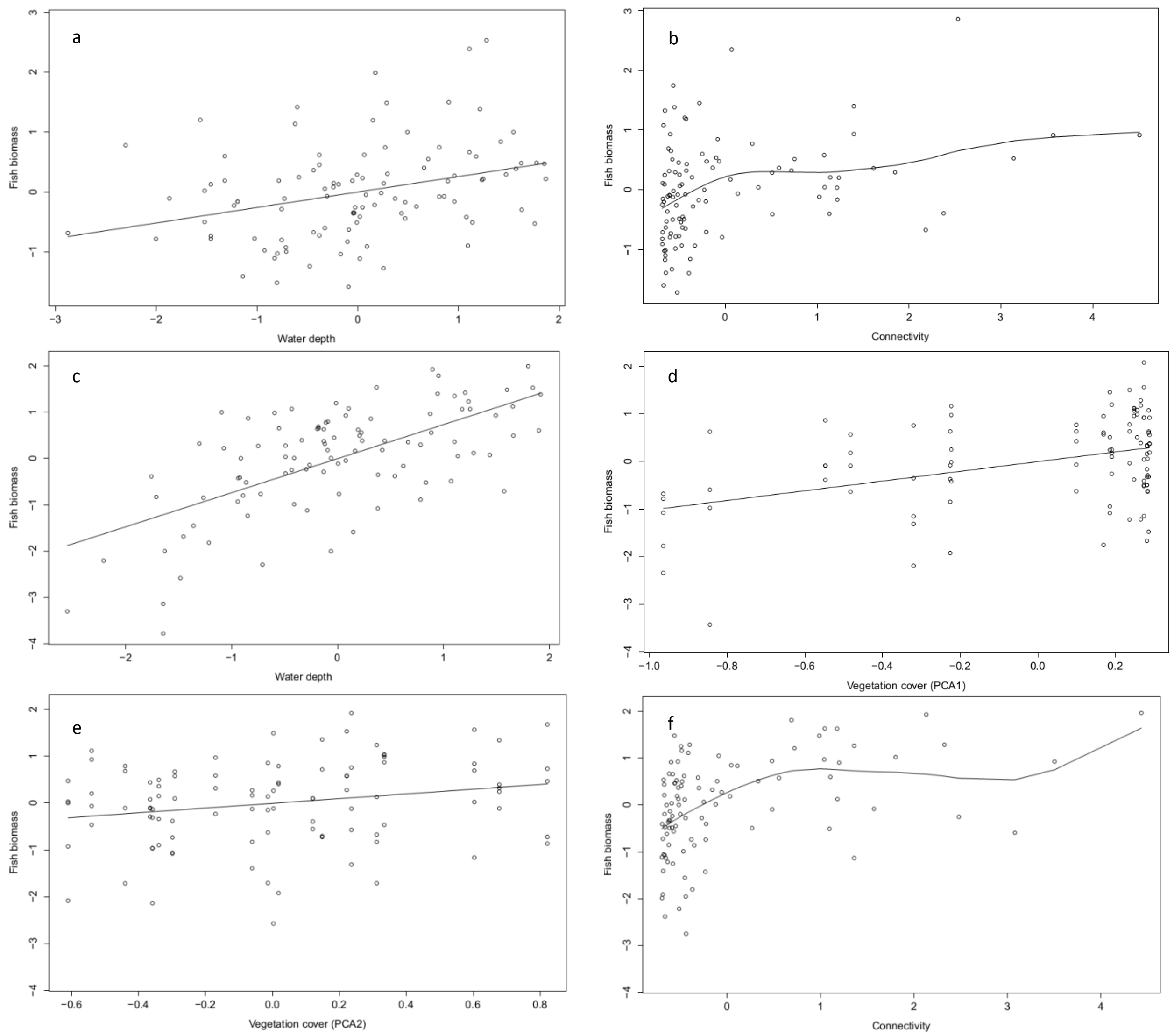


Fig. 5 Relationships between total biomass of small-sized fish and water depth (a) and connectivity (b), and relationships between total biomass of large-sized fish and water depth (c), vegetation cover (d and e) and connectivity. The PCA1 represents the gradient of dominance from exotic to natural vegetation cover and the PCA2 is the gradient of dominance from wet grassland to wet forest on PCA2.

Discussion

Our results shows that the fish community response to mesoscale variation in water depth, vegetation cover and habitat connectivity in Pantanal is size-dependent. The species richness (Fig. 3a; Fig. 3c), body size (Fig. 4a, 4d) and community biomass (Fig. 5a, c) from both small-sized and large-sized fish were positively affected by water depth. But only abundance of large-sized fish responded to changes in the water depth (i.e., shallow plots had less individual than deep ones, Fig. 2c). Further, only large-sized fishes showed significant changes related to the change gradient from exotic vegetation to natural vegetation, which was significantly related to their abundance, species richness, body size and community biomass (Fig. 2d; Fig. 3d; Fig. 4e; Fig. 5d). On the other hand, there was negative relationship between the variation in the gradient from wet grassland to wet forest and the abundance of small-sized fishes (Fig. 2a), and significant and positive relationship of this environmental gradient with body size of both small-sized and large-sized fishes (Fig. 4b, f) and with biomass of only large-sized fishes (Fig. 5e). Abundance, species richness and fish biomass was significantly related to habitat connectivity for both size classes (Fig. 2b, e; Fig. 3b, e; Fig. 5c, f) while only body size of small-sized fishes had a relationship (negative) with habitat connectivity (Fig. 5c).

In temporary aquatic systems such as seasonal wetlands, deep regions hold a higher fish diversity and abundance. This is because a high diversity of habitats is created by the abundance and diversity of aquatic macrophytes (Barbour and Brown 1974; Schessl 1999), which add structural complexity and provides food and shelter against predators in their structural complexity (Tonn and Magnuson 1982; Kodric-Brown and Brown 1993; Mayo and Jackson 2006; Thomaz et al 2008). The positive relationship between body size and fish biomass to water depth has been reported for fishes in shallow water bodies (Power 1984; Englund and Krupa 2000). It could be explained by the predation pressure exerted from terrestrial predators (mainly wading birds and mammals) that forces large-sized fish to occupy deeper waters (Ntiamoa-Baidu 1998; Gawlik 2002), and by presence of piscivorous fish in deeper water making the small-sized fish to change their distribution to shallow water (Power 1987; Englund and Krupa 2000). In Brazilian Pantanal, the high abundance and diversity of piscivorous birds (Signor and Pinho 2011) and predatory fish (Fernandes et al. 2010) in deep water may explain the observed pattern of body size distribution. These distribution patterns showed by the fish community are supposed to minimize predation risk (Power 1987) and increase the life span of the individuals resulting in large-sized fish occupying deeper habitats (Harvey and Stewart 1991).

The plots that are more connected have higher probabilities to be colonized by more species than less connected ones (MacArthur and Wilson 1967; Taylor and Warren 2001; Arrington et al. 2005), because high connectivity allows species with both low and high dispersal ability to colonize the habitat (Baber et al. 2002) and the rescue effect (Brown and Kodric-Brown 1977) may reduce extinction risk. In contrast, patches with lower connectivity will only be colonized by species with higher dispersal ability (Fernandes et al. 2013) and are more likely tobe affected by local extinction events. Finally, the negative relationship between body size and connectivity to small-sized fish can be explained by two not mutually exclusive factors. First, there is a correlation between dispersal distance and body size, i.e. only larger individuals can reach patches more distant and less connected (Griffith 2006); and second, a density-dependent growth can be expected in more connected patches, i.e. the increase in abundance, would lead to a reduction in the body size (Penha et al. in press, Fernandes, I. M. *unpublished data*).

The size-dependent responses of fish communities to exotic plants may reflect the different spatial scales that each environmental factor acts (Dray et al. 2012). Landscape changes from natural to exotic grass seems to have a negligible effect on small-sized fishes because those species respond mainly to factors acting at the micro-scale (local factors) such as availability of shelters and food, and the presence of predators (fine grained species, sense MacArthur and Levins 1964). On the other hand, large-sized species would respond mainly to large-scale factors, which include landscape characteristics such as plant cover (coarse grained species) (MacArthur and Levins 1964). Another factor that can attenuate the effect of the of exotic pasture cover on the small-sized fish fauna is the seasonal alternation of flood and drought periods (Junk et al. 1989). These drastic environmental changes result in the temporal substitution of plant species composition along the hydrological cycle (Schessl 1999; Prado et al. 1994; Rebellato et al. 2012) manly in wet pasture and wet grassland, which associated to the presence of cattle grazing prevents the dominance of exotic or arboreal species (Collins et al. 1995; Marty 2005; Questad et al. 2011; Junk and Nunes da Cunha 2012). During the dry season, the landscape is dominated by short-lived terrestrial plants that do not endure the hydrological stress promoted by the flood, and amphibious species that are adapted to both terrestrial and aquatic environments. By the onset of the floods, these amphibious species are joined by a rich assemblage of strictly aquatic plant species (Rebellato and Nunes da Cunha 2005). Native assemblages of aquatic plants grow both over native grasslands and exotic pastures and so increasing the similarity in vegetation structure across habitats during the flood season. Thus, the high similarity in habitat structure, shelter availability and food supply between native grasslands and exotic pastures during the flood season probably explains the absence of differences in some attributes of the small-sized fish communities between these environments. We believe that it did not affect large-sized fish because these size class has shown a clear preference to wet forest habitat, where replacement of vegetation species is less negligible between the seasons, in contrary to what happens in exotic and native grassland. Finally, the almost absence of aquatic macrophytes in wet forests possibly results in less cover (shelter, refuges) for the small-sized fish in aquatic habitats dominated by larger fish (many of which with predatory habits).

Conclusions

The presence of different types of vegetation cover results in a highly heterogeneous landscape in the Brazilian Pantanal. Nevertheless, the increasing introduction of exotic grasses for cattle grazing threatens the native vegetation and led to landscape homogenization, forest fragmentation and habitat loss. Our results demonstrated that such impacts did not strongly affect the distribution of small-sized fishes (SL< 80 mm as adults), which was mainly influenced by water depth and connectivity. On the other hand, the community subset represented by large-sized fishes (SL> 80 mm as adults) was affected by the replacement of native vegetation to exotic plants and by habitat connectivity. Although the introduction of exotic pastures in place of native grasses does not seem to affect small-sized fish, it negatively affects large-sized species when these exotics plants replace forests. This may be due to the lower densities of terrestrial predators in wet forests, which turns them safer and more effective dispersion routes for larger fish (as well as important foraging grounds; q.v. Goulding, 1980). Therefore, conservation policies should focus on the protection of these habitats, and the preservation of the natural hydrological dynamics and connectivity of the floodplain, so fish species (and other organisms) can successfully complete their life-cycles and maintain sustainable population sizes.

Acknowledgments

We would like to thank the Pantanal Research Center for the financial support. We would also like to thank the National Council for Scientific and Technological Development (CNPq) for productivity grants given to Jansen Zuanon (Proc. 307464/2009-1) and the Postgraduate scholarship given to Izaias Fernandes. Our sincere thanks to S. Magela, M. Bini, F. Costa, W. E. Magnusson and C. E. C. Freitas and two anonymous referees for reviews of earlier versions of the manuscript that greatly improved it.

Referênces

Adriaensen F. Chardon JP, De Blust, G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape Urban Plan 64 (4): 233–247

Alho CJR, Mamede S, Bitencourt K, Benites M (2011) Introduced species in the Pantanal: implications for conservation. Braz J Biol 71(1): 321-325

Agostinho AA, Gomes LC, Zalewski M (2001) The importance of floodplains for the dynamics of fish communities of the upper river Paraná. Ecohydrol hydrobiol 1:209-217

Arrington DA, Winemiller KO, Layman CA (2005) Community assembly at the patch scale in a species rich tropical river. Oecologia 144(1): 157-167

Baber JM, Childers DL, Babbitt KJ, Anderson DH (2002) Controls on fish distribution and abundance in temporary wetlands. Can J Fish Aquat Sci 59:1441-1450

Babbitt KJ, Baber MJ, Childers DL, Hocking D (2009) Influence of agricultural upland habitat type on larval anuran assemblages in seasonally inundated wetlands. Wetlands 29(1): 294–301

Barbour CD, Brown JH (1974) Fish species diversity in lakes. Am Nat 473-489

Bodin Ö, Saura S (2010) Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. Ecol Model 221(19): 2393-2405

Brock MA, Nielsen DN, Shiel RJ, Green JD, Langley JD (2003) Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. Freshw Biol 48:1207–1218

Brooks ML, D'Antonio C, Richardson DM, Grace JB, Keeley JE, DiTomasso JM, Hobbs RJ, Pellant M. Pyke D (2004) Effects of invasive alien plants on fire regimes. BioScience 54:677–688

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58(2):445-449

Casatti L, Ferreira CP, Carvalho FR (2009) Grass-dominated stream sites exhibit low fish species diversity and domi-nance by guppies: an assessment of two tropical pastureriver basins. Hydrobiologia 632(1):273–283

Collins SL, Glenn SM, Gibson DJ (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76:486–492

Cucherousset J, Paillisson JM, Paillisson A, Chapman LJ (2007) Fish emigration from temporary wetlands during drought: the role of physiological tolerance. Arch Hydrobiol 168(2):169–178

Dray S, Pélissier R, Couteron P et al (2012) Community ecology in the age of multivariate multiscale spatial analysis. Ecol Monogr 82(3): 257-275

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Ann Rev Ecol Evol S 487-515

Englund G, Krupa JJ (2000) Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshw Biol 43(1): 75-83

Etten JV.(2012) gdistance: distances and routes on geographical grids. R package version 1.1-3. http://CRAN.R-project.org/package=gdistance

Fantin-Cruz I, Girard P, Zeilhofer P, Collischonn W (2010) Dinâmica de inundação. In: Fernandes IM, Signor CA, Penha J (eds) Biodiversidade no Pantanal de Poconé. Centro de Pesquisas do Pantanal, Cuiabá. pp. 25-35

Fantin-cruz I, Girard P, Zeilhofer P, Collischonn W, Nunes da Cunha C (2010) Unidades fitofisionômicas em mesoescala no Pantanal Norte e suas relações com a geomorfologia. Biota Neotrop 10(2): 31–38

Fernandes IM, Machado FA, Penha J (2010) Spatial pattern of a fish assemblage in a seasonal tropical wetland: effects of habitat, herbaceous plant biomass, water depth, and distance from species sources. Neotrop Ichthyol 8(2):289-298

Fernandes IM, Henriques-Silva R, Penha J, Zuanon J, Peres-Neto, PR (2013). Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. Ecography (in press)

Foltête JC, Girardet X, Clauzel C (2014) A methodological framework for the use of landscape graphs in land-use planning. Landscape Urban Plan (in press)

Gawlik DE (2002) The effects of prey availability on the numerical response of wading birds. Ecol Monogr 72:329–346

Gilpin ME (1980) The role of stepping-stone islands. Theor Pop Biol 17 247–253

Girard P (2011) Hydrology of surface and ground waters in the Pantanal floodplains. In: Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (org) The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland.Sofia: Pensoft Publishers. pp. 103-126

Griffith, D. 2006. Pattern and process in the ecological biogeography of European freshwater fish. J Anim Ecol 75: 734–751

Goulding M (1980) The fish and the forests – Explorations in Amazonian Natural History. Berkeley: California Academy Press

Harris MB, Arcangelo C, Pinto ECT, Camargo G, Ramos Neto MB, Silva SM (2005) Estimativas de perda da área natural da Bacia do Alto Paraguai e Pantanal Brasileiro. Relatório técnico. Conservação Internacional, Campo Grande

Harvey BC, Stewart AJ (1991) Fish size and habitat depth relationships in headwater streams. Oecologia 87(3): 336-342

Hejda M, Pysek P, Jarosík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97:393-403

Heckman CW (1994) The Seasonal Succession of Biotic Communities in Wetlands of the Tropical Wet-and-Dry Climatic Zone: I. Physical and Chemical Causes and Biological Effects in the Pantanal of Mato Grosso, Brazil. Inte Rev Ges Hydrobio 79(3):397-421

Henning JA, Gresswell RE, Fleming IA (2007) Use of seasonal freshwater wetlands by fishes in a temperate river floodplain. J Fish Biol 71:476–492

Hoffmann WA, Lucatelli VM, Silva FJ et al (2004). Impact of the invasive alien grass Melinis minutiflora at the savanna-forest ecotone in the Brazilian Cerrado. Divers Distrib 10(2):99-103

Jackson DA 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. Ecology 74:2204–2214

Jackson DA, Harvey HH (1997) Qualitative and quantitative sampling of lake fish communities. Can J Fish Aquat Sci 54:2807-2813

Jenkins KM, Boulton AJ (2007) Detecting impacts and setting restoration targets in arid-zone rivers: Aquatic micro-invertebrate responses to reduced floodplain inundation. J Appl Ecol 44: 823–832

Junk WJ, Bayley PB, Sparks RS (1989) The flood pulse concept in river – floodplain systems. Pp. 110-127. In: Dodge DP (Ed.) Proceedings of the International Larger River Symposium. (LARS). Can J Fish Aquat Sci 106

Junk WJ, Nunes da Cunha C, Wantzen KM, Petermann P, Strussmann C, Marques MI, Adis J (2006) Biodiversity and Its Conservation in the Pantanal of Mato Grosso, Brazil. Aquat Sci 68:278-309

Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (2011) The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Sofia: Pensoft Publishers

Junk WJ, Nunes da Cunha CN (2012). Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? Wetl Ecol Manag 20(2):111-122

Kodric-Brown A, Brown JH (1993). Highly structured fish communities in australian desert springs. Ecology 74(6):1847-1855

Landi M, Zoccola A, Bacaro G, Angiolini C (2014) Phenology of Dryopteris affinis ssp. affinis and Polystichum aculeatum: modeling relationships to the climatic variables in a Mediterranean area. Plant Spec Biol 29: 129–137

Lapointe NWR, Corrum LD, Mandrak NE (2006). A comparison of methods for sampling fish diversity in shallow offshore waters of large rivers. N Am J Fish Manage 26:503-513

Lehmann A (1998) GIS modeling of submerged macrophyte distribution using Generalized Additive Models. Plant Ecol 139:113-124

MacArthur RH, Levins R (1964) Competition, habitat selection and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51:1207–1210

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

Magusson WE, Lima AB, Luizao RC, Luizão F. Costa FRC, Castilho CV, Kinupp VF (2005) RAPELD, uma modificação do método de Gentry para inventários de biodiversidade em sítios para pesquisa ecológica de longa duração. Biota Neotrop 5 (2): 1-6

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford

Marty JT (2005) Effects of Cattle Grazing on Diversity in Ephemeral Wetlands. Conser Biol 19(5):1626–1632

Mayo JS, Jackson DA (2006) Quantifying littoral vertical habitat structure and fish community associations using underwater visual census. Environ Biol Fish 75:395-407

Ntiamoa-Baidu Y, Piersma T, Wiersma P, Poot M, Battley P, Gordon C (1998) Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. Ibis 140:89–103

Opperman JJ, Luster R, McKenney BA, Roberts M, Meadows AW (2010) Ecologically Functional Floodplains: Connectivity, Flow Regime, and Scale. J Am Water Resour As 46(2): 211-226

Pagotto MA, Silveira RML, Nunes da Cunha C, Fantin-Cruz I (2011) Distribution of Herbaceous Species in the Soil Seed Bank of a Flood Seasonality Area, Northern Pantanal, Brazil. Inter Rev Hydrobiol 96(2):149-163

Penha JMF, Da Silva CJ, Bianchini Júnior I (1998) Análise do crescimento da macrófita aquática Pontederia lanceolata em área alágavel do Pantanal Mato-grossense, Brasil. Braz J Biol 58(2):287-300

Power ME (1984) Depth distributions of armored catfish predator-induced resource avoidance. Ecology 65(2):523-528

Power ME (1987) Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp: 333-51

Prado AL, Heckman CW, Martins FR (1994) The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: II. The aquatic macrophyte vegetation in the Pantanal of Mato Grosso, Brazil. Internatertionale Revue gesamten Hydrobiologie 79(4):569-589

Prugh LR (2009) An evaluation of patch connectivity measures. Ecol Appl 19:1300–1310

Questad EJ, Foster BL, Jog S, Kindscher K, Loring H (2011) Evaluating patterns of biodiversity in managed grasslands using spatial turnover metrics. Biol Conserv 144:1050–1058

Rebellato L, Nunes da Cunha C (2005) Efeito do “fluxo sazonal mínimo da inundação” sobre a composição e estrutura de um campo inundável no Pantanal de Poconé, MT, Brasil. Acta Bot Bras 19(4):789-799

Rebellato L, Nunes da Cunha C, Figueira JEC (2012) Respostas da comunidade herbácea ao pulso de inundação no Pantanal de poconé, Mato Grosso. Oecologia Australis 16(4):797-818

Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location , scale. J Roy Stat Soc C-App 54(3): 507–554

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Samson F, Knopf F (1994) Prairie conservation in North America. Bioscience 44:418–421

Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape Urban Plan 83: 91-103

Schessl M (1999) Floristic composition and structure of floodplain vegetation in northern Pantanal of Mato Grosso, Brasil. Phyton 39(2):303-336

Seidl AF, Silva JDSVD, Moraes AS (2001) Cattle ranching and deforestation in the Brazilian Pantanal. Ecol Econ 36(3):413-425

Shröder T (2001) Colonizing strategies and diapause of planktonic rotifers (Monogononta, Rotifera) during aquatic and terrestrial phases in a floodplain (Lower Oder Valley, Germany). Inter Rev Hydrobiol 86:635–660

Signor CA, Pinho JB (2011) Spatial diversity patterns of birds in a vegetation mosaic of the Pantanal, Mato Grosso, Brazil. Zoologia 28(6): 725-738

Silva JSV, Seidl AF, Moraes AS, (2000) Evolucao da Agropecuaria do Pantanal Brasileiro, 1975–1985. EMBRAPA-CPAP, Corumba, MS

Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol *28*(1):58–66

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ (2001) Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Can J Fish Aquat Sci 58(2): 325-333

Steinman AD, Conklin J, Bohlen PJ, Uzarski DG (2003) Influence of cattle grazing and pasture land use on macroinvertebrate communities in freshwater wetlands. Wetlands 23(4):877–889

Taylor CM, Warren ML (2001) Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. Ecology 82:2320–2330

Taylor PD, Hafrig L, Henein K, Merriam G (1993) Connectivity as a vital element of landscape structure. Oikos 68:571:573

Theobald D, Crooks R, Norman J (2011) Assessing effects of land use on landscape connectivity: loss and fragmentation of western US forests. Ecol Appl 21(7):2445–2458

Thomaz SM, Dibble ED, Evangelista LR, Higuti J, Bini LM (2008) Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. Fresh Biol 53(2):358-367

Tockner K, Malard F, Ward JV (2000) An extension of the flood pulse concept. Hydrol Process 14:2861–2883

Tonn WM, Magnuson JJ (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 1149-1166

Walters DJJ, Kotze DC, O'Connor TG (2006) Impact of land use on vegetation composition, diversity, and selected soil properties of wetlands in the southern Drakensberg mountains, South Africa. Wetl Ecol Manag 14:329–348

Weaver MJ, Magnuson JJ, Clayton MK (1993) Analyses for differentiating littoral fish assemblages with catch data from multiple sampling gears. T Am Fish Soc 122:1111-1119

Zeilhofer P. Moura RM (2009) Hydrological changes in the northern Pantanal caused by the Manso dam: Impact analysis and suggestions for mitigation. Ecol Eng 35(1):105-117

Zimmerman D, Pavlik C, Ruggles A, Armstrong MP (1999) An experimental comparison of ordinary and universal Kriging and inverse distance weighting. Math Geol 31(4):375-389

Zhao Q, Liu S, Deng L et al (2012) Landscape change and hydrologic alteration associated with dam construction. Inter J Appl Earth Obs 16:17-26

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer

CAPÍTULO III

Fernandes, I.M., Henriques-Silva, R., Penha, J., Zuanon, J. & Peres-Neto, P.R. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities . A ser submetido para publicação no periódico *Ecography*.

Abstract

The metacommunity framework has greatly advanced our understanding about the importance of local and regional processes structuring ecological communities. However, information on how metacommunity structure and the relative strengths of their underlying mechanisms change through time is largely lacking. Dynamic systems that undergo environmental temporal changes and disturbances, such as floodplains, serve as natural laboratories to explore how their metacommunity structure change in time. Here we applied the Elements of Metacommunity Structure framework and variation partitioning analysis to assess how temporal changes in the local environmental factors and regional dispersal processes in the rain season influence a seasonal floodplain-fish metacommunity. Across four months, relevant environmental factors were measured across 21 patches where over 3500 individual fish were sampled. Connectivity was measured using landscape resistance-based metrics and additional spatial variation in metacommunity structure was assessed via spatial autocorrelation functions. The metacommunity structure changed from nestedness, at the beginning of the flood season, to a quasi-Clementsian gradient at the end. Our analyses show that connectivity is only important in the beginning of the flood season whereas environment is only important at the end. These results suggest that this metacommunity is structured by changes between dispersal limitation and environmental filtering through time.

Keywords: Temporary habitats, connectivity, spatial variation, species distribution, dispersal limitation, environmental filtering

Understanding the mechanisms structuring how species from a regional pool assemble into local communities is a major goal of community ecology (Ricklefs 1987, Leibold et al. 2004). Patterns of species coexistence and distribution are affected mainly by two broad classes of factors that differ in the spatial and temporal scales at which they operate (Chase 2003). The first class is commonly referred as the " local factors", such as local environmental conditions that species require in order to maintain a net positive population growth within the community (e.g. soil characteristics, temperature, habitat size) and biotic interactions that range from intraspecific and interspecific competition for local resources up to predator-prey relationships (Chase and Leibold 2003). The second class constitutes the "regional factors", which operate at broader scales and regulate the arrival of organisms into the various local communities. They encompass dispersal filters, that dictate how permeable landscapes are to species movement and their probability of arriving at local communities (Taylor et al. 1993, Kennedy et al. 2011).

The metacommunity framework serves as a way to integrate both sets of factors (Leibold et al. 2004) and to investigate their relative importance for the distribution of species and their co-existence (e.g., Cottenie 2005, Beisner et al. 2006, Peres-Neto et al. 2006). Insights regarding the relative importance of local and regional mechanisms underlying the composition of metacommunities may be obtained by analyzing non-random patterns of multi-species distributions across geographical and/or ecological gradients (e.g., nestedness, Clementsian gradients and others; Leibold and Mikkelson 2002, Presley et al. 2009, Henriques-Silva et al. 2013). For any given landscape, the structural pattern that best fits a given metacommunity depends on the group of species being studied, as dispersal ability and environmental tolerance vary greatly across taxonomic classes (Presley et al. 2012). Additionally, it has been recently shown that these patterns are consistent and predictable on the basis of regional differences across large spatial extents (Henriques-Silva et al. 2013) and spatial scales (Meynard et al. 2013). Yet, these studies and other traditional analysis of metacommunity structure (e.g., Leibold et al. 2002, Presley et al. 2009) view these distributional patterns as static metacommunity properties. However, communities are dynamic, changing in richness and composition even over very short timescales (Bloch et al. 2007, Azeria and Kolasa 2008).

On one hand, snapshot studies (one single sample in time) have assumed that the relative importance of underlying mechanisms dictating metacommunity structure is stable through time (but see Vanschoenwinkel et al. 2010, Erös et al. 2012). Given that natural systems may show considerable variability in environmental and spatial processes (Vanschoenwinkel et al. 2010, Pandit and Kolasa 2011) on a wide range of temporal scales, community studies based on single snapshots may misrepresent the importance of particular processes or factors, especially when communities are sampled across different periods and/or time scales. On the other hand, most studies analyzing metacommunity structures over time have focused on a single pattern (e.g., nestedness; Azeria and Kolasa 2008, Elmendorf and Harrison 2009) and whether these single patterns are different from random. Unfortunately, this approach may lack power in detecting structure in the sense that if the data do not fit the particular pattern of interest, the metacommunity structure may be interpreted as random whereas alternative non-random structures different from nested (e.g., Clementsian, Gleasonian, chequerboards) may well fit the data.

Hypotheses regarding the temporal stability of metacommunity structure and the relative importance of assembly processes can be tested using natural systems that undergo considerable ecological dynamics in a reasonable timescale, such as inter-tidal, rock-pool, temporary ponds or floodplains systems (McCauley et al. 2008, Fernandes et al. 2010, Vanschoenwinkel et al. 2010). One of the main consequences of perturbations is their effect on population densities, either directly through mortality or indirectly by changing habitat structure and resource availability. Floodplains differ from many temporary systems because they are characterized by temporal perturbations in the form of a recurrent and predictable dry dictating seasonal predictable changes in their habitats (Junk et al. 1989), which in turn affect the community structure of a wide range of organisms (Girard et al. 2010). In the wet phase, many terrestrial habitats are transformed into transient aquatic habitats by the expansion of permanent waterbodies (e.g. rivers, lakes) as well as by the local rainfall (Junk et al. 1989). Fish seek refugia in permanent ponds during the dry phase but can then expand their ranges into the temporary habitats, which are essential to feeding, growth and reproduction (Agostinho et al. 2001). Although these temporary waterbodies disappear for the most part during the dry season (seven months – June to December), they present regional persistence for about five months out of the year, thus forming to what we refer as a seasonal metacommunity. As such, these systems also serve as a natural system akin to defaunation experiments to understand the temporal dynamics in metacommunity structure in the good tradition of early experimental studies such as the seminal work of Simberloff and Wilson (1969).

During the beginning of the season, the landscape has a considerable degree of heterogeneity because each temporary habitat patch presents particular physicochemical characteristics, low connectivity and distinct biota that are recruited from nearby permanent ponds (Layman et al. 2010). Later in the flooding period, the ephemeral habitats become much more connected between them and with permanent waterbodies as well. Consequently, the among-habitat variability in limnological characteristics and dispersal limitation are reduced (Thomaz et al. 2007, Layman et al. 2010). In this study we set out to evaluate and quantify the structural changes in a floodplain-fish metacommunity throughout the wet season using the EMS approach (Presley et al. 2010 Henriques-Silva et al. 2013). We also quantified the overall importance of environmental and spatial factors over time as a way to determine how changes in these factors are associated to changes in metacommunity structure. We predict that spatial factors will be more important at the beginning of the wet season due to a lower connectivity and community composition will be highly constrained by dispersal limitation. Later in the wet season, environmental factors should predominate as species should be able to colonize all habitats and environmental filtering will be the main structuring factor. As a consequence, we predict that in the first months of the wet season the fish floodplain metacommunity structure should exhibit a nested structure where species that have low dispersal abilities or lack adaptations to tolerate hypoxic conditions will be present only in the deepest and more connected patches and thus have limited distributional ranges. Moreover, their narrow ranges should represent subsets of the broad-range species that have high dispersal ability (or adaptations against hypoxic conditions) and are found even in shallow or isolated patches. Throughout the wet season, we predict that the metacommunity structure should change from negative turnover (i.e. nested structure) to positive turnover across species ranges (i.e. Gleasonian gradients, Clementsian gradients or Evenly-spaced gradients) as species will be less constrained by dispersal limitation and will be sorted throughout habitats according to their environmental niches. Overall, we show that our results are in line with these expectations.

Methods

Field survey

Located in the central portion of South America, the Pantanal is among the largest wetlands on the planet and its ecological dynamics are governed by a predictable monomodal flood pulse (Junk et al. 2006). The water expansion across a highly heterogeneous vegetation creates a high diversity of habitats for aquatic species (Fernandes et al. 2010). For this study, we used the Pantanal Long-Term Sampling Sites (PLTSS) dataset, which span an area of 25 km^2 (56º 21' W, 56º 18' E, 16º 19' N, 16º 22' S) and consists of 30 plots (250m x 1m) that are distributed in a grid format (Fig. 1) and have a minimum distance of 1km between each other (see Fernandes et al. 2010 for more details). We chose this particular size and shape of plots in order to minimize the variation of elevation within any plot. Within and around the PLTSS there are 26 permanent ponds, ranging from 0.01 to 0.36 ha as well as one lake with approximately 220 ha that act as colonization sources for the plots (I. M. Fernandes *unpublished data*). The fishing gear used in the present study are known to efficiently sample strip-like plots such as ours (see Appendix 1 for a detailed description of the sampling protocol) and the distance among plots is large enough for them to be considered as separated fish communities, as the species in the region are mostly small and do not move across sampled plots for activities such as daily foraging. As such, we considered that each plot represented a sample of relatively distinct patches within this seasonal metacommunity. Among these plots, 21 (70%) became temporary aquatic habitats (Fig. 1) during the flood season and were surveyed monthly between January and July 2009. For the present study, we only used the data between January and April 2009 as most patches were dry in the remaining months. We also considered additional data for the years of 2008, 2010 and 2011 for which a single sample was carried at the peak of the flood period (March). These data were used to assess whether metacommunity structure for this period was consistent across years and thus provided additional support for the temporal pattern uncovered in this study.

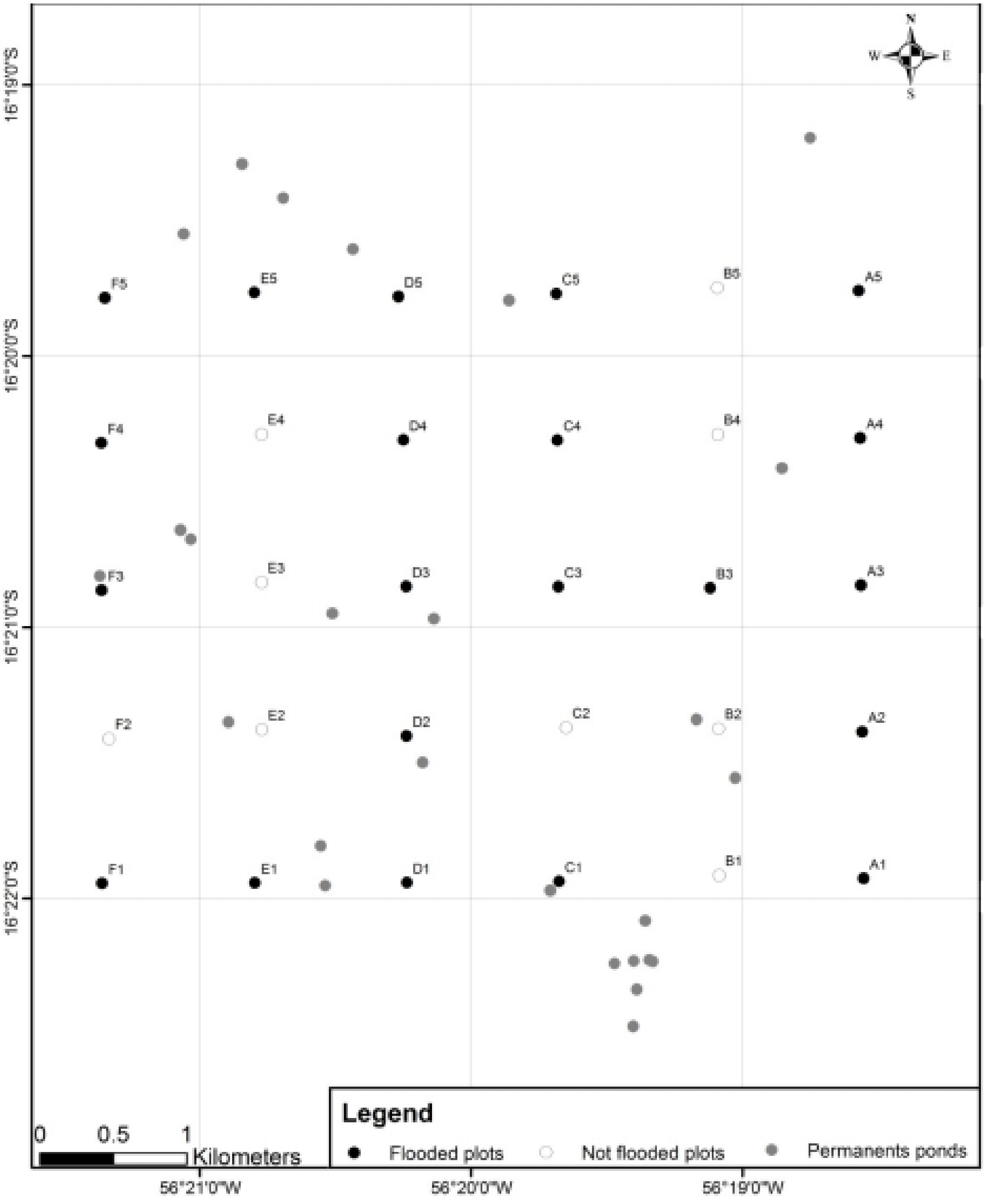


Figure 1. Map of the PLTSS grid. Dark and white circles represent plots that were flooded and not flooded, respectively, in 2009. Grey circles represent the permanent ponds. The code for each plot matches the ones from Figure 2.

Elements of Metacommunity Structure

We analyzed the incidence matrix (i.e., species-by-site matrix) of each month (March 2008, January-April 2009, March 2010 and March 2011) using the EMS framework developed by Leibold and Mikkelson (2002) and improved by Presley et al. (2010). In short, matrices were ordinated via correspondence analysis (CA) which maximizes the positioning of sites and species along the axes based on the degree to which their communities share similar species compositions and species share similar ranges, respectively. Then, three statistics (i.e., elements), namely coherence, range turnover and range boundary clumping, are evaluated under null models (1000 permutations, $\alpha = 0.05$) that constrain site richness equal to the observed value, which has been shown to have appropriate type I error rates and adequate power (Gotelli and Graves 1996). Finally, the pattern that best fit the data is determined based on the comparison between the observed values of these elements with those obtained from the null matrices which are used to obtain significance values. See Appendix 2 for a detailed description on how the EMS statistics are computed and how results are interpreted. In order to apply the EMS framework, we used a matlab script made available by the authors from Presley et al. (2010) at http://faculty.tarleton.edu/higgins/metacommunity-structure.html.

In order to assess the mechanisms underlying species distributions and metacommunity structure we measured and computed a series of predictors that were grouped into three sets: environmental, spatial and connectivity factors. The rationale behind the subdivision between connectivity and spatial variables is explained further below in the “Spatial factors” section.

Environmental variables

Elevation, depth, patch age and vegetation cover were measured (see Appendix 1 for details) in each patch (plot) as these variables are known to be highly associated with fish biodiversity in floodplain systems (Crowder and Cooper 1982, Snodgrass et al. 1996, Baber et al. 2002). Elevation normally has a negative relationship with duration and magnitude of the inundation (Girard et al. 2010) whereas the patch age and water depth in temporary aquatic habitats are known to influence fish diversity through the probability of colonization for the former and habitat complexity for the latter (Snodgrass et al. 1996, Baber et al. 2002). Vegetation cover has been shown to be important in temporary aquatic habitats by creating habitat complexity while also influencing water quality (Crowder and Cooper 1982). We measured the percentage of each type of vegetation cover in a 450m circular buffer around each plot. A principal component analysis (PCA) was applied on vegetation data in order to reduce the number of predictors. The first two PCA axes were used in further statistical analyses as they accounted for most of the variation (61.8%) in vegetation cover among plots (see Appendix 1 for more details). Prior to any statistical analysis, elevation, depth and patch age variables were log-transformed while arcsine transformation was applied to the square root of vegetation cover data in order to improve data normality.

Connectivity factors

Landscape connectivity is the degree to which the landscape facilitates or precludes movement among patches (Taylor et al. 1993). Connectivity can be measured in different ways (Prugh 2009) but can be broadly classified into two main classes namely structural and functional. While functional connectivity incorporates specific data about individuals moving in or out of focal patches, or throughout a landscape, structural connectivity measures the spatial arrangement of different types of habitat or patches in a landscape as a proxy of how these features may affect dispersal dynamics (Theobald et al. 2011). For each month, we measured the structural landscape connectivity by applying the "*Ti* metric" (Theobald et al. 2011), which is a modified version of Hanski's (1994) incidence function model:

$$Ti = \sum_{j=1}^{n} \mathrm{wij}/(\mathrm{dj} \times \mathrm{di})$$

where w_{ij} is the effective distance between patches i and j, d_j is the depth of patch j, d_i is the depth of patch i. Lower values of *Ti* indicate less isolated (i.e. more connected) sites whereas high values suggest the opposite. Effective distance (least-cost distance) was calculated using information on vegetation cover, water level and elevation. Vegetation cover data was extracted from Google Earth while flood and elevation layers were constructed from the plot data through interpolation using ordinary kriging assuming a spherical model to build the semivariogram (Zimmerman et al. 1999). Effective distance is calculated based on factors that facilitate or restrict fish movement across the landscape as terrestrial areas increase the resistance and movement cost while flooded pristine vegetation increases landscape permeability thereby reducing movement cost. As such, effective distance between two patches represents the minimum cumulative effort (least-cost distance) for a fish to move across the resistance layer

(Theobald et al. 2011). In order to create the resistance layer, the vegetation layer was classified by assigning a resistance value (cost) of 1 to wet forest and a value of 2 to wet pasture and wet grassland, while both dry forest and dry pasture received the maximum resistance value (100). We chose these resistance values because larger fish species are likely to avoid open habitats (i.e. wet pastures and wet grasslands) where terrestrial predators are more abundant (I. M. Fernandes *unpublished data*). The depth and elevation layers were reclassified with resistance values ranging from 1 to 10 where higher resistance values were assigned to shallower regions located at higher elevations. After reclassification, the three layers were combined to build the final resistance layer. Given its greater level of accuracy, vegetation data was given a higher weight (0.5) on the final resistance layer while depth and elevation, which were estimated via interpolation (0.4 and 0.1 respectively) were given a lower weight (see Adriaensen et al. 2003 for more details about these methods). All these analytical steps were performed in ArcGIS (ESRI 2006). The least-cost layer was calculated among plots and permanent ponds using the “costDistance” function of the 'gdistance' package in the R Statistical Software.

Along with the *Ti* metric, we also computed two other metrics that account for the influence of potential sources of colonization for each plot: the number of ponds in a 1km radius (hereafter named pond density) and the distance to the nearest neighboring pond weighted by its area (hereafter named *NN*).

Spatial factors

We constructed spatial predictors through spatial eigenfunction analysis using Moran’s Eigenvector Maps (MEM), which allows representing complex spatial patterns at multiple spatial scales (Peres-Neto & Legendre 2010). We used the “pcnm” package in the R Statistical Software in order to compute MEM. The procedure resulted in six positively autocorrelated MEM (due to a smaller number of sites in early season) for January and 10 for the remaining months. Note that MEM when used as predictors may represent unmeasured environmental factors that are spatially structured rather than the signature of dispersal per se (Peres-Neto and Legendre 2010). However, MEM and other spatial predictors based on geographic positioning (e.g., geographic polynomials) may not always capture the dispersal signal (Moritz et al. 2013). If connectivity predictors and MEM represent dispersal processes, their shared contribution in explaining species abundances patterns should be much greater than their unique contribution in explaining species distributions in variation partitioning analysis (see below). However, if MEM represents unmeasured environmental predictors, than their independent contribution should be relatively greater than their shared one.

Statistical analyses

We used two complementary statistical analyses to uncover the underlying drivers of metacommunity structure and their relative importance at each month. We first computed Spearman-rank correlations ($\alpha = 0.05$) between each variable from the three sets of predictors (environmental, spatial and connectivity) and the canonical scores extracted from the correspondence analysis used in EMS framework. Secondly, we used variation partitioning (Borcard et al. 1992) to assess the relative contribution of environmental, connectivity (*Ti* metric, pond density and *NN*) and spatial predictors (MEMs) on the species distribution matrix at each sampling period. This analysis decomposes the total variation of multi-species distributional tables into shared and unique contributions of these sets of variables. The analysis was based on a redundancy analysis (RDA) on Hellinger-transformed abundance data (Legendre and Gallagher 2001), as it has been shown to provide unbiased estimates in variation partitioning (Peres-Neto et al. 2006). A separate variable selection within each group (i.e., environmental, MEM and connectivity) was performed using the “forward.sel” function of the 'packfor' library for R (Peres-Neto & Legendre 2010). Variable selection was based on a Monte Carlo test based on 1000 permutations and the contribution of each set of predictors was reported using adjusted values based on the number of predictors and sampling sites (Peres-Neto et al. 2006).

Results

Elements of metacommunity structure

A total of 3538 individuals distributed across 58 species and 17 families were collected throughout the sampling period in 2009 (Appendix 3). Species richness at the metacommunity level, as well as abundance, increased throughout the wet season from January (26 species and 460 individuals) to April (50 species and 1631 individuals). During the sampling period, species richness across patches throughout the sampling period varied between 1 and 20 species, with an average value ranging from 5.11±4.48 in January to 14.09±5.17 in April. The average plot depth across months varied between 15.86±10.16 cm and 26.24±13.79 cm. In the peak of the flood period for the other years, a total of 56 species (across 2104 individuals), 49 (887) and 55 (1320) were sampled in March 2008, 2010 and 2011, respectively. The EMS analysis revealed significant changes in the fish floodplain metacommunity structure throughout the four sampling periods of 2009 (Fig. 2, Table 1). At each month, the metacommunity structure was significantly different from random and assigned to a particular pattern according to our early predictions (see Introduction). Coherence was statistically significant in all months, indicating that species in general responded to the major gradient of variation (i.e., first CA axis; see Appendix 2). In January, the pattern that best characterized the metacommunity structure was nestedness (Table 1, Fig 2a), with significantly negative range turnover and clumped species loss (see Appendix 2). In February, species range turnover was negative but not significant as in the previous month and as a result the metacommunity structure was found to be quasi-nested with clumped species loss (Table 1, Fig. 2b). The clumped species loss pattern suggests that species have common tolerances to the environmental gradient depicted by the correspondence analysis and quasi-structures emerge when the overall range turnover is not distinguishable from randomness and indicate weaker structuring factors than in regular structures (Presley et al. 2010). Finally, the metacommunity structure in both March and April showed positive range turnovers, with a larger value in April; however neither was significant and the pattern that best fitted both months was quasi-Clementsian (Table 1, Fig. 2c, 2d). For the years in which only the flood peak was sampled (March), the pattern that best fit the metacommunity structure was Clementsian (2008), quasi-nested (2010) and quasi-Clementsian (2011) (Table 1, Fig. 3).

Table 1. Results for the EMS framework for each month from the wet season in 2009 and for March of 2008, 2010 and 2011. Abs = Number of embedded absences, Re = Number of replacements, Mo = Morisita Index, *p* = probability, μ = mean value for the null model, σ = standard deviation value for the null distribution. Significant ($P \leq 0.05$) results are bold. Note that coherence is calculated by the number of embedded absences and in coherent metacommunities the mean number of embedded absences from the null model will be higher than the observed value. Therefore, when standardized the most coherent metacommunity will have the lowest values of coherence and in order to facilitate interpretation, the standardized values of coherence were multiplied by -1. Jan = January, Feb = February, Mar = March and Apr = April.

Elements	Parameters	Jan 2009	Feb 2009	Mar 2009	Apr 2009	Mar 2008	Mar 2010	Mar 2011
Coherence	Abs	81	201	287	333	514	323	435
	p	**0.0253**	**0.0104**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	μ	131.29	261.01	415.46	540.93	696.52	405.52	633.90
	σ	22.48	23.46	25.67	22.33	25.57	23.04	27.99
Range Turnover	Re	684	2625	4939	6097	15110	5033	8226
	p	**<0.0001**	0.0944	0.6622	0.2156	**<0.0001**	0.33	0.30
	μ	1503.44	3690.62	4600.11	5185.50	9577.57	5865.30	7178.49
	σ	189.59	637.02	775.73	757.85	1429.68	859.78	757.85
Boundary Clumping	Mo	2.41	1.68	1.77	1.61	2.07	1.56	1.36
	p	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	Structure	nested	quasi-nested	quasi-Clementsian	quasi-Clementsian	Clementsian	quasi-nested	quasi-Clementsian

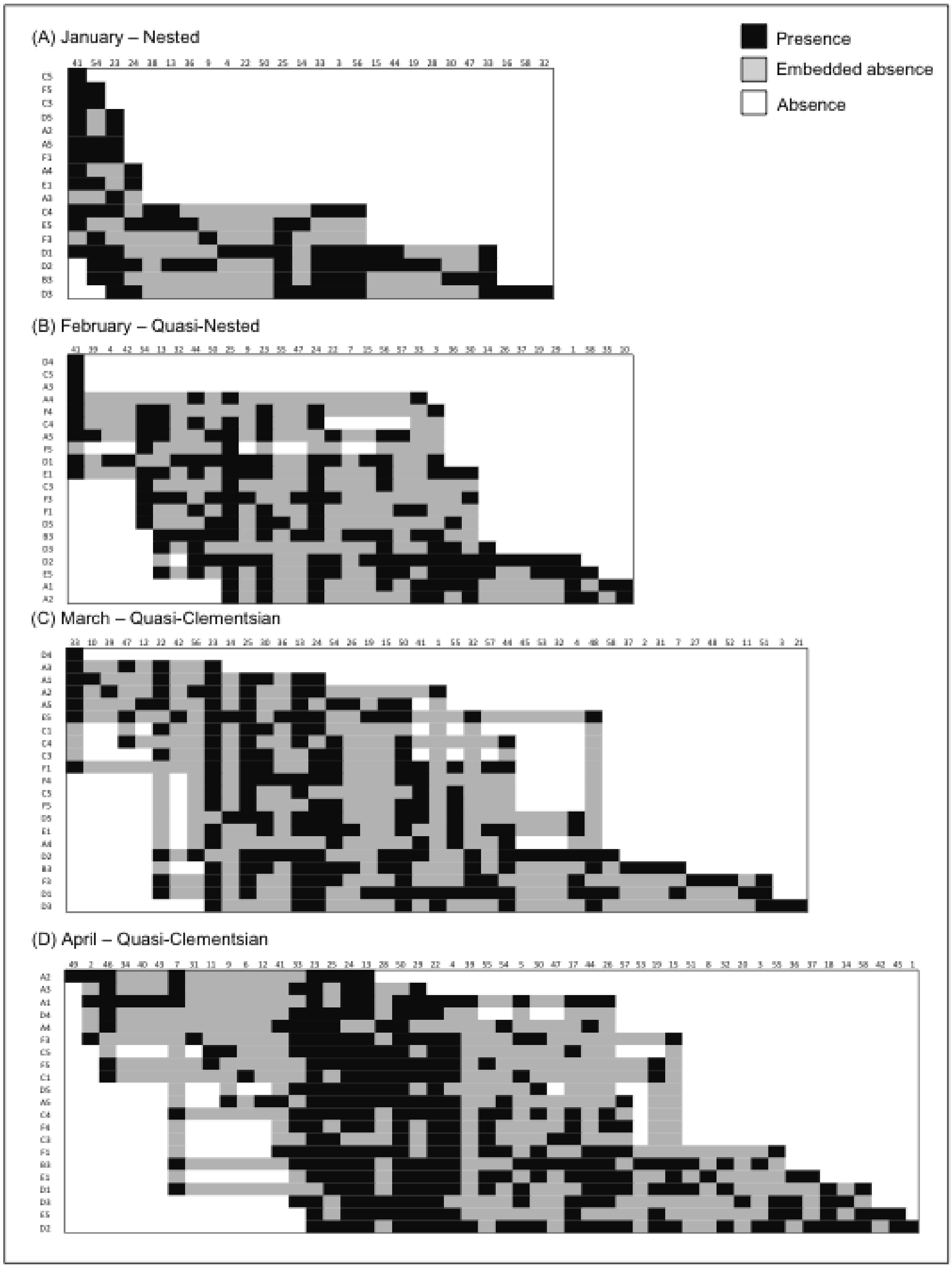


Figure 2. Distributional profiles of species as ordered via analysis of correspondence for (a) January, (b) February, (c) March and (d) April. Species and plots are presented in columns and rows, respectively. See Appendix 3 for species names. Black and white areas represent species

presence and absence, respectively while gray areas represent embedded absences within species ranges (See Appendix 2).

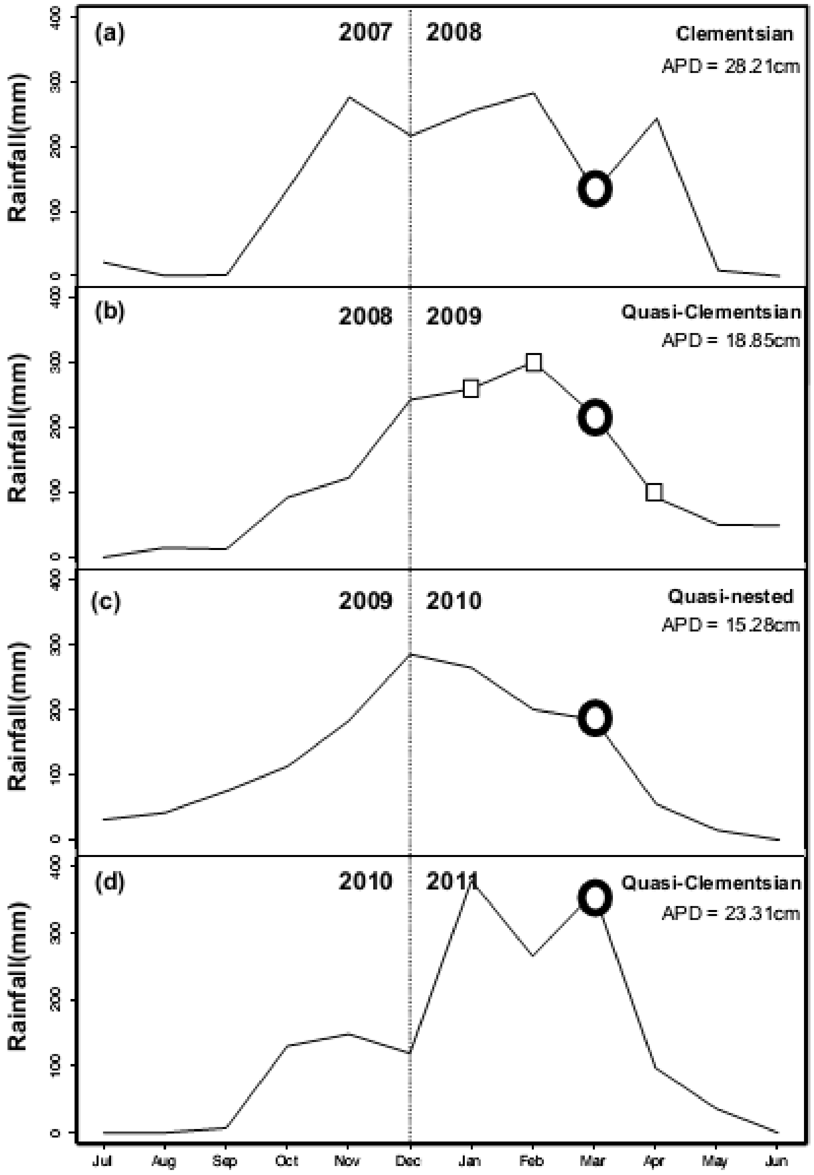


Figure 3. Average monthly rainfall across years from 2007 to 2011. Black circles represent the sampling dates in March. The metacommunity structure found in each year is depicted in the top-right corner. (a) July 2007 – June 2008; (b) July 2008 – June 2009; (c) July 2009 – June 2010; (d) July 2010 – June 2011. White squares in (b) indicate the sampling campaigns from January, February and April 2009. APD = average plot depth.

Table 2. Result of the variation partitioning analysis showing the contribution of environmental factors [E], spatial factors [S] and connectivity [C] to the variation in species abundances across the metacommunity through time. Components with a + sign indicate the shared contribution of two factors (see Fig. 2) . *Ti* = connectivity metric; Age = patch age ; PC2 = 2 axis of the PCA for the vegetation data; Pond. den. = number of ponds in a 1km buffer around each plot.

Component	January		February		March		April	
	R^2	p	R^2	p	R^2	p	R^2	p
E	0.13	0.006	0.13	0.001	0.14	0.001	0.09	0.001
E+S	0.0	--	0.0	--	0.02	--	0.07	--
S	0.0	--	0.0	--	0.04	0.026	0.15	0.001
C	0.14	0.002	0.07	0.01	0.03	0.015	0.04	0.001
C+E	0.16	--	0.07	--	0.0	--	0.12	--
C+S	0.0	--	0.0	--	0.0	--	0.0	--
E+S+C	0.0	--	0.0	--	0.02	--	0.0	--
R	0.57	--	0.73	--	0.75	--	0.53	--
Variables Selected	Depth [E] PC2 [E] *Ti* [C] Pond den. [C]		Depth [E] PC2 [E] *Ti* [C]		Depth [E] PC2 [E] Age [E] *Ti* [C] MEM2 [S]		Depth [E] PC2 [E] *Ti* [C] MEM1 [S] MEM6 [S] MEM10 [S]	

Relative contribution of structuring factors to species distributions

Variation partitioning indicated that the relative contribution of environmental factors [E] to the variation in species abundances across the metacommunity remained mostly constant, decreasing only slightly in the last month (Table 3, Fig 4). However, the contribution of spatial factors [S] and connectivity [C] changed through time (Table 3, Fig. 4). In January and February, only environmental factors and connectivity were significant. The unique contribution of environmental factors throughout the season was mainly due to depth and the second vegetation axis PC2 (Table 3, Fig. 4). Connectivity metrics decreased in contribution from 14% of the explained variation in January (*Ti* and pond density were selected as significant predictors) down to 4% in April (only *Ti* was selected as significant). Finally, in March and April, spatial predictors were significant and accounted for 4% (MEM2) and 15% (MEM 1, MEM 6 and MEM10) of the variation in species abundances, respectively.

Table 3. Spearman-rank correlation between predictors and canonical scores extracted from the first axis of the correspondence analysis used to ordinate species distribution in the EMS framework. Significant relationships are depicted in bold.

Variables	January 2009		February 2009		March 2009		April 2009	
	r	*p*	r	*p*	r	*p*	r	*p*
Altitude	**0.50**	**0.018**	**0.46**	**0.039**	0.14	0.523	0.25	0.266
Depth	**-0.81**	**<0.001**	**-0.67**	**0.001**	**-0.50**	**0.019**	**-0.71**	**<0.001**
Age	**-0.59**	**0.012**	**-0.44**	**0.052**	**-0.44**	**0.042**	**-0.72**	**<0.001**
PC1	0.32	0.206	0.42	0.065	0.19	0.395	0.35	0.109
PC2	-0.17	0.500	-0.30	0.187	0.28	0.212	0.06	0.784
Pond density	**-0.58**	**0.014**	-0.30	0.197	**-0.52**	**0.015**	**-0.49**	**0.023**
NN	-0.37	0.141	0.10	0.644	**-0.55**	**0.010**	-0.35	0.108
Ti metric	**0.76**	**<0.001**	**0.62**	**0.003**	**0.52**	**0.016**	**0.75**	**<0.001**
MEM1	0.13	0.59	-0.004	0.984	-0.19	0.398	**-0.43**	**0.047**
MEM2	0.31	0.217	-0.03	0.894	0.35	0.109	**0.52**	**0.016**
MEM3	0.24	0.352	-0.20	0.389	0.28	0.206	0.35	0.113
MEM4	0.03	0.888	-0.16	0.477	**0.44**	**0.045**	0.24	0.282
MEM5	-0.20	0.418	-0.31	0.170	-0.34	0.122	-0.35	0.118
MEM6	0.02	0.936	-0.09	0.676	-0.20	0.361	-0.30	0.172
MEM7	---	---	-0.12	0.599	0.94	0.682	**0.43**	**0.048**
MEM8	---	---	0.01	0.959	0.04	0.850	-0.03	0.885
MEM9	---	---	---	---	0.031	0.894	-0.29	0.192
MEM10	---	---	---	---	-0.053	0.819	0.06	0.775

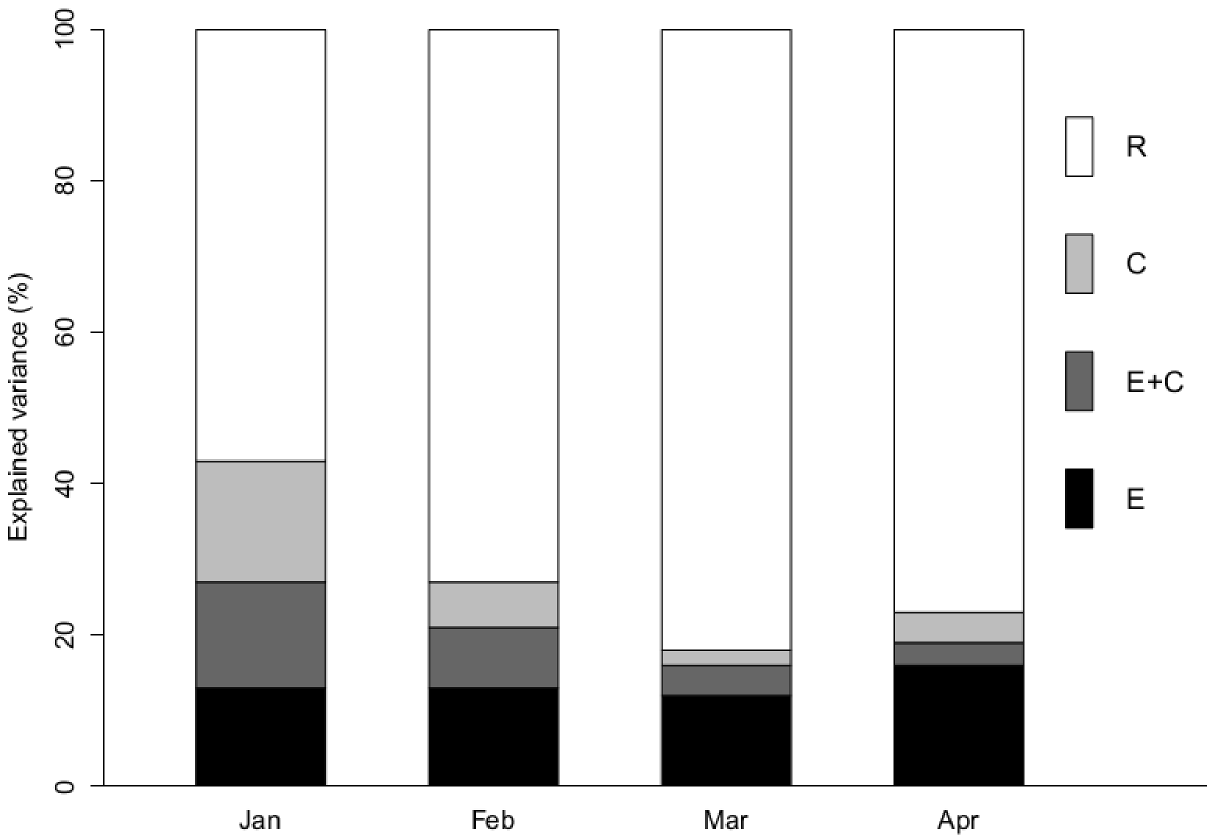


Figure 4. Result of the variation partitioning analysis showing the contribution of environmental factors [E], spatial factors [S] and connectivity [C] to the variation in species abundances across the metacommunity through the four months of 2009 wet season. Components with a + sign indicate the shared contribution of two or more sets of predictors (see also Table 2) . Jan = January, Feb = February, Mar = March and Apr = April.

Drivers of metacommunity structure

The results from the correlation are fairly similar to those obtained via variation partitioning. The correlation between January canonical scores and depth was extremely high (r = -0.81; p < 0.001), thus supporting our hypothesis that depth should be one of the main factors influencing the metacommunity structure at the beginning of the wet season. The strength of this correlation decreased somewhat over the following months: February (r = - 0.67; p < 0.001), March (r = -0.40; p = 0.019) and April (r = -0.71; p < 0.001), indicating that water depth became less important for metacommunity structure as the season advanced (Table 3). Pond density was significantly related to the main gradient of variation as well in January (r = -0.58; p = 0.014), March (r = -0.52; p = 0.015) and April (r = -0.49; p = 0.023) while the *Ti* metric contributed significantly correlations across all months (Table 3). Finally, between one and three MEM were significantly related to the metacommunity's major gradient of variation in March and April, respectively and none in the first two months (Table 3). Overall, the major difference in contrast to the variation partitioning results was the absence of correlation with PC2 (vegetation gradient), suggesting that vegetation is more related to species' abundances rather than their distribution.

Discussion

Metacommunity structure

Different metacommunity structures can emerge from the relationship between species distributions and environmental gradients (Presley et al 2010) and in this study we showed that metacommunity structure may also change over time due to structural changes in their landscapes. Moreover, these structural changes can be related to predictable ecological processes related to the flood regime in this system, which directly affects the degree of environmental heterogeneity and landscape connectivity (Layman et al. 2010). The floodplain fish metacommunity went from nested to quasi-nested in the beginning of the wet season up to quasi-Clementsian during the peak of the flood. In January, and to a lesser degree in February, the metacommunity was characterized by a hierarchical structure of narrow-range species whose occurrences represented subsets of broadly distributed species (Fig. 2a, 2b). However, during subsequent months some of the broadly distributed species retreated their ranges (e.g. *Neofundulus parvipinnis*; *Stenolebias damascenoi*; species 41 and 54 on Fig. 2, respectively) while some narrow-range species (e.g. *Hemigrammus tridens*; species 22 on Fig. 2) dispersed across the landscape. This process accounted for the change in range turnover that, as predicted, was negative at the beginning of the wet season but gradually increased through time (Fig. 2; Table 1). Finally, the consistency of significant positive boundary clumping across all months (Table 1) indicates that species might be sharing physiological and/or evolutionary constraints resulting in a shared response to a common environmental gradient (Presley et al. 2010). Indeed, throughout all months the vegetation axis (PC2) was a significant factor explaining fish abundance distribution (Table 2). This axis represents a gradient of vegetation variation from wet grasslands to wet forests (Appendix 1) which associated with the flood regime, creates contrasting habitats that are likely to select different groups of fish species depending on their habitat preferences.

Although changes of species distributions are expected in such dynamic systems, this may not necessarily impose changes to the overall metacommunity structure. For instance, a study performed on terrestrial gastropods within tropical forests that are frequently disturbed by hurricanes and logging activities found that the degree of nestedness changed through time but the pattern, in general, was persistent (Block et al. 2007). Nestedness was also found to be temporally stable in invertebrate communities inhabiting rock pools, despite it being a dynamic system with high temporal turnover (Azeria and Kolasa 2008). However, because these studies only considered nestedness, the possibility that other patterns with different structuring mechanisms could fit even better their data was not considered. Other studies such as Keith et al. (2011) and Newton et al. (2012) applied the EMS technique in order to assess the temporal variability in the structure of English woodland and calcareous grassland metacommunities, respectively. Both studies reported that these plant metacommunities followed a Clementsian structure and, more importantly, that these structures were stable for a relatively long period (i.e. 70 years). Surprisingly, these results were found despite the fact that significant changes in both local and regional diversity occurred over this period of time, casting doubt on the utility of EMS approach as a broad indicator of conservation status (Keith et al. 2011, Newton et al. 2012). However, metacommunity structures not only depend on species diversity but also on the processes underlying landscape-scale community organization. Although apparently long, 70 years were probably not enough to account for meaningful temporal variability in the fundamental mechanisms that influence plant metacommunities, which might explain the lack of structural changes. In stark contrast, we were able to detect significant changes in metacommunity structure in an extremely short term because the structural changes in our landscape are massive as these systems go from flooded to dry within a single year. We also applied the EMS analysis using the pooled fish distribution data across all four months and detected a quasi-Clementsian structure. Therefore, if we had not taken into account the temporal dynamics of this system we would have missed a signal suggesting that dispersal limitation is important at the beginning of the wet season.

Drivers of metacommunity structure

The major distributional gradient in our system was highly correlated with depth and connectivity (Table 3). Spatial factors modeled by MEM, which were non-significant in the beginning of the season, ended up explaining 15% of species variation in the last month (April). In contrast, the connectivity factors were important mostly in January and explained over 14% of the variation in species abundances (Fig. 4, Table 2), decreasing drastically in the subsequent months. Therefore, because the effects of connectivity and MEM contrasted across months, we suspect that the latter are not related to dispersal processes. This conclusion is further supported by the fact that the shared contribution between connectivity and MEM [C+S] was null across all months (Fig. 4, Table 3). Therefore, metacommunity variation related to MEM in our study system is likely to represent unmeasured environmental factors that are themselves spatially structured (see Peres-Neto and Legendre 2010 for a discussion on this matter). As such, by adding the fractions explained by environmental factors and spatial eigenvectors [E]+[E+S]+[S] together in March and April, there is a substantial increase in the importance of environment, which accounts for more than 20% (March) and 30% (April) of the variation in species abundances, respectively. This result strengthens our predictions, where dispersal processes, estimated by connectivity factors, are important at the beginning of the wet season whereas the environment (represented by environmental predictors MEM) are relevant at the end.

The nested pattern detected at the beginning of the wet season was influenced by a combination of local and regional factors. The importance of local environmental factors on wetland fish communities has been well documented (Baber et al. 2002). Depth and patch age are both positively related to wetland fish diversity, where the former can be viewed as habitat size because a greater water volume may provide more habitat diversity and complexity (Barbour and Brown 1974) while the latter is directly related to an increase in chance that fish disperse and successfully colonize patches through time (Baber et al. 2002, Arrington et al. 2005, Layman et al. 2010). Both factors have been reported to promote nestedness in wetland metacommunities for many taxa (Snodgrass et al. 1996, Baber et al. 2004) and it may be the case in the Pantanal wetland as well. Shallower patches (i.e., lower depth) or the ones that were flooded later (i.e., lower patch age) harbored fewer species than the ones that were flooded earlier or that were deeper. In addition, the species composition of poor-species patches represented subsets of richer sites, creating a nested structure (Fig. 2a). As for regional factors, connectivity or isolation associated with differential abilities among species to disperse have been found to underlie the nested structure in other systems as well (e.g. Kodric-Brown and Brown 1993). Indeed, variation partitioning indicated that pond density was only important in January (Table 2), suggesting that proximity to more sources of colonization was an important structuring factor during that month. Due to the low degree of connectivity among patches in the beginning of the rain season, only species with high dispersal abilities or specific adaptations can colonize most patches, while poor dispersers are restricted to dwell in the highly connected or deeper patches. For instance, both *Hoplerythrinus unitaeniatus* and *Hoplias malabaricus* (species 23 and 24 in Fig. 2; Appendix 2) can tolerate hypoxic conditions by diffusing atmospheric oxygen into their bloodstream through a vascularised swim bladder and also perform overland movements using lateral body undulation (Kramer et al. 1978, Lima-Filho et al. 2012). Such traits may explain why these species have relatively larger distributional ranges during the initial months of the rainy season when most patches are poorly connected and shallow. Others, such as killifishes (i.e. species 38, 41, 53, 54 and 57 in Fig. 2; Appendix 2), have drought-resistant eggs that are deposited in the muddy substrate in the end of the wet season and remain buried during the dry period, waiting for the next wet season to hatch (Wourms 1972). In addition, these species present annual lifecycles, thus their larvae and juveniles have rapid growth rates, which allow them to quickly colonize newly formed habitats and explain their broad distribution in January and February (Fig. 2a, 2b). Evolutionary strategies that enable persistence or rapid colonization in systems affected by drought are common among fish species (Wourms 1972, Kramer et al. 1978) as well as for others taxa such as zooplankton, algae and macrophytes (Chase 2007). In contrast, species of the tetras lacking any of these adaptations such as *Aphyocharax anistsi*, *Hemigrammus tridens* and *Serrapinnus* spp (i.e. species 4, 22 and 50 in Fig. 2; Appendix 2) were restricted to the deepest patches and had much smaller ranges.

During the last half of the wet season quasi-Clementsian structure was the pattern that best fitted the floodplain fish metacommunity. The rise of the water level increases the connectivity across habitat patches, providing opportunities for dispersion and thus reducing dispersal limitation, explaining the decrease in importance of connectivity metrics after January (Table 2). During this period, a highly connected landscape if formed, allowing the expansion of some species (e.g. tetras) ranges throughout March and April. Conversely, some broadly distributed species (e.g., killifish) observed their ranges reduced during these months (Fig 2c, 2d), potentially excluded by competitive interactions with late colonizer species (Arrington et al.

2005). Indeed, the killifish, which were responsible for 47% and 36% of the total abundance of fish sampled in January and February, respectively, decreased to about 14% and 4% of the total abundance in the two last months. This process created some degree of turnover among species ranges and changed the pattern from nested to a quasi-Clementsian structure at the metacommunity scale (*sensu* Presley et al. 2010). A Clementsian structure is found on metacommunities where major suites of species replace each other as groups across space. Such pattern is generally due to joint responses of species to the environmental gradient (Presley et al. 2010). Although ephemeral habitats are more similar in their limnological characteristics during the late wet season, the growth of macrophytes, the vegetation gradient of the landscape and debris increase habitat complexity by creating microhabitats that select for different group of fish species (Arrington et al. 2005, Dibble and Pelicice 2010). If such habitat features are spatially structured they may be captured by the MEM that were found to be important during March and April. Indeed, the highest explained variation from environmental factors was found in April, thus supporting the hypothesis of environmental filtering regulating the floodplain fish metacommunity at the end of the wet season as indicated by the Clementsian structure. Alternatively, competitive interactions can also promote Clementsian pattern if pairs of competing species do not occur independently of each other, rather forming “clusters of forbidden combinations” (Gilpin and Diamond 1982). However, in order to assess the possible role of competition further research is needed using phylogenetic or trait-based approaches (e.g., Ingram and Shruin 2009).

The analysis performed with the additional data from other years (Fig. 3) reinforces our general conclusions based on the 2009 data. In 2008, the year where the average plot depth (APD) was the highest (28.21 cm), the fish metacommunity exhibited a Clementsian structure, indicating that species experienced sufficient opportunity to disperse and consequently select for their preferred habitats, creating the significant range turnover, which was not found in 2009 (APD = 18.85 cm). In contrast, 2010 was the driest year (APD = 15.28 cm), which created limited opportunities for fish to disperse across plots. Consequently, up to March 2010 the fish metacommunity structure was still quasi-nested while in the other years it had already changed to quasi-Clementsian or Clementsian structure (Fig. 3). These results suggest that the metacommunity structure in fish-floodplain systems is predictable and recurrent across years on the basis of the relative importance of environmental (local) versus connectivity (regional) factors. Indeed, it has been reported that cichlid assemblages in the Pantanal may undergo substantial changes over one season but have a low inter-annual variability (Lourenço et al. 2012) and a similar result was found for fish assemblages in a Venezuelan neotropical floodplain system (Rodriguez and Lewis 1994). One important point that cannon be investigated with our data is whether and how chances in the dynamics of this seasonal metacommunity through time affect the larger regional metacommunity. If dispersal limited species are precluded to expand their ranges due to low connectivity during one year they will not be able to take fully advantage of this temporary resource-rich landscape. This may have long-term consequences to their regional demographics, as they may not be able to grow and/or produce enough individuals to cope with the dry season.

The majority of the species that dwell in this system are small-sized fish (<30 cm; I.M. Fernandes *unpublished data*) and thus rarely perform long distance dispersal (i.e. dispersal distance is known to be correlated with body size in fish; Griffith 2006). Therefore, we consider that the sampling scheme used here was broad enough to encompass the dispersal processes, environmental heterogeneity and biotic interactions underlying the metacommunity structure of our study system. In addition, the findings from this study are not restricted to this system. Temporal variability in environmental and spatial processes is common in probably most ecological systems, as environmental variables changes across many different temporal scales and species tend to respond to these changes. The differences among systems will lie on which temporal scale these processes operate. Therefore, as long as the appropriate temporal and spatial scales are assessed for the particular system of interest, one can evaluate how the relative importance of different underlying factors will influence the metacommunity structure through time.

Finally, our results together with the findings of other studies (see results from Vanschoenwinkel et al. 2010, Erös et al. 2012) emphasize that many ecosystems undergo great temporal variability in the relative contribution of environmental and dispersal processes. In addition, others have found that the relative importance of these two types of processes also depend on the spatial scale (Meynard et al. 2013) and disturbance regimes (McCauley et al. 2008). Together, these findings suggest that the ongoing debate regarding neutral (i.e., spatial) versus niche (i.e., environment) factors for assembly processes (Cottenie 2005, Alonso et al. 2006, Ricklefs 2006) may only be relevant, if at all, for very large spatial scales.

Acknowledgements - We would like to thank the Pantanal Research Center for the financial support and the National Council for Scientific and Technological Development (CNPq) for Postgraduate scholarship as well as the Coordination for the Improvement of the Higher Level Personnel (CAPES) that provided sandwich scholarship for I. M. Fernandes (#BEX: 6140/11-4). JZ receives a productivity grant from CNPq (#307464/2009-1). – Our sincere thanks to Jason Sansom, S. M. Thomaz, L. M. Bini, F. R. C. Costa, W. E. Magnussun and C. E. C. Freitas for reviews of earlier versions of the manuscript that greatly improved it.

References

Adriaensen, F. et al. 2003. The application of 'least-cost' modelling as a functional landscape model. — Landscape and Urban Planning 64: 233-247.

Alonso, D. et al. 2006. The merits of neutral theory. — Trends in Ecology & Evolution 21: 451-457.

Arrington, D. A. et al. 2005. Community assembly at the patch scale in a species rich tropical river. — Oecologia 144: 157-167.

Azeria, E. T. and Kolasa, J. 2008. Nestedness, niche metrics and temporal dynamics of a metacommunity in a dynamic natural model system. — Oikos 117: 1006-1019.

Baber, M. J. et al. 2002. Controls on fish distribution and abundance in temporary wetlands. — Canadian Journal of Fisheries and Aquatic Sciences 59: 1441-1450.

Baber, M. J. et al. 2004. The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. — Oikos 107: 16-27.

Barbour, C. D. and Brown, J. H. 1974. Fish species diversity in lakes. — The American Naturalist 108: 473-489.

Beisner, B. E. et al. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. — Ecology 87: 2985-2991.

Bloch, C. P. et al. 2007. Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness. — Oikos 116:

Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. — Ecology 73: 1045-1055.

Chase, J. M. 2003. Community assembly: when should history matter? — Oecologia 136: 489-498.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. — Proceedings of the National Academy of Sciences 104: 17430-17434.

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

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

Crowder, L. B. and Cooper, W. E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. — Ecology 63: 1802-1813.

Dibble, E. D. and Pelicice, F. M. 2010. Influence of aquatic plant-specific habitat on an assemblage of small neotropical floodplain fishes. — Ecology of Freshwater Fish 19: 381-389.

Elmendorf, S. C. and Harrison, S. P. 2009. Temporal variability and nestedness in California grassland species composition. — Ecology 90: 1492-1497.

Erös, T. et al. 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization - stream fish in a human-modified landscape. — Freshwater Biology 57: 1914-1928.

Fernandes, I. M. et al. 2010. Spatial pattern of fish assemblage in a seasonal tropical wetland: effects of habitat, herbaceous plant biomass, water depth, and distance from species sources. — Neotrophical Ichthyology 8: 289-298.

Gilpin, M. E. and Diamond, J. M. 1982. Factors contributing to non-randomness in species co-occurences on islands. — Oecologia 52: 75-84.

Girard, P. et al. 2010. Small-scale spatial variation of inundation dynamics in a floodplain of the Pantanal (Brazil). — Hydrobiologia 638: 223-233.

Gotelli, N. J. and Graves, G. R. 1996. Null Models in Ecology. — Smithsonian Institution Press.

Griffith, D. 2006. Pattern and process in the ecological biogeography of European freshwater fish. — Journal of Animal Ecology 75: 734-751.

Hanski, I. 1994. A practical model of metapopulation dynamics. — Journal of Animal Ecology 63: 151-162.

Henriques-Silva, R. et al. 2013. A community of metacommunities: exploring patterns in species distribution across large geographical areas. — Ecology 94: 627-639.

Ingram, T. and Shruin, J. B. 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. — Ecology 90: 2444-2453.

Junk, W. J. et al. 1989. The flood pulse concept in river - floodplain systems. — p. 110-127 *in* D. P. Dodge [ed.] Proceedings of the international large river Symposium. Can. Spec. Pub. Fish. Aquat. Sci. 106.

Junk, W. J. et al. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. — Aquatic Sciences 68: 278-309.

Kennedy, C. M. et al. 2011. Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. — Ecological applications 21: 1837-1850.

Kodric-Brown, A. and Brown, J. H. 1993. Highly structured fish communities in australian desert springs. — Ecology 74: 1847-1855.

Kramer, D. L. et al. 1978. The fishes and the aquatic environment of the central Amazon basin, with particular reference to respiratory patterns. — Canadian Journal of Zoology 56: 717-729.

Layman, C. A. et al. 2010. Linking fish colonization rates and water level change in littoral habitats of a Venezuelan floodplain river. — Aquatic Ecology 44: 269-273.

Legendre, P. and Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. — Oecologia 129: 271-280.

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

Leibold, M. A. and Mikkelson, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. — Oikos 97: 237-250.

Lima-Filho, J. A. d. et al. 2012. Air-breathing behavior of the JeJu fish *Hoplerythrinus unitaeniatus* in Amazonian streams. — Biotropica 44: 512-520.

Lourenço, L. S. et al. 2012. Persistence and stability of cichlid assemblages in neotropical floodplain lagoons. — Environmental Biology of Fishes 93: 427-437.

McCauley, S. J. et al. 2008. Metacommunity patterns in larval odonates. — Oecologia 158: 329-342.

Meynard, C. N. et al. 2013. Disentangling the drivers of metacommunity structure across spatial scales. — Journal of Biogeography 40: 1560-1571.

Moritz, C. et al. 2013. Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. — Oikos 122: 1401-1410.

Newton, A. C. et al. 2012. Structure, composition and dynamics of a calcareous grassland metacommunity over a 70-year interval. — Journal of Ecology 100: 196-209.

Pandit, S. N. and Kolasa, J. 2011. Opposite effects of environmental variability and species richness on temporal turnover of species in a complex habitat mosaic. — Hydrobiologia 685: 145-154.

Peres-Neto, P. R. and Legendre, P. 2010. Estimating and controlling for spatial structure in the study of ecological communities. — Global Ecology and Biogeography 19: 174-184.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. — Ecology 87: 2614-2625.

Presley, S. J. et al. 2012. Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. — Global Ecology and Biogeography 21: 968-976.

Presley, S. J. et al. 2009. Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple ordination axes. — Oecologia 160: 781-793.

Presley, S. J. et al. 2010. A comprehensive framework for the evaluation of metacommunity structure. — Oikos 119: 908-917.

Prugh, L. R. 2009. An evaluation of patch connectivity measures. — Ecological Applications 19: 1300-1310.

Ricklefs, Robert E. 1987. Community diveristy: relative roles of local and regional processes. — Science 235: 167-171.

Ricklefs, Robert E. 2006. The unified theory of biodiverisity: do the numbers add up? — Ecology 87: 1424-1431.

Rodriguez, M. A. and Lewis, W. M. J. 1994. Regulation and stability in fish assemblages of neotropical floodplain lakes. — Oecologia 99: 166-180.

Simberloff, D. and Wilson, E. O. 1969. Experimental zoogeography of islands: the colonization of emtpy islands. — Ecology 50: 278-296.

Snodgrass, A. J. W. et al. 1996. Factors affecting the occurence and structure of fish assemblages in isolated wetlands on the upper coastal plain, U. S. A. — Canadian Journal of Fisheries and Aquatic Sciences 53: 443-454.

Taylor, P. D. et al. 1993. Connectivity is a vital element of landscape structure. — Oikos 68: 571-573.

Theobald, D. M. et al. 2011. Assessing effects of land use on landscape connectivity: loss and fragmentation os western US forests. — Ecological Applications 21: 2445-2458.

Thomaz, S. M. et al. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. — Hydrobiologia 579: 1-13.

Vanschoenwinkel, B. et al. 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. — Journal of the North American Benthological Society 29: 1267-1278.

Wourms, J. P. 1972. The developmental biology of annual fishes. — Journal of Experimental Zoology 182: 389-414.

Zimmerman, D. et al. 1999. An experimental comparirson of Odinary and Universal Kriging and Inverse Distance Weighting. — Mathematical Geology 31: 375-390.

Síntese

Esse estudo mostrou que o efeito de fatores ambientais e espaciais sobre a temperatura da água, oxigênio, condutividade e pH mudam ao longo do período de cheia. No início e final da estação cheia, quando os habitats aquáticos estão mais isolados, a influência de fatores ambientais (locais) é mais pronunciada, principalmente para temperatura da água e oxigênio enquanto que no auge da cheia fatores espaciais foram mais importantes para todas as variáveis. Para condutividade e pH fatores espaciais foram sempre mais importante do que fatores ambientais.

A profundidade da coluna da água é importante para a diversidade de espécies de pequeno porte (< 50 mm) com maiores diversidades sendo encontradas em locais mais profundos. Peixes maiores têm seu comprimento e biomassa influenciados positivamente pela quantidade de vegetação arbórea presente na planície de inundação, enquanto que locais mais conectados possuem maior diversidade de espécies do que locais menos conectados.

Contrário a outros estudos, esse estudo demonstram que os padrões encontrados em estrutura de metacomunidades não são estatísticos temporalmente e que ao longo do processo de montagem de metacomunidades diferentes padrões podem surgir. Fatores ambientais, conectividade e fatores agindo em escala espacial devem ser considerados para explicar os padrões encontrados, entretanto mudanças no grau de conectividade foi o principal fator que permitiu a existência de diferentes padrões na estrutura das quatro metacomunidades aqui estudadas.

Apêndices

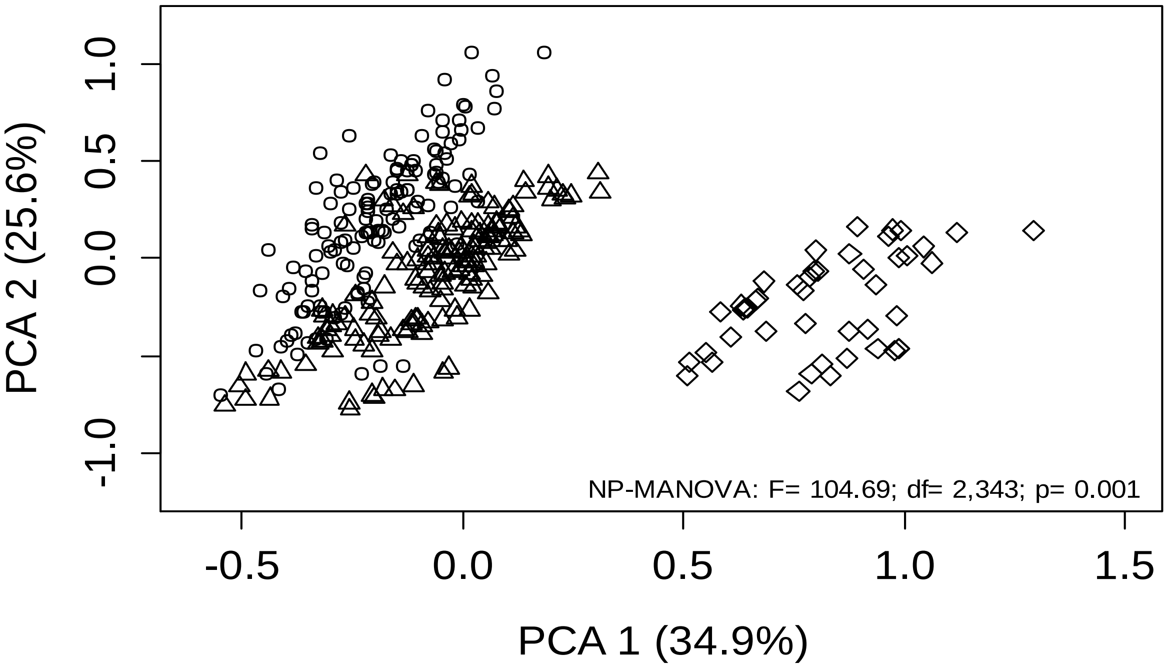
Capítulo I

Appendix A - Description about temporal variation in limnological variables

Differences in environmental characteristics among the three sampling period were evaluated through non-parametric multivariate analysis of variance (NP-MANOVA; Anderson 2001) and principal components analysis (PCA) was used to reduce the dimensionality of the data and gave a visual representation of the compared groups using NP-MANOVA. In this analyze was used only temperature, oxygen, conductivity, pH and depth with distance matrix constructed using Euclidian distance. Soil variables and vegetal cover were not used because these were measured just one time and we considered that important changes not occurred in sampling period.

Clearly, the environmental characteristics of the study area change between the three sampled period (NP-MANOVA: $F_{2,243}$=104; p=0.001). There is clear separation among receding period and rising/flood period and a light difference between rising and flood period in environmental characteristics of the floodplain water (Figure A).

Figure A - Plots distribution in bidimensional space based in principal components analysis (PCA) with environmental factors (oxygen, conductivity, pH, hydroperiod and depth) for rising (○), flood (Δ) and receding (◊) period. The difference between the three sampled period was tested using non-parametric multivariate analysis of variance (Anderson, 2001) and result is showing. The two first axis explained 60.4% of the variation and were selected based in broken stick model (Jackson et al., 1993).



PCA 2 (25.6%)
1.0
0.5
0.0
-1.0
NP-MANOVA: F= 104.69; df= 2,343; p= 0.001
-0.5
0.0
0.5
1.0
1.5
PCA 1 (34.9%)

Appendix B - Spearman correlation between first PCA axis and vegetal cover (landscape variables) in different buffer showing that all measures have high and significant negative correlation with first axis. Based on broken stick model (Jackson et al 1993) one axis is sufficient to represent landscape in all other analyses. Values in parentheses represent the percentage of variation explained in each axis.

Landscape variables	PCA1 - Rising (91.5%)		PCA1 - Flood (90.9%)		PCA1 - Receding (93.5%)	
	r	p	r	p	r	p
B5	-0.86	<0.001	-0.74	<0.001	-0.76	<0.001
B10	-0.89	<0.001	-0.77	<0.001	-0.79	<0.001
B25	-0.93	<0.001	-0.87	<0.001	-0.87	<0.001
B50	-0.94	<0.001	-0.93	<0.001	-0.93	<0.001
B100	-0.98	<0.001	-0.96	<0.001	-0.96	<0.001
B150	-0.98	<0.001	-0.96	<0.001	-0.97	<0.001
B300	-0.95	<0.001	-0.95	<0.001	-0.94	<0.001
B500	-0.94	<0.001	-0.93	<0.001	-0.92	<0.001

Appendix C - Spearman correlation between first and second PCA axes and soil characteristics. Clay, sand and silt have high correlation with first axis while organic matter is correlated with second axis. Thus, first axis was used in analyses to represent clay, sand and silt and was named soil1 variable while PCA2 was used with measure of the matter organic content and it was named soil2. The numbers of the axes were selected based in broken stick model (Jackson et al 1993). Values in parentheses represent the percentage of variation explained in each axis.

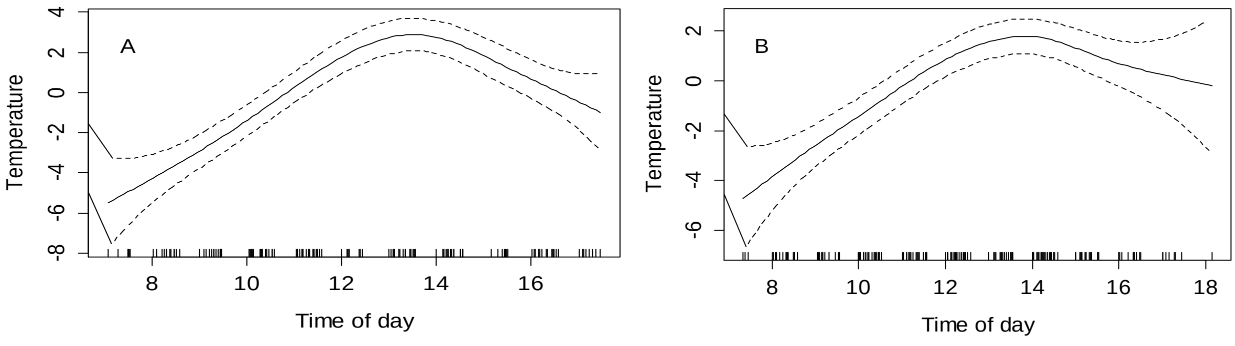
Soil Variables	PCA1 (69.4%)		PCA2 (23.5%)	
	r	p	r	p
Clay	0.93	<0.001	-0.07	0.726
Sand	-0.99	<0.001	0.12	0.610
Silt	0.90	<0.001	-0.13	0.513
Organic matter	0.30	0.126	0.95	<0.001

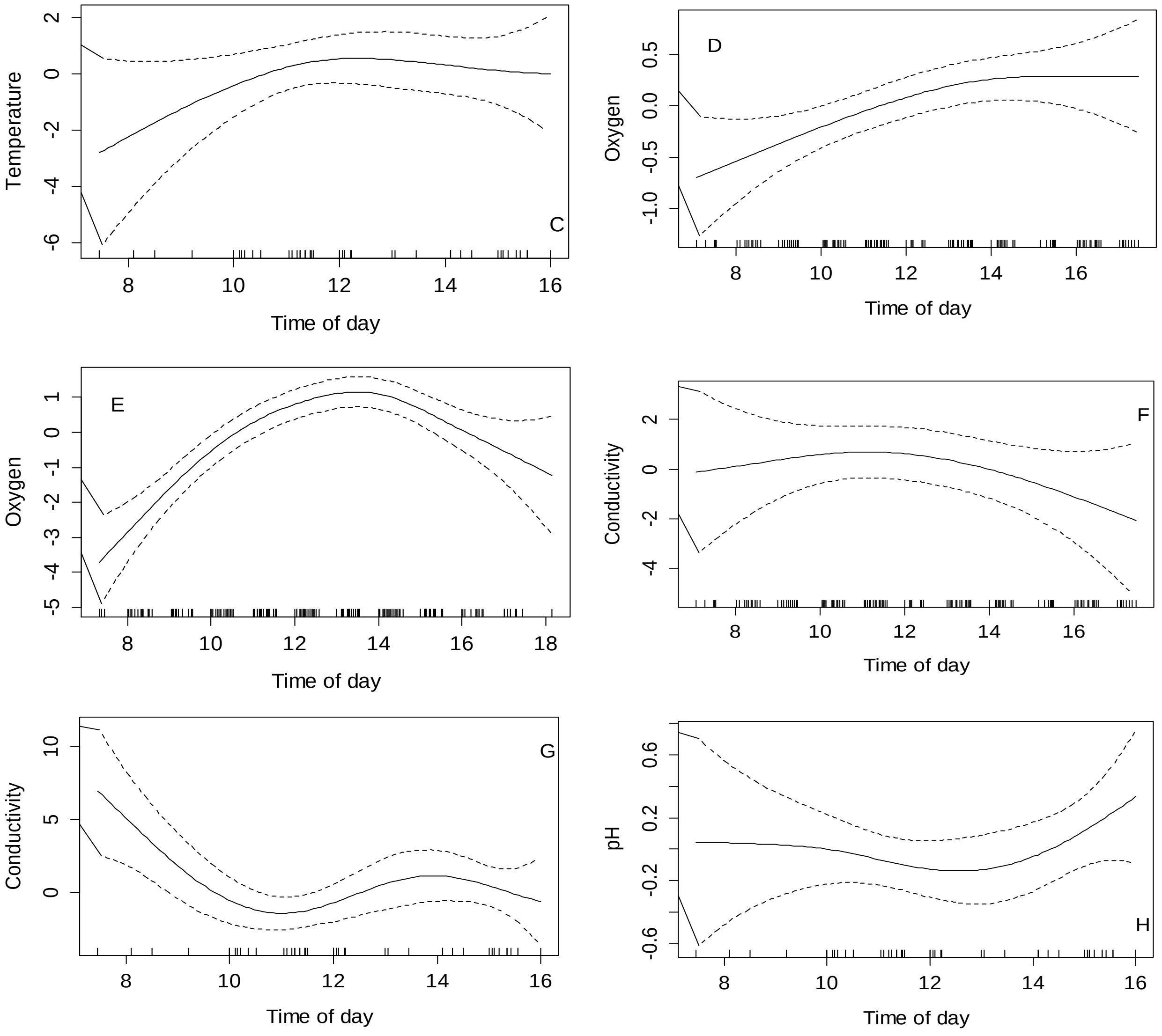
Appendix D - Daily variation in limnological variables

Generalized additive models (GAMs, Hastie and Tibshirani, 1986) was used to evaluate the relationship between time of the day and temperature, oxygen (OD), conductivity (CD) and pH (PH). When effect of the time of the sampling on the variables aforementioned was found, the residual of the analysis was extracted and utilized on the next analyzes. But when did not have relationship between time of the sampling and variables, the raw data of the variable were utilized. GAM models are data-driven rather than model-drive (Yee and Mitchell, 1991). This nonparametric category of model allows determination of the shape of the response curves from the data instead of fitting an a priori parametric model which is limited in its available shape of response (Lehman 1991). Thus, GAM is a excellent tool when the relationship between one or more variable is unknown.

The time of the day in which the sample were performed had a strong effect on temperature (in three sample period), oxygen (rising and flood period), conductivity (rising and receding period) and for pH in receding period (Figure D).

Figure D - Result of the GAM regression for temperature (A, B and C) oxygen (D an E), conductivity (F and G) and pH (H) in rising (A, D and B), flood (B and E) and receding (C, G and H) period showing the variation throughout the day.





Oscillations on water temperature, oxygen content, conductivity and pH during diurnal period is well known process (Schroeder 1975; Boyd et al., 1978; Chang & Ouyong, 1988; Erez et al., 1990). As we hope, higher water temperature coincides with time of day with higher solar irradiation, but oxygen show a surprising increasing throughout of day. Low oxygen content in the morning was found because during the night period the plant and other organisms utilize the oxygen that was produced during of day reducing the oxygen available. In photosynthesis absence during the night period coupled with breathing and decomposition process increase the available of the ions soluble in the water which can make clear the patterns displayed by conductivity, where higher value of the conductivity were found on the beginning of the morning, but strong reduction was observed throughout of day. Despite pH show daily variation just on the end of the inundation, this was inverse to oxygen and can be a relationship with a possible carbon dioxide (CO_2) increase due to photosynthetic rate reduction and increase of respiration process (Erez et al., 1990).

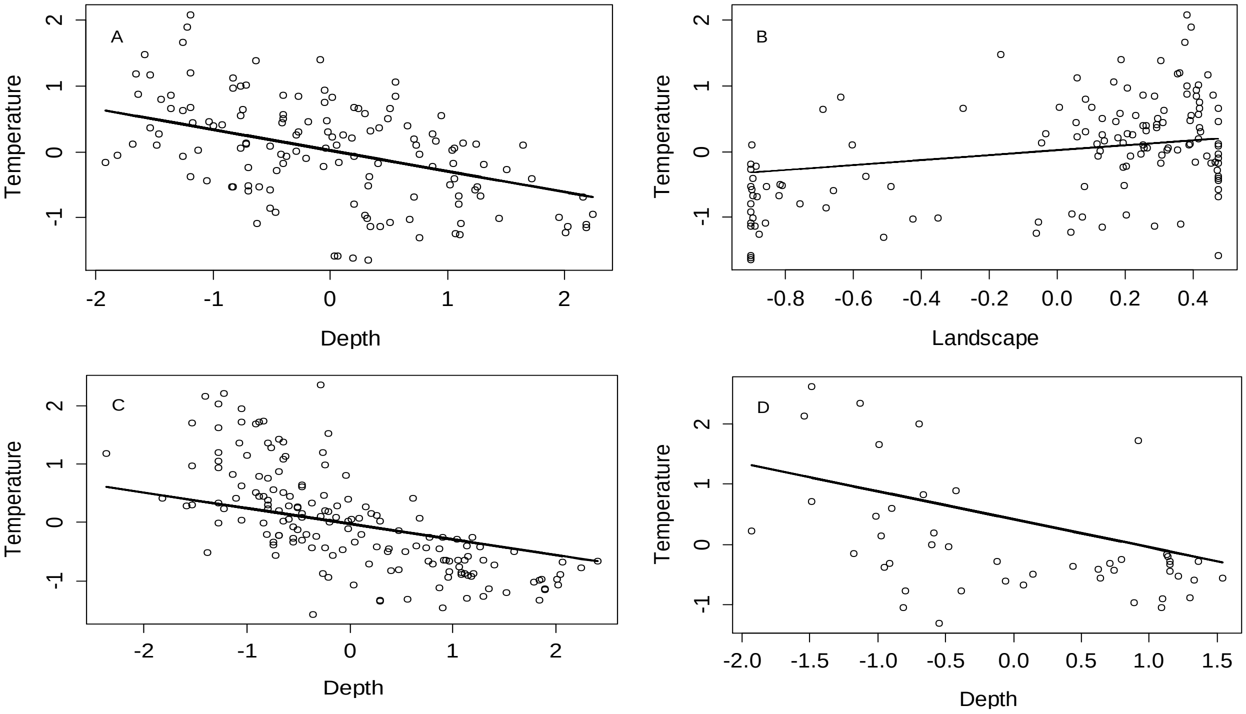
Appendix E - Result of the Akaike Information Criterion (AICc) where comparison among models without structure autocorrelation and models with autocorrelation structure were realized. Based on the Akaike Information Criterion (AICc), rational quadratic was the best spatial correlation structure just for oxygen in rising period. Spherical structure was the best for conductivity in receding period and and Exponential structure was the best for pH in flood period. While Gaussian structure was the best for oxygen in flood period, for conductivity during rising and flood periods and for pH in rising and receding periods. The best models are shown in bold.

	Rising			Flood			Receding		
				Temperature					
Models	AICc	ΔAICc	wAIC	AICc	ΔAICc	wAIC	AICc	ΔAICc	wAIC
Model	279.9	77.9	<0.001	311.2	97.7	<0.001	117.5	21.5	<0.001
Model+corRatio	202.6	0.7	0.174	**213.4**	**0.0**	**0.400**	97.8	1.8	0.236
Model+corExp	202.6	0.7	0.169	214.0	0.6	0.302	100.3	4.3	0.066
Model+corSpher	202.0	0.0	0.244	218.2	4.8	0.036	99.0	3.0	0.128
Model+corLin	**202.2**	**0.0**	**0.245**	**---**	**---**	**---**	**---**	**---**	**---**
Model+corGaus	202.7	0.8	0.168	214.3	0.9	0.259	**96.0**	**0.0**	**0.569**
				Oxygen					
Model	396.0	2.3	0.072	325.2	64.8	<0.001	115.6	11.8	<0.001
Model+corRatio	393.7	4.7	0.232	260.5	0.2	0.414	**103.8**	**0.0**	**0.354**
Model+corExp	393.7	4.7	0.232	262.9	2.5	0.128	104.1	0.3	0.299
Model+corSpher	**393.7**	**4.7**	**0.232**	269.8	9.4	0.004	121.6	17.8	<0.001
Model+corLin	---	---	---	---	---	---	---	---	---
Model+corGaus	393.7	4.7	0.232	**260.4**	**0.0**	**0.453**	103.8	0.0	0.346
				Conductivity					
Model	335.2	85.5	<0.001	467.0	106.0	<0.001	133.8	25.6	<0.001
Model+corRatio	250.2	0.5	0.254	361.1	0.4	0.231	109.1	0.9	0.172
Model+corExp	251.6	1.9	0.125	360.9	0.2	0.254	108.7	0.5	0.207
Model+corSpher	250.2	0.5	0.250	361.1	0.4	0.233	**108.2**	**0.0**	**0.265**
Model+corLin	253.4	3.7	0.049	---	---	---	108.7	0.4	0.213
Model+corGaus	**249.7**	**0.0**	**0.320**	**360.7**	**0.0**	**0.283**	110.4	0.8	0.155

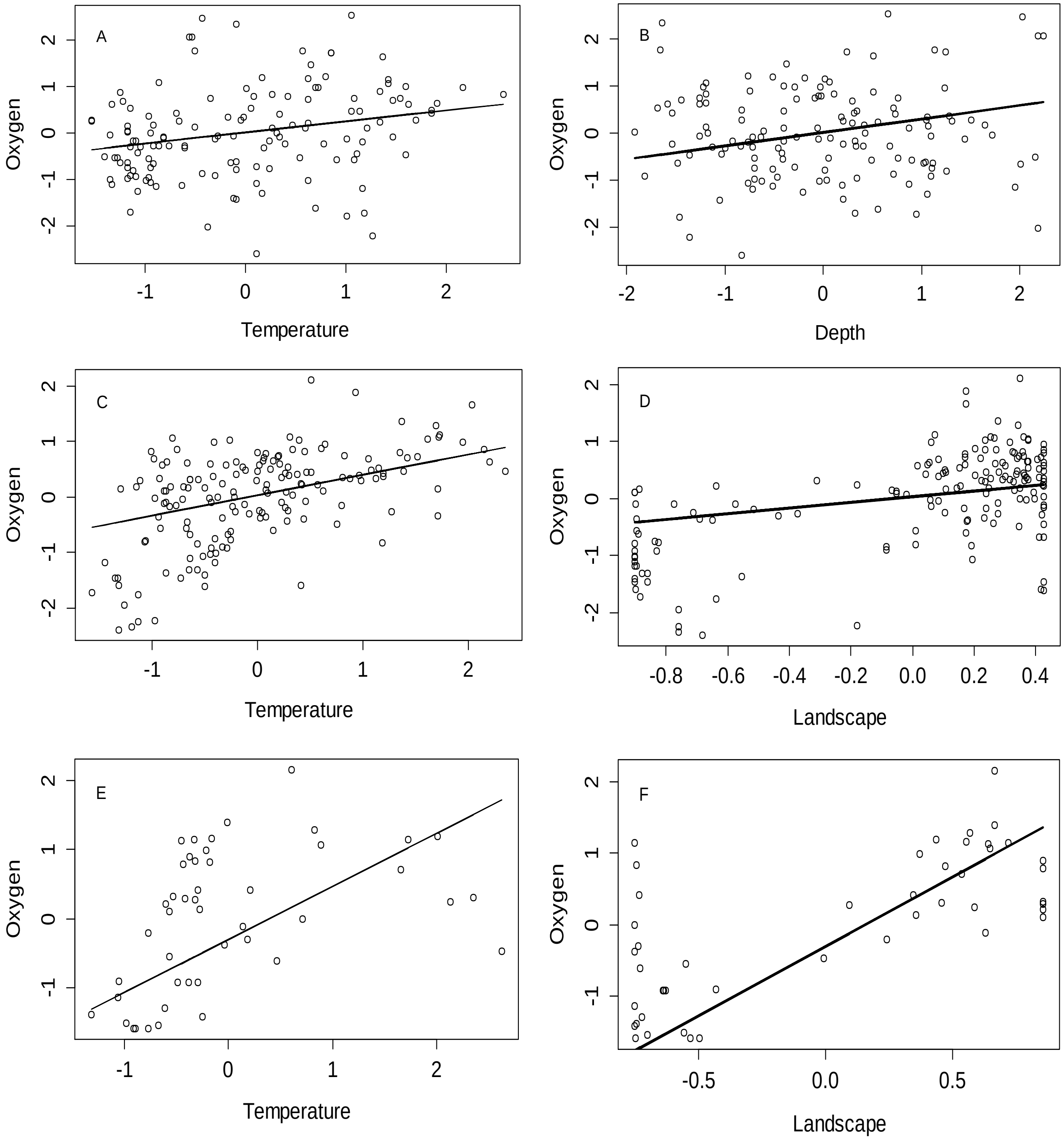
pH									
Model	257.0	21.3	<0.001	481.3	47.1	<0.001	106.6	13.6	<0.001
Model+corRatio	235.8	0.1	0.345	434.7	0.4	0.314	94.7	1.0	0.225
Model+corExp	236.2	0.5	0.288	**434.3**	**0.0**	**0.375**	95.5	1.9	0.146
Model+corSpher	261.7	26.0	<0.001	439.3	5.1	0.030	94.4	0.8	0.253
Model+corLin	261.7	26.0	<0.001	439.3	5.1	0.030	---	---	---
Model+corGaus	**235.7**	**0.0**	**0.368**	435.0	0.7	0.260	**93.6**	**0.0**	**0.375**

--- The model not converge

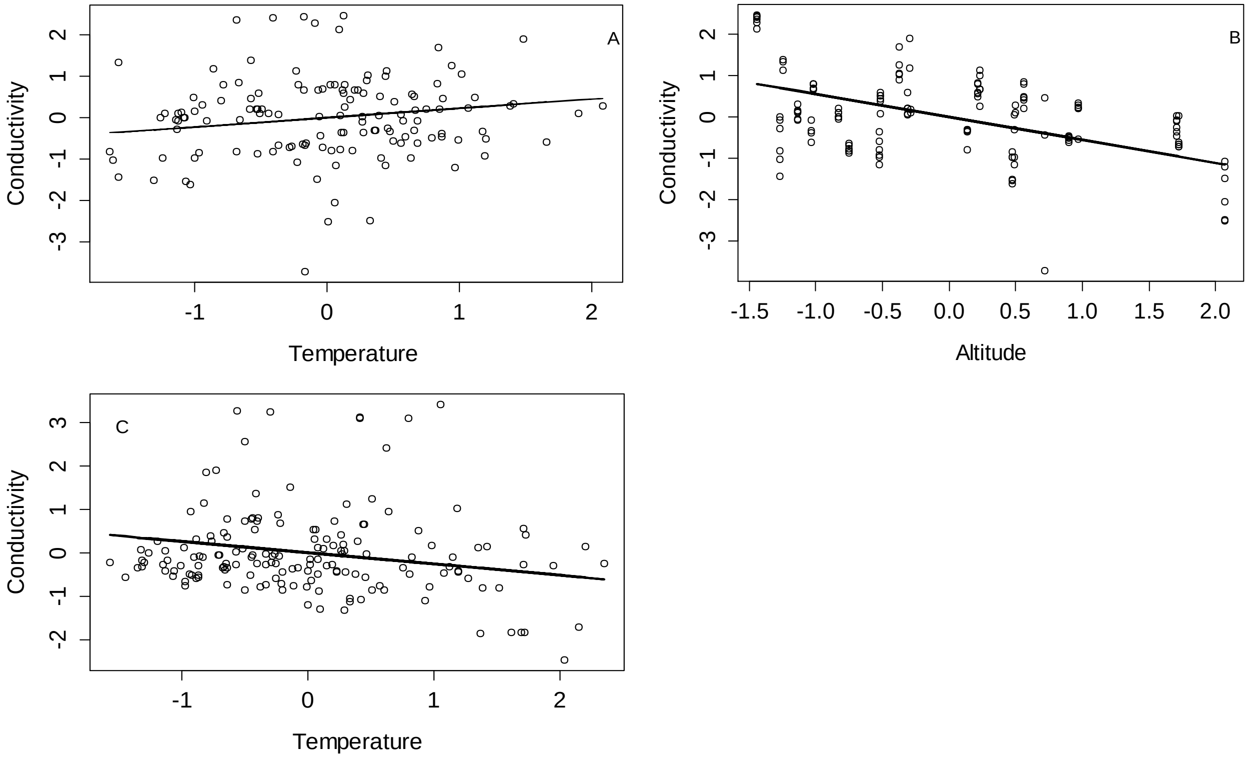
Appendix F - Relationship between temperature and exploratory variable for rising, flood and receding period. Figures A and B show the relationship of the oxygen with depth and landscape in the rising period. C showing the relationship of the temperature with depth in flood period while D, showing the relationship of the temperature with depth in receding period. The variables are presented without measurement units because the variables were standardized using *z-scores* transformation (Legendre & Legendre 1998).



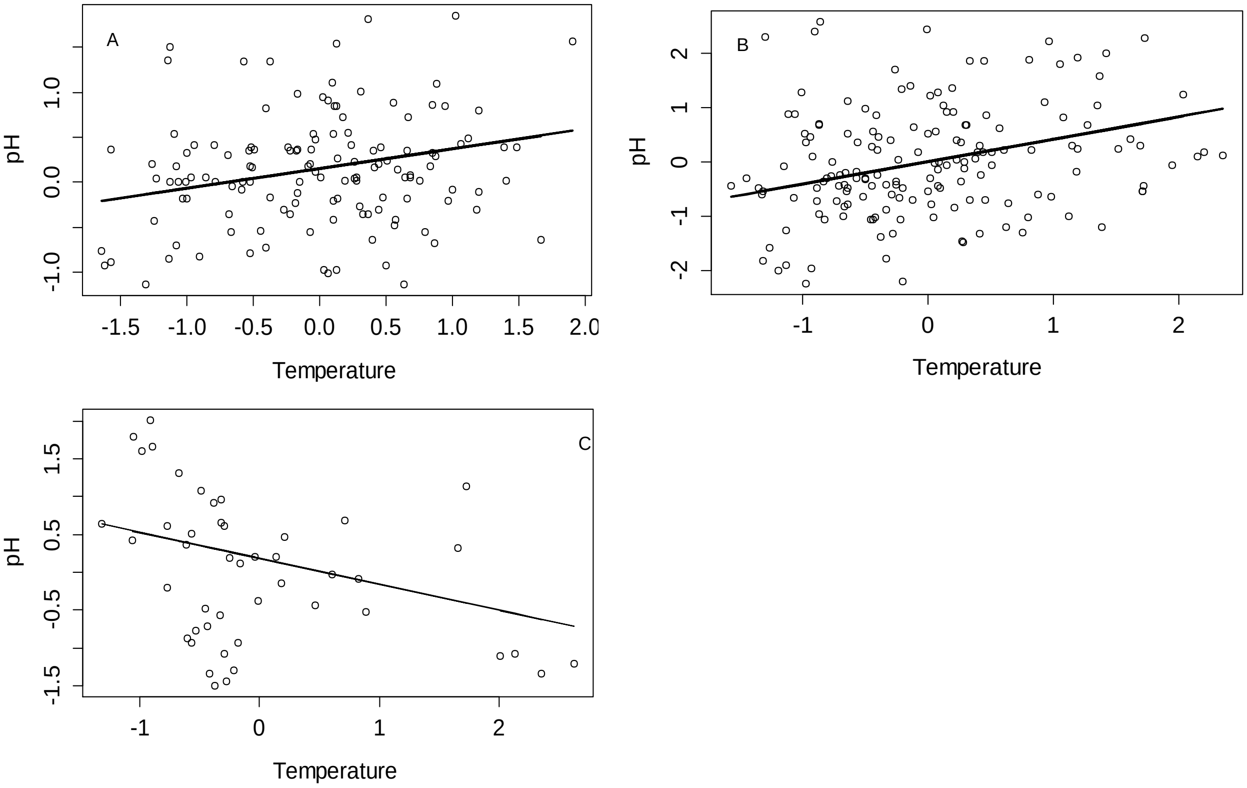
Appendix G - Relationship between oxygen and exploratory variable for rising, flood and receding period. Figures A and B show the relationship of the oxygen with temperature and depth in the rising period. C and D show the relationship of the oxygen with temperature and landscape in the flood period, while E, F and G, show the relationship of the oxygen with temperature, landscape and organic matter content in soil. The variables are presented without measurement units because the variables were standardized using *z-scores* transformation (Legendre & Legendre 1998).



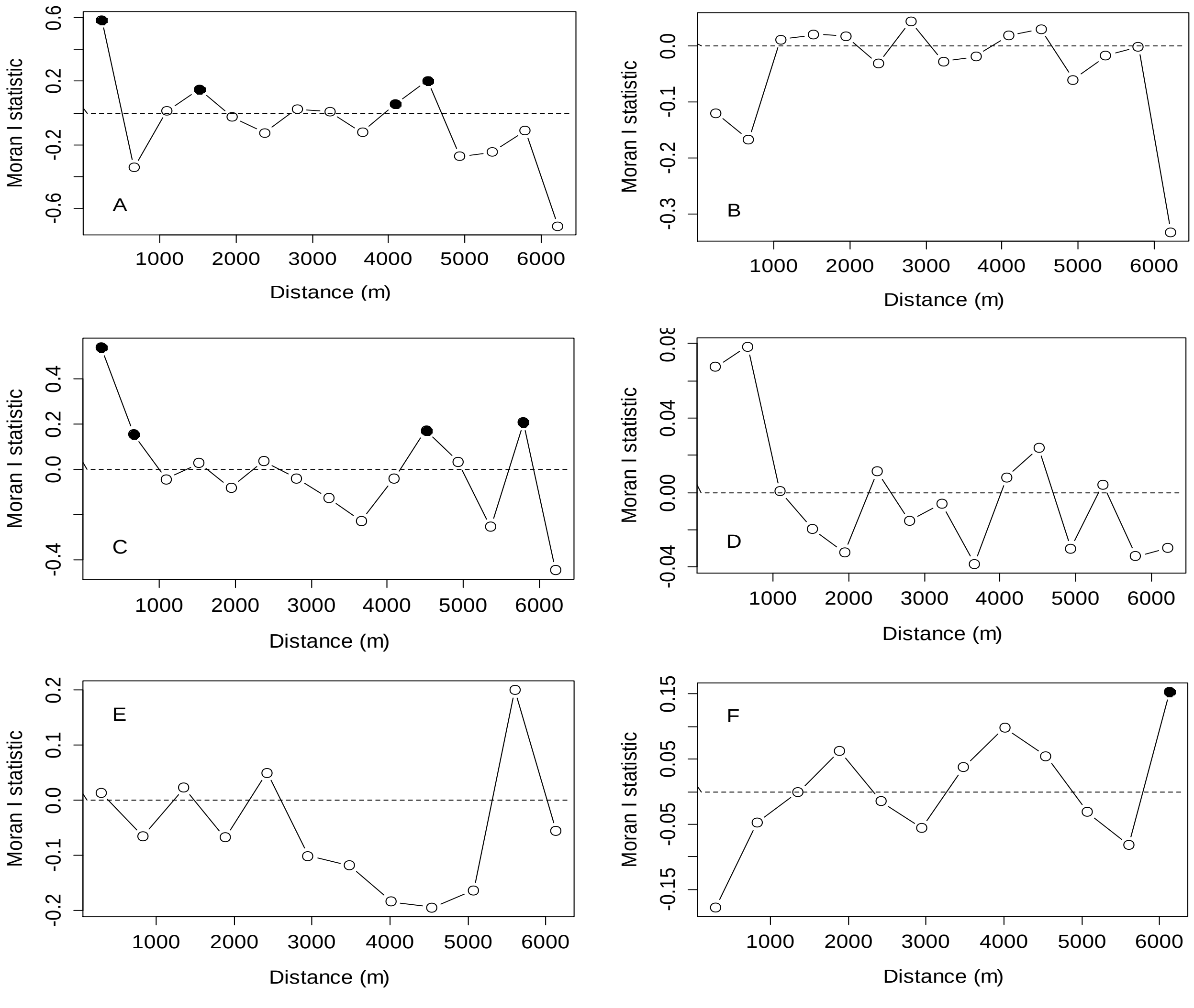
Appendix H - Relationship between conductivity and exploratory variables that showed relationship significant in generalized least squares (GLS) for rising (A and B) and flood (B) period. In receding period conductivity not showed relationship with environmental variables. The variables are presented without measurement units because the variables were standardized using *z-scores* transformation (Legendre & Legendre 1998).



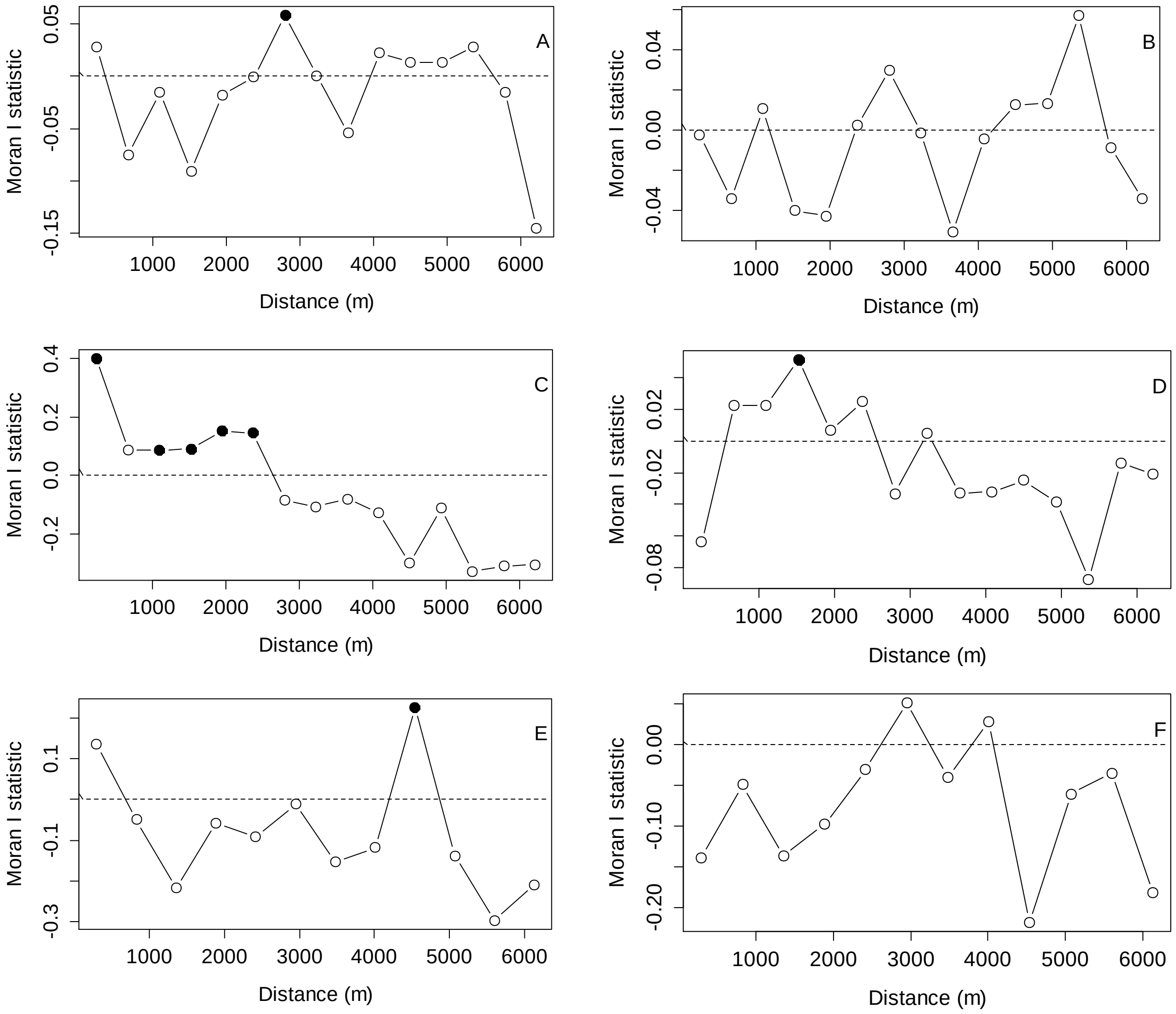
Appendix I - Relationship between pH and temperature for rising (A), flood (B) and receding period. Only temperature showed significant relationship with pH. The variables are presented without measurement units because the variables were standardized using *z-scores* transformation (Legendre & Legendre 1998).



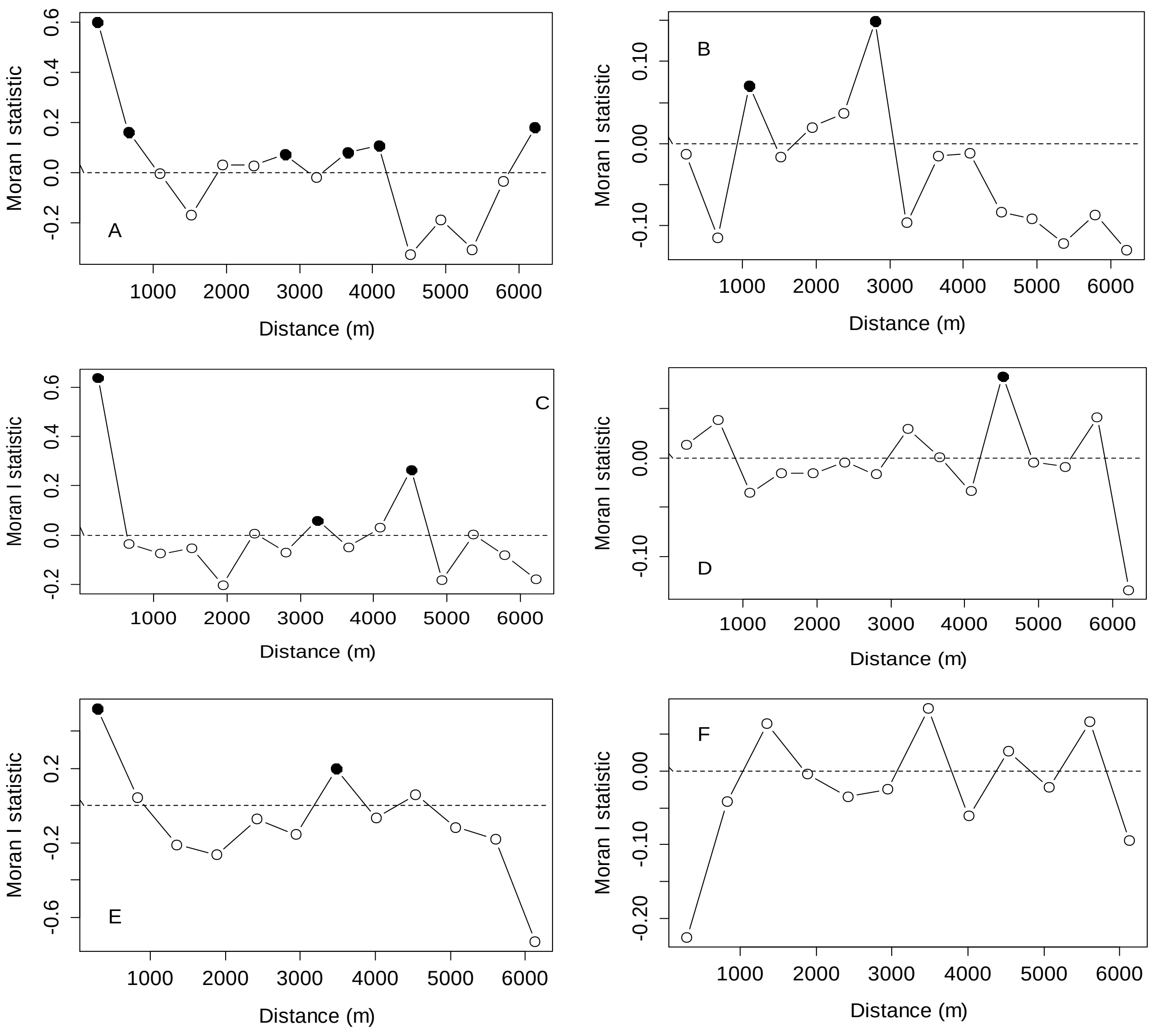
Appendix J - Moran's I Correlograms for temperature in rising, flood and receding periods. A and B are correlograms for the rising period without (A) and with (B) spatial correlation structure. C and D are correlograms for flood period without (C) and with (D) spatial correlation structure, and E and F are correlograms for receding period without (E) and with (F) spatial correlation structure. Closed symbols indicate significant Moran's I coefficient (at a significance level of $p<0.05$, after Bonferroni correction; see Olden, 1984)



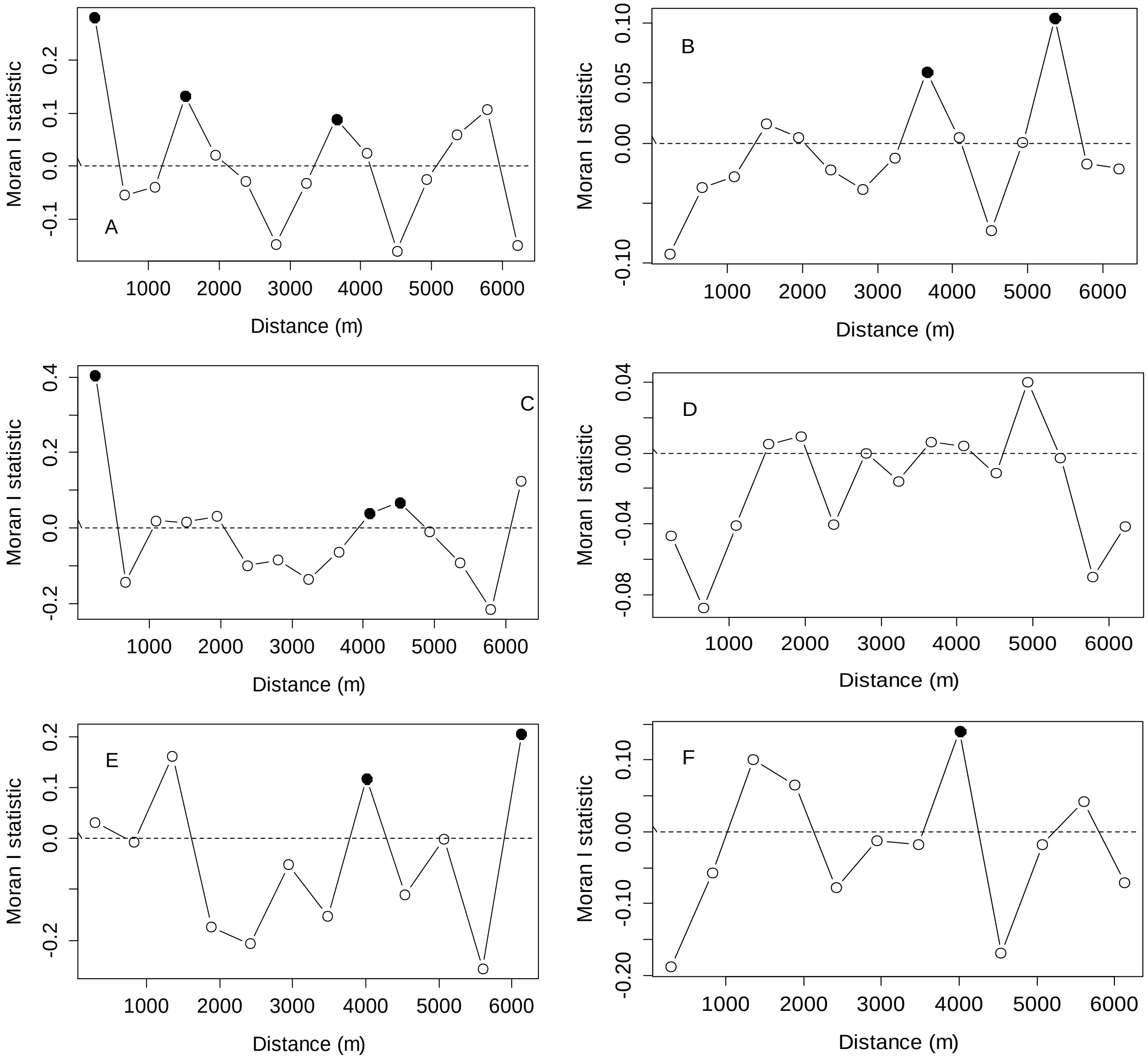
Appendix K - Moran's I Correlograms for oxygen in rising, flood and receding period. A and B are correlograms for model without (A) and with (B) spatial correlation structure for rising period. C and D are correlograms for flood period without (C) and with (D) spatial correlation structure. E and F are correlograms for receding period without (E) and with (F) spatial correlation structure. Closed symbols indicate significant Moran's I coefficient (at a significance level of $p<0.05$, after Bonferroni correction; see Olden, 1984)



Appendix L - Moran's I Correlograms of for conductivity in rising, flood and receding period. A and B are correlograms for rising period without (A) and with (B) spatial correlation structure. C and D are correlograms for flood period without (C) and with (D) spatial correlation structure, and E and F are correlograms for receding period without (E) and with (F) spatial correlation structure. Closed symbols indicate significant Moran's I coefficient (at a significance level of $p<0.05$, after Bonferroni correction; see Olden, 1984)



Appendix M - Moran’s I Correlograms of for pH in rising, flood and receding period. A and B are correlograms for rising period without (A) and with (B) spatial correlation structure. C and D are correlograms for flood period without (C) and with (D) spatial correlation structure. E and F are correlograms for receding period without (E) and with (F) spatial correlation structure. Closed symbols indicate significant Moran’s I coefficient (at a significance level of $p<0.05$, after Bonferroni correction; see Olden, 1984)



Appendix N - Variation partition for temperature, oxygen, conductivity and pH in rising, flood and receding period. OD, oxygen; CD, conductivity; PH, ph; R, rising; F, flood; E, receding. [E] purely environmental component , [E+S] component representing spatially structured environmental variation, [S] purely spatial component and [R] the residual fraction of variation not explained by spatial or environmental factors.

Response variable	Environmental factors	Spatial predictors	Variation components			
			E	E+S	S	R
Temp (R)	Depth, landscape	22, 4, 1, 8, 5, 12, 7, 8	0.12**	0.25	0.13**	0.50
Temp (F)	Depth	6, 21, 5, 7, 9, 10, 16, 4, 14, 19, 17, 1, 24, 8	0.14**	0.37	0.24**	0.25
Temp (E)	Depth	3	0.23**	0.01	0.06**	0.7
OD (R)	Temperature, depth	4,17	0.11**	0.01	0.04*	0.84
OD (F)	Temperature, landscape	7, 5, 21, 6, 26, 4, 14, 18, 8, 20, 9	0.06**	0.39	0.12**	0.43
OD (E)	Temperature, landscape	3, 4	0.40**	0.16	0.05*	0.39
CD (R)	Altitude, temperature	10, 20, 9, 13, 11, 3, 26, 2	0.29**	0.00	0.45**	0.26
CD (F)	Temperature	14, 9, 11, 2, 12, 5, 13, 28, 16, 16	0.02**	0.00	0.58**	0.40
CD (E)	---	4	---	---	0.15**	0.85
PH (R)	Temperature	30, 19, 3, 8, 9, 2, 4	0.01†	0.02	0.38**	0.59
PH (F)	Temperature	18, 26, 7, 34, 3, 6, 20	0.07**	0.00	0.25**	0.68
PH (E)	Temperature	---	0.12*	---	---	0.88

† non significant * P<0.05 ** P<0.01 --- Not had variable with significant relationship.

References

Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. Aust. Ecol. 26,32–46.

Boyd, C.E., Romaire, R. P., Johnson, E,. 1978. Predicting early morning dissolved oxygen concentration in channel catfish ponds. Trans. Am. Fish. Sot. 107(3), 484-492.

Chang, W. Y. B., Ouyang, H., 1988. Dynamics of dissolved oxygen and vertical circulation in fish ponds. Aquaculture 74, 263-276.

Erez, J., Krom, M. D., Neuwirth, T., 1990. Daily oxygen variations in marine fish ponds, Elat, Israel. Aquaculture 84, 289–305.

Hastie, T. J., Tibshirani, R.J., 1986. Generalized additive models. Stat. Sci. 1, 297-318

Hurvich, C. M., Tsai, C. L., 1989. Regression and time series model selection in small samples. Biometrika 76,297–307.

Jackson, D. A., 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. Ecology 74, 2204–2214

Lehman, A., 1998. GIS modeling of submerged macrophyte distribution using Generalized Additive Model. Plant. Ecology 139, 113–124.

Olden, N.L., 1984. Assessing the significance of a spatial correlogram. Geog. Anal. 16,1–16.

Schroeder, G.L., 1975. Nighttime material balance for oxygen in fish ponds receiving organicwastes. Bamidgeh 27, 65-74.

Yee, T. W., Mitchell, N. D. 1991. Generalized additive models in plant ecology. J. Veg. Scien. 2, 587–602.

Capitulo III

Appendix 1: Detailed sampling procedure of fish species and environmental variables

Plot sampling

Plots were sampled monthly during the flood season in 2009, between January and July and once in March on the years of 2008, 2010 and 2011. Due to variability in the duration and amplitude of flood, the number of the plots sampled in each month from 2009 varied: 17 plots for January, 20 to February, 21 plots for March and April, 10 plots in May, three plots in June and two in July. The number of plots flooded in March 2008, 2010 and 2011 were 23, 18 and 22 respectively.

Fish were collected using two methods: throw traps and gill nets. A throw trap consist of a cubic metal structure ($1m^3$) with the four sides covered by a 1.5 mm nylon mesh and was employed six times along the strip-like plot at every 50 meters (from 0 m up until 250 m). Individuals captured in this trap were collected with the aid of a triangular fish trap that was used until no additional fish specimen was revealed after 10 consecutive sweeps. Moreover, seven gill nets (20.0 x 1.5m) were distributed (mesh size of 12, 15, 18, 20, 25, 30 and 50 mm between opposite knots) along each plot between 1600 and 1700 hours and removed the following day between 0800 and 0900 hours, remaining exposed for about 16 hours. Each technique was used on a different day, so that they did not interfere with one another. The combination of active and passive sampling methods allowed the capture of both mobile and sedentary species as well as individuals from different size classes (Lapointe et al. 2006). Individuals captured were euthanized with Eugenol, fixed in 10% formalin solution and preserved in 70% ethanol and were identified to the species level.

Environmental variables

Elevation data was acquired with geodetic Global Position System (GPS) with simple frequency, adopting minimal time tracking of 10 minutes or maximum error of 50 mm. As each plot has approximately the same topographical elevation along its length, only one measure was enough to represent the entire plot. Water depth was measured using a measuring tape fixed to a pole and the patch depth was represented by the average value of six measurements performed across them, one at each location where the throw trap was launched. Patch age was estimated as the number of days a patch has been inundated, starting from the first sampling date.

Information on the vegetation cover was extracted from Google Earth^{TM} and transformed into a raster grid. Based in the vegetal structure and inundation, six types of vegetation cover were identified: wet grassland, wet forest, wet pasture, wet grassland with pasture, dry forest and dry pasture. While grassland and pasture include mainly grasses and aquatic macrophytes (submerged, emergent and floating), forest are composed by shrubs and trees without undergrowth. The percentage of each vegetation type was measured using 450 m circular buffer around the center of each plot.

Vegetation cover types were highly correlated among each other, thus we applied a principal components analysis (PCA) to reduce the dimensionality of the data. Two axes were extracted (using the broken stick model, Jackson et al. 1993) and accounted for 61.8% of the variation in vegetation data. The first axis was positively related to wet grasslands, dry forests and negatively related to dry and wet pastures while the second axis was positively correlated with wet forests and presented a negative relationship with wet grassland-pastures (Table S1).

Table S1 - Coefficients and p-values for the correlation between the first and second axis of the PCA and different types of the vegetation cover.

Vegetal cover	PCA1 (36.9%)		PCA2 (24.9%)	
	r	p	r	p
Wet grassland	0.80	<0.001	-0.35	0.095
Dry forest	0.70	<0.001	-0.29	0.170
Dry pasture	-0.62	0.001	-0.27	0.211
Wet forest	-0.007	0.972	0.89	<0.001
Wet grassland with pasture	-0.05	0.800	-0.62	0.001
Wet pasture	-0.83	<0.001	-0.07	0.740

References not found in the main text

Jackson, D.A., 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. – Ecology 74: 2204–2214.

Lapointe, N. W. R., Corkum, L. D. and Mandrak, N. E. 2006. A comparison of methods for sampling fish diversity in shallow offshore waters of large rivers. – North American Journal of Fisheries Management 26: 503-513.

Appendix 2: Analysis of Metacommunity Structure

The EMS algorithm analyzes the metacommunity structure using an incidence matrix (presence-absence data), which is first ordinated via a correspondence analysis (CA). Each CA axis is a gradient construct describing patterns of variation across species and sites within metacommunities by maximizing the positioning of sites along axes based on the degree to which their communities share species compositions and the positioning of species sharing similar ranges (Leibold and Mikkelson 2002). For each month (i.e. each incidence matrix), species and sites were ranked according to their position along the primary CA axis (i.e., the one that summarizes most of the variation in the incidence matrix). The EMS framework is based on three statistics, namely coherence, turnover and boundary clumping. By assessing the significance of these statistics and their values, we can determine in a hierarchical manner which metacommunity pattern (checkerboard, nestedness, Clementsian gradients, Gleasonian gradients, evenly-spaced gradients and random) best describes the major pattern of species variation (i.e., first CA axis). Here, significance of each statistics was assessed via a null model that permutes species across sites 1000 times within the incidence matrix while maintaining site richness, which has been shown to have acceptable levels of Type I error (Gotelli and Graves 1996, Presley et al. 2009). Each permuted matrix is ordinated via correspondence analysis, which is in turn used to calculate the values of the three elements for the random incidence matrices. P-values were calculated to assess how extreme the observed value was among the random values and for each of the three statistics, significance was assessed on the basis of an $\alpha = 0.05$.

Coherence was evaluated by counting the number of embedded absences in all species ranges and community compositions for each month (see Fig. 1 in Henriques-Silva et al. 2013 for more details). Significant negative coherence (i.e. more embedded absences than the null distribution) indicates that a checkerboard distribution (Diamond 1975) is the pattern that best fits the data. If coherence is non-significant, then the metacommunity is randomly structured regarding the gradient analyzed (Leibold and Mikkelson 2002). Finally, a significantly positive coherence (i.e. less embedded absences than the null distribution) suggests that species are distributed according to the same gradient (Leibold and Mikkelson 2002), which is further differentiated by evaluating the species range turnover and boundary clumping. Note that these two elements were analyzed using the species perspective, which contrasts turnover and boundary clumping among species ranges rather than community compositions (see Presley et al. 2009 for a discussion on this matter). Turnover is calculated by counting the number of replacements (i.e. the number of times a species replace another at the edge of their ranges; see Fig 1 in Henriques-Silva et al. 2013 and Presley et al. 2010 for further details on rationale). The observed number of replacements is then compared to the ones generated by each null metacommunity. A lower number of observed replacements (i.e. negative range turnover) suggests that nestedness (Patterson and Atmar 1986) characterizes the metacommunity structure whereas if the observed metacommunity exhibits a higher number of replacements (i.e. positive turnover across species ranges) the data is further contrasted to range boundary clumping. Note that if range turnover is not significant the metacommunity will exhibit quasi structures (e.g. quasi-nested, quasi-Gleasonian, quasi-Clementsian and quasi-evenly-spaced; *sensu* Presley et al. 2010). These quasi-structures have the same characteristics as their associated idealized structures but with weaker structuring processes (see Presley et al. 2010 for a discussion). This last element is tested using the Morisita's Index which has an expected value of 1. If the observed index is not significantly different than 1, range boundaries are randomly distributed, indicating a Gleasonian gradient. Conversely, if the observed value is significantly higher or lower than 1, it shows that the species range boundaries are clumped or overdispersed as in a Clementsian or Evenly-spaced distributions, respectively (Leibold and Mikkelson 2002). We highlight that nested metacommunities may exhibit clumped, stochastic or hyperdispersed species loss among sites, which are analogous to Clementsian, Gleasonian and evenly-spaced gradients with the difference that these patterns of range dispersion are found only at one side of the distributional gradient (see Presley et al. 2010 for further details). Gleasonian and Clementsian structures differ regarding the response of species to the major gradient of variation defined by the CA: in the former the species respond independently from one another whereas in the latter groups of species respond similarly (Leibold and Mikkelson 2002). Finally, evenly-spaced gradient suggests that species exhibit a trade-off between environmental tolerance and competitive ability along the gradient of variation (Tilman 1982). Significance for the observed Morisita index is evaluated using a Chi-squared goodness-of-fit test that compare the observed distribution to an expected distribution of range boundary locations (Presley et al. 2009).

References not found in the main text

Diamond, J. M. 1975. Assembly of species communities *in*. Ecology and evolution of communities (eds Cody, M. L, & Diamond, J. M.). Belknap Press of Harvard University Press, pp. 203-209.

Gotelli, N. J. and Graves, G. R. 1996. Null Models in Ecology. — Smithsonian Institution Press.

Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. — Biological Journal of the Linnean Society 28: 65-82.

Tilman, D. 1982. Resource competition and community structure. — Princeton Univ. Press.

Appendix 3: List of species with codes (from Fig. 2) and regional abundances across the four sampling periods in 2009.

Species	Family	Code	January	February	March	April
Acestrorhynchus pantaneiro	Acestrorhynchidae	1	0	7	4	2
Aequidens plagiozonatus	Cichlidae	2	0	0	1	4
Anadoras weddellii	Doradidae	3	18	21	2	2
Aphyocharax anistsi	Characidae	4	1	1	20	49
Aphyocharax paraguayensis	Characidae	5	0	0	0	9
Apistogramma borellii	Cichlidae	6	0	0	0	1
Astyanax asuncionensis	Characidae	7	0	3	7	6
Brachyhypopomus spB	Hypopomidae	8	0	0	0	1
Bujurquina vittata	Cichlidae	9	3	8	0	3
Callichtys callichtys	Callichthyidae	10	0	9	1	0
Chaetobranchopsis australis	Cichlidae	11	0	0	1	2
Characidium aff. *Zebra*	Crenuchidae	12	0	0	1	1
Cichlasoma dimerus	Cichlidae	13	5	17	48	168
Corydoras aeneus	Callichthyidae	14	17	24	5	3
Corydoras hastatus	Callichthyidae	15	3	14	47	36
Corydoras latus	Callichthyidae	16	1	0	0	0
Crenicichla lepidota	Cichlidae	17	0	0	0	15
Cyphocharax gillii	Curimatidae	18	1	0	1	20
Gymnocorymbus ternetzi	Characidae	19	1	2	3	8
Gymnogeophagus balzanii	Cichlidae	20	0	0	1	1
Gymnotus carapo	Gymnotidae	21	0	0	1	0
Hemigrammus tridens	Characidae	22	9	23	37	195
Hoplerythrinus unitaniatus	Erythrinidae	23	26	36	64	108

Hoplias malabaricus	Erythrinidae	24	10	30	56	63
Hoplosternum littorale	Callichthyidae	25	62	67	108	79
Hyphessobrycon elachys	Characidae	26	0	1	5	41
Hyphessobrycon eques	Characidae	27	0	0	1	0
Laetacara dorsigera	Cichlidae	28	2	0	0	16
Leporinus lacustris	Anostomidae	29	0	3	9	26
Lepthoplosternum pectoralle	Callichthyidae	30	1	10	11	12
Loricariichthys platymetopon	Loricariidae	31	0	0	1	1
Markiana nigripinnis	Characidae	32	26	9	11	9
Megalechis personata	Callichthyidae	33	25	28	9	14
Megalechis picta	Callichthyidae	34	0	0	0	1
Megalechis thoracata	Callichthyidae	35	0	3	0	0
Merodoras nheco	Doradidae	36	5	7	4	3
Metynnis mola	Characidae	37	0	1	0	2
Moema heterostigma	Rivulidae	38	2	0	0	0
Moenkhausia bonita	Characidae	39	0	1	1	5
Moenkhausia sanctaefilomenae	Characidae	40	0	0	0	1
Neofundulus parvipinnis	Rivulidae	41	32	17	11	3
Parauchenipterus striatulus	Auchenipteridae	42	0	1	3	1
Phenacogaster tegatus	Characidae	43	0	0	0	1
Plesiolebias glaucopterus	Rivulidae	44	39	119	49	39
Poptella paraguayensis	Characidae	45	0	0	1	3
Pyrrhulina australis	Lebiasinidae	46	0	0	0	10
Rhamdia quelen	Heptapteridae	47	1	3	3	2
Roeboides sp.	Characidae	48	0	0	1	0
Satanoperca pappaterra	Cichlidae	49	0	0	0	1

Serrapinnus spp.	Characidae	50	2	47	214	612
Serrasalmus maculatus	Serrasalmidae	51	0	0	4	3
Serrasalmus marginatus	Serrasalmidae	52	0	0	1	0
Steindachnerina conspersa	Characidae	53	0	0	1	1
Stenolebias damascenoi	Rivulidae	54	145	87	52	20
Synbranchus marmoratus	Synbranchidae	55	0	1	10	11
Trachelyopterus coriaceus	Auchenipteridae	56	16	16	4	4
Trigonectes balzannii	Rivulidae	57	0	4	4	8
Triportheus nematurus	Characidae	58	7	3	6	5