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Interações ecológicas entre a macrófita invasora lírio-do-brejo (*Hedychium coronarium* – J. Köenig, 1783) e macroinvertebrados aquáticos de zona litoral: implicações na estruturação comunitária e herbivoria.

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“A seleção natural procura a cada dia, momento e, em todo o lugar, as mais tênues variações, rejeitando as nocivas, conservando e ampliando todas as que forem uteis, trabalhando silenciosa e imperceptivelmente, quando e onde quer que se ofereça a oportunidade, pelo aperfeiçoamento de cada ser vivo com relação a suas condições de vida orgânica e inorgânica.”

Charles Darwin

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Resumo

A interferência antrópica é o processo chave da disseminação de diversas espécies invasoras, as quais estão entre as principais causas do declínio da biodiversidade. Macrófitas aquáticas invasoras podem alterar a estrutura das comunidades associadas e processos ecológicos. Através dos trabalhos realizados no reservatório do Fazzari (Universidade Federal de São Carlos) foram analisados os possíveis impactos da espécie vegetal invasora lírio do brejo (*Hedychium coronarium*) sobre a diversidade taxonômica e funcional da comunidade de macroinvertebrados aquáticos presentes na zona litoral. No Capítulo I e II são explorados os aspectos de alterações de habitat e suas implicações para sua função de habitat para comunidade de insetos aquáticos. Já nos Capítulos III e IV, são exploradas as questões de qualidade de recurso alimentar para a macrofauna. Nestes últimos, pretendeu-se analisar as implicações das mudanças na composição taxonômica e funcional dos herbívoros bem como sua importância na estrutura das redes tróficas da comunidade em geral. O principal impacto da macrófita invasora lírio-do-brejo sobre a estrutura taxonômica e funcional da comunidade de macroinvertebrados aquáticos, provavelmente esteve relacionado à alteração de habitat promovida pela sua rápida propagação. Através da menor diversidade funcional e das características de expressiva participação de larvas predadoras observadas na margem invadida pelo lírio do brejo, é possível inferir que a macrófita invasora poderia promover maior complexidade de habitat. Sendo assim, sua presença nas zonas litorais de ecossistema lêntico parece desempenhar uma importante influência na estruturação comunidade de insetos aquáticos. Quanto ao seu aspecto como recurso alóctone, pode-se afirmar que suas folhas demonstraram melhor qualidade de recurso alimentar para a macrofauna quando comparada a espécie nativa (*Pontederia cordata*). Esta característica demonstrou ser um importante fator na colonização de herbívoros generalistas. A baixa qualidade nutricional da espécie nativa influenciou na colonização de herbívoros especialistas, resultando numa comunidade mais dissimilar. Ambas as espécies de macrófitas pareçam sustentar uma estrutura comunitária de macroinvertebrados similar, composta principalmente por táxons onívoros. Entretanto, a composição química das folhas, em especial, baixa concentração de nitrogênio, altas concentrações de polifenóis, celulose e lignina da espécie nativa teve uma influência negativa na riqueza de traços funcionais dos herbívoros e redução da relação predador-presa, indicando um efeito “bottom-up”. Os resultados destacaram a importância da seleção de espécies nativas com alto valor nutritivo na utilização de programas de restauração para a conservação da biodiversidade dos ecossistemas de água doce.

ABSTRACT

Biological invasions are the main cause of biodiversity erosion, which is widespread in several invasive species that have antropogenic interference as a key process. Invasive macrophyte species can shift structures of associated communities, and they can interfere in many ecological process in aquatic ecosystems. For these issues, macroinvertebrate taxonomic and functional analyses can show the ecological alteration processes that occur between macrofauna and these plant species. Through the surveys performed at the Fazzari reservoir (Universidade Federal de São Carlos), the potential impact of the invasive macrophyte white ginger lily (*Hedychium coronarium* - J. Koenig, 1783) on the taxonomic and functional diversity of freshwater macroinvertebrates dwelling the littoral zone of the reservoir was assessed. In chapters I and II of this doctoral thesis, habitat alterations caused by the white ginger lily are explored and its effect on the role of the habitat in aquatic insect assemblages is discussed. Chapters III and IV explore aspects of the resource quality of white ginger lily on associated macroinvertebrates. The final experiment also assess the implication of the resource quality provided by white ginger lily in the taxonomic and functional changes of herbivore species and their effect on macroinvertebrate food webs. The main impact of this invasive macrophyte species on the functional and structure assemblage of macroinvertebrates was related to habitat alterations caused because of white ginger lily's faster vegetative growth. Its presence in the littoral zone seemed to show an important influence on the aquatic insect structure assemblages as well as on habitat losses. Through lower functional diversity indices and significant participation of predator larvae in the invaded reservoir banks, it was possible to infer that this invasive macrophyte promoted higher habitat complexity and lower band loss in the littoral zone. For its allochthonous resource quality aspects, its leaves demonstrated better quality when compared with the native pickerelweed (*Pontederia cordata* – L.), which presents similar ecological characteristics. The higher quality resource of this invasive macrophyte was shown to be an important factor to generalist herbivore species, which differed in taxonomic composition of specialist herbivore species present in the native macrophyte leaves. Although invasive and native macrophyte species seemed to support similar macroinvertebrates structures, which were composed mainly of omnivore species, pickerelweed leaves, which are of lower nutritional quality, were shown to be unfavorable to the herbivore species. The leaf chemical traits of the native species, such as lower N% and higher P% and polyphenols, negatively influenced the herbivore functional richness, as well as caused a decrease in predator-prey rations in the food web structure. This indicated a bottom-up effect. The results suggest that the role of macrophytes in the habitat and resource quality provided by macrophyte leaf species has an important influence on the life history of macroinvertebrates and freshwater herbivores, which in turn directly interfere with changes in the entire macroinvertebrate structure. Additionally, the results highlight the importance of selecting native species with a high resource quality in restoration practices for freshwater biodiversity conservation.

1 INTRODUÇÃO

1.1 Biodiversidade e conservação dos ecossistemas lênticos

A superfície da Terra é constituída por 70% de água, das quais menos de 1% são referentes à água doce. Embora represente uma parcela muito pequena da cobertura da superfície do planeta, essa se destaca por abrigar numerosas espécies animais e vegetais (≈ 100.000 spp), representando 6% da diversidade mundial. Devido a superexploração dos recursos hídricos no uso de atividades antrópicas (agricultura, navegação, pescas, abastecimento humano, produção de energia elétrica), os ecossistemas de água doce se encontram em situação de declínio da biodiversidade. As ameaças à biodiversidade nesses ecossistemas podem ser divididas em cinco categorias: superexploração, poluição, modificação do fluxo d'água, destruição ou degradação de habitats e invasões biológicas. A combinação destes fatores geram graves consequências negativas, causando modificações no equilíbrio das comunidades. Tal situação se apresenta num processo considerado mais acelerado do que nos ecossistemas terrestres. Como essas atividades já existem em escala global, o estabelecimento de estratégias para conservação dos ecossistemas de água doce foi considerado de primordial importância durante a conferência internacional "Water for life - Decade for Action" (2005-2015), para sua proteção e manutenção da sua sustentabilidade (DUDGEON et al., 2006).

Os ecossistemas lênticos são ambientes que apresentam baixo fluxo, variam em sua forma e profundidade e incluem lagos, lagoas, áreas alagadas, açudes e represas. Estes se originaram através das modificações geológicas causadas por eventos naturais, como erosão, mudanças glaciais, atividades vulcânicas e, mas também, por intervenção antrópica. No entanto, em decorrência de eventos naturais e também da intervenção antrópica na modificação da estrutura geológica da paisagem, tem-se observado o surgimento de reservatórios naturais e/ou artificiais de água doce. Esses ecossistemas apresentam distintas zonas biológicas que se diferenciam num gradiente de profundidade em relação à distância das margens. Destas se destaca a zona litoral que se localiza próximo às margens, a qual pode ser considerada um ecótono, pois se caracteriza como área de transição entre o ambiente terrestre e aquático (ODUM, 1988). Nesta zona há maior penetração de luz que resulta numa alta produtividade primária, que por sua vez proporciona elevada diversidade de organismos, entre os quais se destacam os macroinvertebrados aquáticos, os peixes e as macrófitas aquáticas.

1.2 O papel ecológico das macrófitas aquáticas nos ecossistemas lênticos

As macrófitas aquáticas estão entre as comunidades bióticas mais diversificadas dos ecossistemas lênticos. Estas possuem características morfológicas que as separam em diferentes formas de vida: emergentes (enraizadas no sedimento, ou em solos alagados, com folhas voltadas para a parte aérea), flutuantes (enraizadas no sedimento, com as folhas flutuando na superfície da água), livre flutuantes (que flutuam na superfície da água sem enraizamento no sedimento) e submersas (plantas que crescem completamente submersas na coluna d'água enraizadas ao substrato) (CHAMBERS et al., 2008). Essas características morfológicas possibilitam a ampla distribuição dessas plantas entre os vários compartimentos da zona litoral, os quais podem ser limitados por fatores ambientais, como tipo de sedimento, luminosidade, turbidez, disponibilidade de nutrientes e ação de herbívoros (CARLSSON et al., 2005; MIDDELBOE; MARKAGER, 1997; CARREIRA et al., 2014).

Entre os diferentes papéis ecológicos das macrófitas na estruturação dos ecossistemas lênticos destaca-se sua atuação na retenção de detrito promovendo maior estabilidade do sedimento do fundo (TRIVINHO-STRIXINO; STRIXINO, 1993). Em suas folhas - onde ocorre a formação de um biofilme, composto por bactérias, protozoários, algas e detritos depositados, - servindo de fonte (primária) de alimento para diversos invertebrados. Além disso, a presença de inúmeras espécies de macrófitas aumenta a heterogeneidade espacial, disponibilizando maior número de habitats (MARGALEF, 1983). A contribuição da estrutura morfológica de uma macrófita para a heterogeneidade do habitat é também amplamente reconhecida (THOMAZ; CUNHA, 2010). Quando analisada a diversidade biológica dos sistemas lênticos, a presença das macrófitas (zona litorânea) e a sua ausência (zona profunda), os resultados poderiam ser similares se comparássemos a diversidade biológica de uma floresta tropical com aquela de uma área de dunas de areia (SCHEFFER, 2004; THOMAZ; CUNHA, 2010).

A complexidade estrutural dos sistemas lênticos pode implicar em importantes consequências para a estrutura da comunidade de macroinvertebrados aquáticos, como, por exemplo, na redução dos efeitos da predação (GILINKI, 1984; DIEHL, 1992; HEINO, 2000). O tipo de vegetação litoral ou o substrato do fundo podem influenciar na ocupação do espaço e na preferência de muitas espécies, e, dessa maneira, determinar diversos padrões de comunidades (MINSHALL, 1984; HOFFMAN et al., 1996; HEINO, 2000). Um dos principais fatores que contribui para o aumento da heterogeneidade de habitat é a morfologia das macrófitas aquáticas. É reconhecida uma relação positiva entre a complexidade

morfológica do vegetal e a abundância e riqueza de macroinvertebrados a ele associados (THOMAZ et al., 2008). Indiretamente, a alta produção de biomassa destes vegetais pode influenciar também na abundância, na diversidade e na biomassa dessa comunidade associada. Esses vegetais, quando entram em decomposição, irão influenciar nas variáveis abióticas do sistema e, assim, pode alterar a estrutura da comunidade (THEEL et al., 2008).

1.3 Macrófitas invasoras: suas influências sobre a comunidade de macroinvertebrados da zona litoral

Define-se como “espécie invasora” todo organismo oriundo de uma determinada zona geográfica ou bioma que não é o de sua origem (exótico) e que adquiriu vantagem competitiva após o desaparecimento de obstáculos naturais para sua proliferação, permitindo rápida dispersão e conquista da dominância nos ecossistemas receptores (VALÉRY et al., 2008). O impacto promovido pela introdução de espécies invasoras não se limita à redução das populações nativas, mas também interfere na estrutura de diversas comunidades nativas residentes, alterando as interações das cadeias alimentares e os processos ecossistêmicos (BUNN et al., 1998; THOMAZ et al., 2009). Devido à ampla abrangência de seus impactos e das dificuldades de previsão e mitigação dos seus efeitos, os estudos ecológicos das espécies invasoras têm se destacado e despertado a atenção e o interesse de gestores ambientais (THOMAZ et al., 2009), possibilitando o desenvolvimento e a criação de técnicas de manejo eficientes e de diretrizes políticas para o seu controle. Pesquisas voltadas para obtenção de informações sobre a influência da introdução de macrófitas invasoras nos ecossistemas lênticos e as suas interações com a biota residente têm sido objeto de estudo nos últimos anos (SCHULTZ; DIBBLE, 2012).

A predominância de espécies invasoras também induz alterações nas características abióticas do sistema, como, por exemplo, redução da disponibilidade de oxigênio. A liberação de compostos químicos secundários, considerados alelopáticos, pelas macrófitas invasoras pode ser também um mecanismo de competição interespecífica que pode resultar na vantagem competitiva da espécie invasora sobre a espécie nativa (DANDELOT et al., 2008). Estes aspectos têm sido considerados fatores importantes para os macroinvertebrados aquáticos. Uma vez que as concentrações de oxigênio na água são reduzidas em razão da decomposição de grandes quantidades de biomassa da planta invasora, e pode levar à redução da abundância e diversidade faunística, simplificando assim, a comunidade. Neste caso, a estrutura da comunidade se modifica, prevalecendo grupos

tolerantes, como, por exemplo, larvas de Chironomidae e Oligochaeta (STIERS et al., 2011; SCHULTZ; DIBBLE, 2012).

Além disso, faz-se importante reconhecer o papel modificador da qualidade do recurso alimentar decorrente da presença de plantas invasoras, uma vez que estas podem ter efeitos diretos nos aspectos ecológicos de herbivoria, bem como modificar a composição da comunidade dos macroinvertebrados herbívoros (LEITE-ROSSI et al., 2016). Espécies invasoras, com altas concentrações de compostos secundários (fenóis, lignina) podem influenciar negativamente nas características da história de vida das espécies herbívoras, tais como crescimento, taxa de fecundidade e mortalidade (MORRISON; HAY, 2011). Embora as relações adversas de macrófitas invasoras estejam bem documentadas para algumas espécies herbívoras (e.g. *Pomacea caniculata*, *Lymnea stagnali* e *Acentria ephemerella*) (CHOI et al., 2002; ELGER et al., 2005), pouco se sabe a respeito dos efeitos sobre outros herbívoros aquáticos (LEITE-ROSSI et al., 2016), bem como implicações sobre a dinâmica de transferência de energia através de redes tróficas. Dentre os diversos tipos de forma de vida de macrófitas aquáticas, os grupos das emergentes e anfíbias se destacam como importantes componentes, devido à alta produção primária (DE SAZALAY; RESH, 2000). Estas servem como base de detritos para diversas cadeias alimentares quando em fase de senescência (NELSON, 2011). Os estudos realizados com essas macrófitas invasoras têm demonstrado que, devido a sua elevada produção de biomassa e ao rápido processo de decomposição podem ocasionar maiores alterações de estrutura dos habitats, redução de oxigênio dissolvido e aumento da disponibilidade de nitrogênio quando comparadas com espécies nativas (EHRENFELD, 2003; NELSON, 2011).

Hedychium coronarium (J. Koenig, 1783) é considerada macrófita aquática invasora do tipo anfíbia, sendo nativa da região do Himalaia, na Ásia tropical, e atualmente com distribuição em todas as Américas (MACEDO, 1997; PIO CORRÊA, 1984, SANTOS et al., 2005). A espécie conhecida pelo nome popular de lírio-do-brejo, mariazinha-do-brejo e gengibre-branco é uma monocotiledônea da família Zingiberaceae, rizomatosa de hábito herbáceo perene (SANTOS et al., 2005). Sua inflorescência em espiga de flores com corolas brancas ou amarelo pálidas e de aroma adocicado são as características responsáveis pelo nome da espécie, originado da palavra grega *Hedychium* que significa “neve doce” e *coronarium* do latim “corona” (KISSMAN; GROTH, 1991), as quais atraem polinizadores noturnos como as mariposas (SANTOS et al., 2005). O lírio-do-brejo apresenta a parte aérea disposta em caule simples e cilíndrico, de coloração avermelhada na base e folhas lanceoladas

dispostas de forma alternada (KISSMAN; GROTH, 1991). A espécie possui reprodução sexuada por produção de sementes e também assexuada pela produção de hastes aéreas que se originam dos rizomas (STONE et al., 1992; SANTOS et al., 2005) e formam fragmentos que se dispersam na água (dispersão hidrocórica), invadindo e colonizando outros locais através de crescimento vegetativo.

O histórico de introdução do lírio-do-brejo no Brasil ainda é incerto. Seus registros mais antigos no país datam de um espécime em Kew Gardens, o qual foi coletado pelo Dr. Glaziou em 1860, e na elaboração da *Flora Brasiliensis* por Martius e Schuman K. entre 1860 e 1904 (ROYAL BOTANY GARDENS, 1912). Segundo Kissman (1991), a introdução do lírio-do-brejo no Brasil deve ter ocorrido de forma acidental, carregada por navios negreiros. Essa espécie que juntamente com outras gramíneas, eram utilizadas para fazer camas para os escravos. Posteriormente o uso da planta demonstrou-se economicamente útil, principalmente na utilização como alimento (rizoma e folhas), na produção de papel (celulose – 43%), na produção de fármacos e aromatizantes (rizoma e flores) (VERMA; BANSAL, 2010). A espécie se tornou comum em regiões litorâneas e em diversas áreas continentais do Sudeste, como por exemplo, em Minas Gerais (SANTOS et al., 2005). Atualmente, a mesma tem sendo considerada uma invasora agressiva em áreas de sub-bosques do Bioma Mata Atlântica (ZENNI; ZILLER, 2010), como também, em áreas alagadas, margem de córregos e represas no Estado de São Paulo.

Considerando a influência das invasões biológicas, que atuam juntamente com outras alterações antrópicas na aceleração dos processos de degradação dos ecossistemas aquáticos continentais, a realização de trabalhos de pesquisa ecológica sobre a atuação dessas invasões sobre as comunidades nativas poderão servir de ferramenta para o estabelecimento de políticas de gestão e estratégias de controle. No entanto, as informações disponíveis até o presente sobre esta espécie invasora estão relacionadas mais a sua fenologia e biologia (SANTOS et al, 2005) e pouco se conhece a respeito de sua influência sobre as comunidades de macroinvertebrados aquáticos (LEITE-ROSSI et al., 2016). Sendo assim, tornam-se importantes as investigações direcionadas ao conhecimento das suas interações com a comunidade de macroinvertebrados, uma vez que o conhecimento das interações e padrões comunitários com a comunidade vegetal poderá indicar o nível de impacto sobre a biodiversidade e processos ecológicos que ocorrem nos ecossistemas de água doce.

1.4 Traços funcionais dos macroinvertebrados: sua importância para a estrutura das comunidades e processos ecossistêmicos

Investigar os padrões de biodiversidade em níveis espaciais e temporais tem sido um dos principais carros-chefe dos estudos ecológicos atuais (HEINO, 2000; JHONSON et al, 2004). Em geral, os estudos focam na quantificação dos padrões de diversidade ou de riqueza de espécies ao longo de um gradiente ou determinado processo ecológico que possa produzir um padrão observável (MAGURRAN, 2013). Tal abordagem tem sido considerada a base das investigações ecológicas que direcionam o entendimento da biodiversidade. No entanto, a biodiversidade não deve ser entendida somente através da diversidade de espécies, uma vez que nela também estão incluídos os aspectos filogenéticos, genéticos e funcionais da comunidade. Além disso, se levado em conta que a diversidade de espécies engloba o simples fato da nomeação das espécies, poucas informações se obteriam a respeito de suas histórias funcionais e evolutivas, pois são esses aspectos que determinam os processos e padrões de biodiversidade observados (SWENSON, 2014).

Os índices de diversidade funcional, com os quais são estimadas as similaridades dos traços entre as espécies de uma comunidade, permitem o entendimento da maneira como um ecossistema funciona ou opera (TILMAN, 2001). Esta abordagem está fundamentada no “templet theory”, na qual Thomaz Southwood (1977) afirma que as estratégias ecológicas das espécies respondem às características do habitat, o qual seleciona ou favorece determinados conjuntos de traços dos indivíduos. Sua principal premissa tem servido de base para o surgimento de outras aplicações teóricas dos ecossistemas de água doce, como por exemplo a teoria do “The River Continuum Concept” (VANNOTE et al., 1980), a qual partiu das premissas de “habitat templet” para compreender os padrões de distribuição das comunidades de macroinvertebrados aquáticos em sistemas lóticos. Através do conhecimento dos traços funcionais dos táxons em diferentes perfis de habitat, os autores concluíram que estes poderiam responder às mudanças ambientais ao longo de um gradiente de contínuo de rios, revelando, assim, diferentes processos ecossistêmicos (VANNOTE et al, 1980). Desde então, os modelos preditivos desses trabalhos teóricos têm servido de base para diversas análises de respostas dos traços funcionais dos macroinvertebrados aquáticos aos impactos causados por interferências antrópicas, bem como na justificativa do uso de índices funcionais para análises dos processos ecológicos nos ecossistemas de água doce (MENEZES et al. 2010).

Referências

- BUNN, S. E.; DAVIES, P. M.; KELLAWAY, D. M.; PROSSER, I. P. Influence of invasive macrophytes on channel morphology in a tropical lowland stream, and potential control by riparian shading. **Freshwater Biology**, v. 39, p. 171-178, 1998.
- CARLSSON, N. O.; LACOURSIERE, J. O. Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. **Biological Invasions**, v.7, p. 233-241, 2005.
- CARREIRA, B. M.; DIAS, M. P.; REBELO, R. How consumption and fragmentation macrophytes by the invasive crayfish *Procambarus clarkia* shape the macrophyte communities of temporary ponds. **Hydrobiologia**, v. 72, p. 89–98, 2014.
- CHAMBERS, P. A.; LACOUL, P.; MURPHY, K. J.; THOMAZ, S.M. Global diversity of aquatic macrophytes in freshwater. **Hydrobiologia**, v. 595, p. 9-26, 2008.
- CHOI, C.; BAREISS, C.; Walenciak, O.; Gross, E. M. Impact of polyphenols on growth of the aquatic herbivore *Acentria ephemerella*. **Journal of Chemical Ecology**, v. 28, p. 2245-2256, 2002.
- DANDELLOT, S.; ROBLES, C.; PECH, N.; CAZAUBON, A.; VERLAQUE, R. Allelopathic potential of two invasive alien *Ludwigia* spp. **Aquatic Botany**, v. 88:, p. 311–316, 2008.
- DE SZALAY, F. A.; RESH, V. H. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. **Freshwater Biology**, v. 45, p. 295-308, 2000.
- DIEHL, S. Fish predation and benthic community structure: the role of omnivory and habitat complexity. **Ecology**, v. 73, p. 1646–1661, 1992.
- DUNDGEON, D. Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. **Science Direct**, v. 2, p. 422-430, 2010.
- EHRENFELD, J. G. Effects of exotic plant invasions on soil nutrient cycling processes. – **Ecosystems**, v. 6, p. 503–523, 2003.
- ELGER, A.; BARRAT-SEGRETAIN, M. H.; WILLBY, N. J. Seasonal variability in the palatability of freshwater macrophytes: a case study. In **Macrophytes in Aquatic Ecosystems: From Biology to Management**. Springer, Netherlands, 2005. p. 89-93.
- GILINSKY, E. The role of fish predation and spatial heterogeneity in determining benthic community structure. **Ecology**, v. 65, p. 455–468, 1984.
- HEINO, J. Lentic macroinvertebrates assemblages structure along gradients in special heterogeneity, habitat size and water chemistry. **Hydrobiologia**, v. 418, p. 229-242, 2000.
- HOFFMAN, R. L.; LISS, W. J.; LARSON, G. L. E.; DEIMLING, K.; LOMNICKY, G. A.. Distribution of nearshore macroinvertebrates in lakes of the northern Cascade Mountains, Washington, U.S.A. **Archieve of Hydrobiology**, v. 136, p. 363–389, 1996.

JOHNSON, R. K.; GOEDKOOP, W.; SANDIN, L.. Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. **Freshwater Biology**, v. 49, p. 1179-1194, 2004.

KISSMANN, K. G; GROTH, D. **Plantas infestantes e nocivas**. São Paulo, Basf Brasileira, 1991, p. 590-593.

LEITE-ROSSI, L. A.; SAITO, V. S.; CUNHA-SANTINO, M. B.; TRIVINHO-STRIXINO, S. How does leaf litter chemistry influence its decomposition and colonization by shredder Chironomidae (Diptera) larvae in a tropical stream?. **Hydrobiologia**, v. 771, p. 119-130, 2016.

MACEDO, J. F. O gênero *Hedychium koening* (Zingiberaceae) no Estado de Minas Gerais. **Daphne**, v. 7, n. 2, p. 27-31, 1997.

MAGURRAN, A. E. **Measuring biological diversity**. Oxford: John Wiley & Sons, 2013.

MARGALEF, R. **Limnologia**. Barcelona: Ed. Omega, 1983.

MENEZES, S.; BAIRD, D. J.; SOARES, A. M. Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. **Journal of Applied Ecology**, v. 47, p. 711-719, 2010.

MIDDELBOE, A. L.; MARKAGER, S. Depth limits and minimum light requirements of freshwater macrophytes. **Freshwater Biology**, v. 37, p. 553-568, 1997.

MINSHALL, G. W. Aquatic insect-substratum relationships. In: RESH, V. H. & ROSENBERG, D. M. (eds), **The Ecology of Aquatic Insects**. Praeger: New York, 1984. p. 358-400.

MORRISON, W. E.; HAY, M. E. Induced chemical defenses in a freshwater macrophyte suppress herbivore fitness and the growth of associated microbes. **Oecologia**, v. 165, p. 427-436, 2011.

NELSON, S. M. Comparison of macrophyte breakdown, associated plant chemistry, and macroinvertebrates in a wastewater dominated stream. **Hydrobiologia**, v. 96, p. 72-89, 2011.

ODUM, E. **Ecologia**. Rio de Janeiro: Guanabara Koogan, 2º ed., 1988. 433 p.

PIO CORRÊA, M. **Dicionário das plantas úteis do Brasil e das exóticas cultivadas**. Rio de Janeiro: Instituto Brasileiro de Desenvolvimento Florestal, v. 6, 1984.

ROYAL BOTANICAL GARDENS. New sources of paper (*Hedychium coronarium*, Koenig, and Allies). **Bulletin of Miscellaneous Information (Royal Gardens Kew)**, p.373-378, 1912

SANTOS, S. B.; PEDRALLI, G.; MEYERS, S. T. Aspectos da fenologia e ecologia de *Hedychium coronarium* (ZINGIBERACEAE) na Estação Ecológica do Tripuí, Ouro Preto-MG. **Planta Daninha**, Viçosa-MG, v. 23, n.2, p.175-180, 2005.

- SCHEFFER, M. **Ecology of shallow lakes**. Norwell: Kluwer Academic Publishers, 2004. 357 p.
- SCHULTZ, R.; DIBBLE, E. Effects of invasive macrophytes on freshwater fish and macroinvertebrates communities: the role of invasive plants traits. **Hydrobiologia**, v. 684, p. 1-14, 2012.
- SOUTHWOOD, T. R. E. Habitat, the templet for ecological strategies? **Journal of Animal Ecology**, v. 46, p. 337-365, 1977.
- STIERS, I.; CROHAIN, N.; JOSENS, G.; TRIEST, L. Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. **Biological Invasions**, v. 13, p. 1–12, 2011.
- STONE, C. P.; SMITH, C. W.; TUNISON, J. T. (Eds). **Alien plant invasions in native ecosystems of Hawaii: management and research**. Honolulu: University of Hawaii, Cooperative National Park Resources Study Unit, 1992. 887p.
- SWENSON, N. G. **Functional and phylogenetic ecology in R**. New York: Springer, 2014.
- THEEL, H. J.; DIBBLE, E. D.; MADSEN, J. D. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. **Hydrobiologia**, v. 600, p. 77–87, 2008.
- THOMAZ, S. M.; CARVALHO, P.; MORMUL, R. P.; FERREIRA, F. A., SILVEIRA, M. J.; MICHELAN, T. S.. Temporal trends and effects of diversity on occurrence of exotic macrophytes in a large reservoir. **Acta Oecologica**, v. 35, p. 614–620, 2009.
- THOMAZ, S. M.; CUNHA, E. R. The role os macrophytes in habitat structuring in aquatic ecosystems: methods of measurements, causes and consequences on animal assemblages´s composition and biodiversity. **Acta Limnologica Brasiliensia**, v.22, n.2, p.218-236, 2010.
- THOMAZ, S. M.; DIBBLE, E. D.; EVANGELISTA, L. R.; HIGUTI, J.; BINI, L. M. Influence of aquatic macrophyte habitat complexity on invertebrates abundance and richness in tropical lagoons. **Freshwater biology**, v. 53, p. 358-367, 2008.
- TILMAN, D. Functional diversity. **Encyclopedia of biodiversity**, v. 3, p. 109-120. 2001
- TRIVINHO-STRIXINO, S.; STRIXINO, G. Estrutura da comunidade de insetos aquáticos associados à *Pontederia lanceolata* Nuttal. **Revista Brasileira de Biologia**, v. 53, p. 103-111, 1993.
- VALÉRY, F.; LEFEUVRE, J. C. L. H.; SIMBERLOFF, D. In Search of a real definition of the biological invasion phenomenon itself. **Biological Invasions**, v. 10, p. 1345–1351, 2008.
- VANNOTE, R. L.; MINSHALL, G. W.; CUMMINS, K. W.; SEDELL J. R.; CUSHING, C. E. The river continuum concept. **Canadian Journal Fish Aquatic Science**, v. 37, p. 130-137, 1980.

VERMA, M.; BANSAL, Y. K. Butterfly Lilly (*Hedychium coronarium* J. Koenig): An endangered medicinal plant. **Plant Archives**, Heonra (Saifai)- Etawah, v.10. n. 2, p.841-843, 2010.

ZENNI, R. D., & ZILLER, S. R. An overview of invasive plants in Brazil. **Brazilian Journal of Botany**, v. 34, n. 3, 431-446, 2011.

2. Objetivos e justificativa

Considerando a crescente ocupação de plantas invasoras nos sistemas aquáticos torna-se necessário o conhecimento de suas implicações para os processos ecológicos nesses ecossistemas de água doce. Em especial para a espécie lírio-do-brejo, em vista da inexistência de informações a respeito das interações ecológicas entre esta macrófita invasora com a comunidade de macroinvertebrados aquáticos este conhecimento se faz importante. Através de coletas entre margem invadida e não invadida de um reservatório, analisou-se a interferência da invasão dessa planta na composição taxonômica (Capítulo I) e nos traços funcionais da comunidade de insetos aquáticos (Capítulo II). Através de experimentos de colonização de folhas dessa macrófita invasora e de uma macrófita nativa orelha-de-veado (*Pontederia cordata*), foi analisada a interferência das diferentes características química das folhas das plantas na especialização das espécies herbívoras (Capítulo III) bem como dos seus efeitos na mudança de composição funcional dos herbívoros que podem alterar a estruturação de redes tróficas da comunidade de macroinvertebrados (Capítulo IV). O estudo foi conduzido para avaliar as seguintes hipóteses:

Capítulo I – Forecasting the impact of an invasive macrophyte species in the littoral zone by aquatic insect species composition.

Hipótese: A presença da macrófita invasora lírio do brejo na zona litoral altera a composição taxonômica de comunidades de insetos aquáticos em decorrência de mudanças na estrutura do habitat.

Neste capítulo são analisadas a riqueza e abundância da comunidade de insetos aquáticos associadas a bancos de vegetação invasora e nativa (floresta parcialmente invadida, macrófita nativa e floresta ripária não invadida). Além disso, é feita a análise de espécies indicadoras para identificar quais espécies associadas ao lírio do brejo poderiam servir de referência para o monitoramento do seu impacto.

Capítulo II – The invasive white ginger lily (*Hedychium coronarium*) simplifies functional trait composition of an insect assemblage in the littoral zone of a Savanna reservoir

Hipótese: A proliferação do lírio-do-brejo modifica as condições ambientais locais, como variáveis abióticas e estrutura do habitat resultando em menor índice de

diversidade funcional. Este resultado se reflete diretamente na seleção de traços de espécies aquáticas adaptadas ao tipo do habitat e da modificação do recurso alimentar causado pela presença dessa macrófita.

Neste capítulo é analisada a composição funcional da comunidade de insetos aquáticos através dos índices de dissimilaridade funcional (FDis), equidade funcional (FEve), divergência funcional (FDiv) e relevância de traços (CMW) nas margens invadidas e não invadidas pela espécie invasora. Estes índices remetem às medidas de ocupação de nicho, bem como indicam quais traços funcionais são predominantes na comunidade associada. A partir dos resultados obtidos são inferidos os principais processos ecológicos relacionados à presença da espécie vegetal invasora na estruturação da comunidade.

Capítulo III – Native macrophyte leaves influence more specialisation of Neotropical shredder chironomids than invasive macrophyte leaves

Hipótese: As diferenças nas composições químicas entre as folhas da macrófita invasora lírio-do-brejo (*Hedychium coronarium*) e macrófita nativa orelha-de-veado (*Pontederia cordata*) influenciam na especialização da comunidade de quironomídeos fragmentadores associados.

Neste capítulo é analisada a estrutura da comunidade de quironomídeos fragmentadores associados às folhas das macrófitas invasora e nativa através das variáveis riqueza e abundância de espécies. O consumo das folhas das espécies vegetais é estimado através de análises do trato digestivo dos táxons fragmentadores, o qual é utilizado para estimar os índices de especialização individual (d') e da comunidade associada (H_2'). Através da análise de correlação do consumo médio das folhas e traços químicos das folhas, são discutidas duas principais teorias de evolução adaptativa dos herbívoros aquáticos: “intake-efficiency” e “heterotrophic facilitation” que podem explicar as diferenças de composição de espécies herbívoras nas duas espécies vegetais.

Capítulo IV - Can herbivore functional traits influence food web complexity? - Implications for an invasive macrophyte species.

Hipótese: A folha de macrófita aquática que apresenta menor qualidade do recurso influencia no decréscimo da diversidade funcional de macroinvertebrados herbívoros e estrutura das redes tróficas. Tal efeito se reflete num impacto negativo, afetando assim, o

processo de transferência de energia na comunidade que ocorre através da estruturação das redes tróficas de macroinvertebrados associados.

Nesse capítulo é analisada a diversidade funcional da comunidade de herbívoros associados a espécie invasora e nativa através avaliação dos índices de número de espécies funcionalmente singulares (sing.sp) e riqueza funcional (FRic). A estrutura das redes tróficas de macroinvertebrados é analisada através de medidas do número total de ligações (L), densidade de ligações (L/S), conectância (C) e da relação entre predador-presa. Através dos resultados das análises de influência dos traços químicos das folhas das espécies de macrófitas nestas variáveis comunitárias são discutidas as interferências da qualidade nutricional das espécies vegetais sobre a diversidade funcional dos herbívoros e sua consequência no processo de transferência de energia através das redes tróficas.

Capítulo I

Forecasting the impact of an invasive macrophyte species in the littoral zone by aquatic insect species composition.

Este capítulo foi submetido à revista Limnologica (em revisão)

Abstract

Invasive macrophytes threaten the freshwater ecosystem biodiversity. We analysed the influence of the invasive white ginger lily (*Hedychium coronarium*) on aquatic insect assemblages living in the littoral zone of a tropical reservoir. We took aquatic insect samples from the littoral zone of four main bank vegetations: white ginger lily monospecific bank, forest partially invaded, spike-rush (*Eleocharis*) monospecific bank and riparian forest. At each bank vegetation, we measured the abiotic variables such as dissolved oxygen, pH, water temperature and depth. We also analysed the aquatic insects through abundance, richness and Simpson diversity. We used the non-Metric MDS analyses to analyse the spatial distribution of each assemblage and ANOSIM to verify differences among the dissimilarity distances. Additionally, we analysed the main taxa associated with invasive macrophytes through indicator species analyses using the IndVal index. We observed that the invasive macrophyte banks presented a higher abundance of associated specimens, as well as a lower dissimilarity of aquatic insect assemblages. We did not observe an influence of abiotic in the aquatic insect community variables. The IndVal index indicated eight aquatic insects as indicator species. *Labrundinia unicolor*, *Ablabesmyia paule* and *Diastatops* were indicator species on invaded banks. The invasion of white ginger lily could have caused a high complexity habitat of the surrounding water, probably by a high production of plant biomass. We suggest using species of aquatic insects as indicator species to monitor the impact of white ginger lily on freshwater systems.

Key words: habitat complexity, Chironomidae, freshwater conservation, biomonitoring, macroinvertebrates, *Hedychium coronarium*

1. Introduction

Invasive species are considered one of the main stressors of freshwater systems and have impaired various ecosystem services, such as energy production, sailing and fishing (Dungeon, 2010). The lentic littoral zone is an important freshwater ecosystem compartment which presents high diversity species and is threatened by invasive species (Vander et al., 1999). Among diverse invasive organisms, the influence of invasive macrophyte species in this freshwater compartment is well recognized (Thomaz and Cunha, 2010).

Some studies report fast vegetative growth of invasive macrophyte species increasing habitat complexity, which results in the disruption of food webs (Kovalenko and Dibble, 2011). Furthermore, the high biomass production of these plants results in the decrease of dissolved oxygen that leads to the exclusion of sensitive species (Schultz and Dibble, 2012). Additionally, invasive macrophytes can alter resource food availability which shifts species assemblage compositions (Leite-Rossi et al., 2016). The ecological interaction between invasive macrophyte species and aquatic insects seems to have important implications on the impact of some ecological process, especially those involving predation (Warfe and Barmuta, 2006), herbivory (Boyero et al., 2012) and decomposition (Leite-Rossi et al., 2016). Because invasive macrophyte species cause changes to aquatic insect assemblages which directly impact these ecological processes, interest of their management in freshwater systems is also of vital importance to biodiversity conservation.

Aquatic insect assemblages are recognised as good indicators of habitat alterations. Their ubiquity in freshwater systems as a consequence of their various habitat adaptations (*e.g.* respiration system, feeding habit, life cycle) enable them to be utilized in many freshwater monitoring studies (Arimoro and Ikomi, 2009). Their use as bioindicators arose from the Saprobian System approach, which was an early model that used some aquatic insect

taxa, such as, *Chironomus* as indicators of anthropogenic disturbance (*e.g.* sewage discharge) (Rosengerb and Resh, 1993). Since then, the applicability of aquatic insect assemblages in biomonitoring studies has developed, demonstrating their importance to freshwater conservation issues such as deforestation, stream discontinuity habitat and restoration programs (Blankely et al., 2006; Navarro-Llacer et al., 2010; Saulino et al., 2016).

In littoral zones of lentic systems, aquatic insect assemblages are believed to respond to habitat changes caused by invasive macrophyte species (Kovalenko et al., 2010). In the present study, we analysed the effect of white ginger lily (*Hedichium Coronarium* - J. Koenig, 1783) on aquatic insect assemblages dwelling in the littoral zone of a tropical reservoir. This invasive amphibious plant species has become dominant in wetlands, riparian zones and lake banks, where it forms dense populations. Concerning its characteristics, this macrophyte species has been considered as an aggressive competitor with native plants (De Castro et al., 2016). Additionally, the ecological interactions with associated community (*e.g.* macroinvertebrates and fish) are still unexplored in ecological studies. Hence, knowledge concerning the influence of white ginger lily in the associated community is needed, as there is a lack of knowledge regarding its influence. Similar to anthropogenic stressors in freshwater systems (*e.g.* erosion, sewage and deforestation), as well as several invasive macrophyte species that cause habitat alterations, white ginger lily could lead to a decrease in the diversity of aquatic insect species. In addition, specific taxa of aquatic insects associated with this invasive plant could be used as indicators of habitat disturbance, taxonomically mirroring the habitat conditions promoted in the littoral zone.

To understand this, we compared aquatic insect assemblages associated with a monospecific bank where white ginger lily was present in a tropical reservoir with three other main bank vegetations: forest bank partially invaded by white ginger lily (few individuals

mixed with forest vegetation), spike-rush (*Eleocharis*, R. Br.) monospecific macrophyte bank and non-invaded riparian vegetation. We assumed that the occupation of white ginger lily in the littoral zone shifts aquatic insect composition assemblages when compared to the native bank vegetations causing loss and alteration of the littoral habitat. In addition, we tried to identify aquatic insect taxa that could serve as indicators of the presence of the invasive plant. These results could be important for conservation practices intended to monitor the invasion by this macrophyte species in the lentic systems.

2. Material and Methods

2.1 Study area

This study was performed in a tropical reservoir located in a preserved area of the Brazilian Savanna vegetation (Cerrado Biome) in the central region of São Paulo State (Brazil). The Fazzari reservoir (21°58'S, 47°53'W) has chemical characteristics such as high levels of dissolved oxygen (> 7mgL), acidic pH (\pm 5.5) and diverse vegetation on its banks. Its total area is 11,370 m², 220 meters long, an average width of 51.5 m and an average depth of 1.10 m and maximum 4 m. The vegetation surrounding its banks consists of four main bank vegetations. The right reservoir bank, which stretches about 80 meters, is completely dominated by the invasive white ginger lily (*H. coronarium*) (WG) followed by a forest partially invaded (IF) by the same invasive plant. The left reservoir bank is surrounded by spike-rush (*Eleocharis*), an amphibious macrophyte (SR), and native riparian forest (RV) consisting of trees, shrubs and ferns.

2.2 Sampling and identification of fauna

Aquatic insects from each vegetation profile were collected at the beginning of the dry season (May/June, 2014). Six sectors of each bank vegetation were randomly sampled, totaling 24 samples. At each bank vegetation, ten-meter-long sectors were scanned using dip

collectors (“D” net - mesh 250 μm). In addition, the abiotic variables such as dissolved oxygen, pH and water temperature were measured using a multisensory probe (HORIBA U010). The depth was measured using a measuring tape.

The specimens were sorted live on transilluminated trays and conserved in 80% ethanol. We carried out the specimen identification to the lowest possible taxonomic level using taxonomic keys for aquatic insects of the Neotropical region (Domingues and Fernandes, 2009; Trivinho-Strixino, 2011; Trivinho-Strixino, 2012; Oliveira et al., 2013; Silva et al., 2014; Trivinho-Strixino and Pepinelli, 2015) and with the help of Odonata specialists.

2.3 Data analyses

The abiotic variables amongst the bank vegetations were compared using a non-parametric test of Mann-Whitney pair-wise analyses.

For each aquatic insect composition assemblage, the total abundance, richness, and Simpson diversity were compared using the non-parametric test of Mann-Whitney pair-wise analyses. To analyse the influence of abiotic variables in these ecological aspects of aquatic insect assemblages, the Pearson’s correlation analyses were used. The coefficient correlations (r) and p -values ($p < 0.05$) were used as a measure to infer significant interaction strength between abiotic and assemblage variables.

To verify the influence of white ginger lily invasion on the spatial distribution of aquatic insect assemblages, the non-Metric Multi Dimensional Scale (nMDS) analysis was performed to compare aquatic insect composition with native vegetation. To do this, the total abundance of taxa found on the bank vegetations was used. The clustering among samples was determined by the dissimilarity distance measured using the Bray-Curtis index. In addition, significant differences of dissimilarity distances in the aquatic insect assemblages were compared using a similarity analyses test (ANOSIM). To do this, the total abundance of

specimens on each bank vegetation was used to measure the dissimilarity distances using the Bray-Curtis index. The significant differences among dissimilarity distances of assemblages were analysed by statistic tests (R) and descriptive level sampling ($p < 0.05$) (Clarke, 1993).

Furthermore, to analyse the influence of white ginger lily on aquatic insect species assemblages, an indicator value of species analysis using the IndVal index was used. This index measures the association between a species and a group of sites, where a statistical significance of this relationship is tested using a permutation test ($nperm = 999$). The IndVal index is an indicator of value species, calculated using a product of two quantities, A and B , with r as the correlation index. Quantity A , defined as the mean abundance of the species in the target site group, divided by the sum of the mean abundance over all the groups, was used. It represents the probability that the surveyed site belongs to the target site group given the fact that the species has been found. This conditional probability is called the “specificity” or “positive predictive value” of the species as an indicator of the site group. Quantity B is defined as the relative frequency of occurrence (presence-absence) of the species inside the target group. It represents the probability of finding the species in sites belonging to the site group. This second conditional probability is called the “fidelity” or “sensitivity” of the species as an indicator of the target site group (Cáceres and Legendre, 2009; De Cáceres, 2013).

To do this, a data matrix consisting of bank vegetations in rows and aquatic insect species in columns was utilized. The IndVal indices were calculated using the “indicpecies package” (De Cáceres et al., 2015), which is available on the R platform (R Development Core Team, 2014).

3. Results

Water near the spike-rush banks presented higher dissolved oxygen than other bank vegetations (WG [U= 0, p= 0.005], IF [U= 0, p= 0.005], RV [U= 4.5, p= 0.04]). The littoral zone of the white ginger lily banks was deeper than other riparian bank vegetations (U= 0.5, p= 0.006) due to its vegetative growth that goes into the shallower areas of the littoral zone of the reservoir. Additionally, it has a lower pH compared to other bank vegetations (IF [U= 5, p= 0.04], SR [U= 5, p= 0.04], RV [U= 3, p= 0.02]) (Table 1).

Table 1. Abiotic variable bank vegetations in the littoral zone of a tropical reservoir in the Brazilian Savanna. WG – white ginger lily, IF – invaded forest, SR – spike-rush, RV – riparian vegetation.

Abiotic variables	WG	IF	SR	RV
dissolved oxygen (mg/L)	7.40 ±0.43	7.37 ±0.47	8.70 ±0.22 *	8.00 ±0.43
pH	5.30 ±0.24*	5.55 ±0.17	5.55 ±0.16	5.77 ±0.21
depth (cm)	0.39 ±0.03 *	0.37 ±0.09	0.30 ±0.11	0.28 ±0.07
water temperature (°C)	18.70 ±0.40	18.50 ±0.41	18.50 ±0.29	18.30 ±0.27

(*) p<0.05

Sixty seven aquatic insect taxa were identified (Table 2). White ginger lily banks showed higher abundances ($n= 167.5 \pm 55.00$) of specimens than other bank vegetations (IF, $n= 74 \pm 24.30$ [U= 2, p= 0.01], SR, $n= 65.5 \pm 26.40$ [U= 1, p= 0.008], RV, $n= 56.80 \pm 27.71$ [U= 1, p= 0.008]) (Figure 1). No significant differences were observed among the bank vegetations in richness and Simpson diversity ($p>0.05$). The Pearson's correlation analyses showed that richness on the partially invaded forest bank had a strong and positive relationship to dissolved oxygen ($r= 0.93$, $p= 0.006$). Additionally, the same results were observed on the spike-rush bank, for the abundance ($r= 0.82$, $p=0.04$), richness ($r= 0.85$, $p= 0.03$) and Simpson diversity ($r= 0.94$, $p<0.001$).

Table 2. Aquatic insect taxa collected in different bank vegetations in a tropical reservoir in the Brazilian Savanna. WG – white ginger lily, IF – invaded forest, SR – spike-rush, RV – riparian vegetation.

Taxa	Bank vegetation profile			
	WG	IF	SR	RV
<i>Campsurus</i> Walker, 1853	x	x	x	x
<i>Caenis</i> Stephens, 1835	x	x	x	x
<i>Ulmeritus</i> Traver, 1956	x	x	x	
<i>Callibaetis</i> Eaton, 1875			x	
<i>Aedomyia</i> Theobald, 1901	x	x	x	x
<i>Dasyhelea</i> Kieffer, 1911	x	x	x	x
<i>Gyrinus</i> Latreille, 1810	x	x	x	x
<i>Desmopachria</i> Babington, 1841	x	x	x	
<i>Andonectes</i> Guéorguiev, 1971	x			
<i>Laccophilus</i> Leach, 1815	x	x	x	x
<i>Pronoterus</i> Sharp, 1882	x	x		
<i>Mesonoterus</i> Sharp, 1882	x		x	x
<i>Hydrocanthus</i> Say, 1823	x			x
Scirtidae			x	x
<i>Macronema</i> Pictet, 1836	x	x	x	x
<i>Cyrnellus</i> Banks, 1913	x	x	x	x
<i>Oecetis</i> McLachlan, 1877	x	x	x	x
<i>Protoneura</i> Selys, 1857	x		x	x
<i>Oxyagron</i> Selys, 1876		x		
<i>Telebasis</i> Selys, 1865	x	x	x	x
Cont. Table 2				
<i>Acanthagrion</i> Selys, 1876	x	x	x	x
<i>Diastatops</i> Rambur, 1842	x	x	x	x
<i>Miathyria</i> Kirby, 1889	x	x	x	x
<i>Erythrodiplax</i> Brauer, 1842	x	x	x	x
<i>Macrothemis</i> Hagen, 1868		x		
<i>Orthemis</i> Hagen, 1861		x		
<i>Idiataphe</i> Cowley, 1934		x	x	
<i>Gynothemis</i> Calvert, 1909		x		x
<i>Lestes</i> Leach, 1815	x	x		
<i>Belostoma</i> Latreille, 1807			x	x
<i>Notonecta</i> Hungeford, 1933	x		x	x
<i>Limnocois</i> Stål, 1860	x		x	x
<i>Tenagobia</i> Bergroth, 1899	x			
<i>Aedokritus coffeatus</i> Trivinho-Strixino, 1997	x		x	x
<i>Asheum beckae</i> Sublette & Sublette 1964	x	x	x	x
<i>Caladomyia kapilei</i> Trivinho-Strixino, 2012	x	x	x	x
<i>Caladomyia riotarumensis</i> Reiff, 2000	x	x	x	

<i>Chironomus</i> Meigen	x	x	x	x
<i>Cladopelma forcipes</i> (Rempel, 1939)	x		x	
<i>Endotribelos bicolor</i> Trivinho-Strixino & Pepinelli, 2015	x	x	x	x
<i>Goeldichironomus maculatus</i> Trivinho-Strixino & Strixino, 1991	x	x		
<i>Polypedilum</i> sp5 cf Trivinho-Strixino, 2011	x	x	x	
<i>Polypedilum (Tripodura)</i> sp3 cf Trivinho-Strixino, 2011		x	x	x
<i>Polypedilum</i> sp3 cf Trivinho-Strixino, 2011	x	x		x
<i>Polypedilum</i> sp4 cf Trivinho-Strixino, 2011				x
<i>Stenochironomus</i> Kieffer, 1919	x	x	x	
<i>Ablabesmyia depaulai</i> Neubern, 2013	x	x	x	x
<i>Ablabesmyia laurindoi</i> Neubern, 2013	x	x	x	x
<i>Ablabesmyia metica</i> Roback, 1983	x			
<i>Ablabesmyia strixinoae</i> Neubern, 2013	x	x	x	x
<i>Clynotanypus</i> Kieffer, 1913				x
<i>Coelotanypus</i> Kieffer, 1913	x		x	x
<i>Labruninia carolae</i> Silva, 2014	x	x		x
<i>Labrundinia paulae</i> Silva, 2014			x	x
<i>Labrundinia</i> sp Fittkau, 1962	x	x	x	
<i>Labrundinia tenata</i> Silva, 2013	x	x		x
<i>Labrundinia unicolor</i> Silva, 2013	x	x	x	x
<i>Larsia</i> Fittkau, 1962			x	
<i>Monopelopia</i> Fittkau, 1962	x	x	x	x
<i>Pentaneura</i> Philippi, 1865			x	x
<i>Procladius</i> Skuse, 1889			x	x
<i>Fissimentum desiccatum</i> Cranston & Nolte, 1996		x		x
<i>Fissimentum</i> sp 3 cf Trivinho-Strixino, 2011				x
Cont. Table 2				
<i>Fissimentum</i> sp 2 cf Trivinho-Strixino, 2011			x	x
<i>Tanytarsus</i> sp v. d. Wulp, 1874		x	x	x
<i>Tanytarsus obiriciae</i> Trivinho-Strixino & Sonoda, 2006			x	

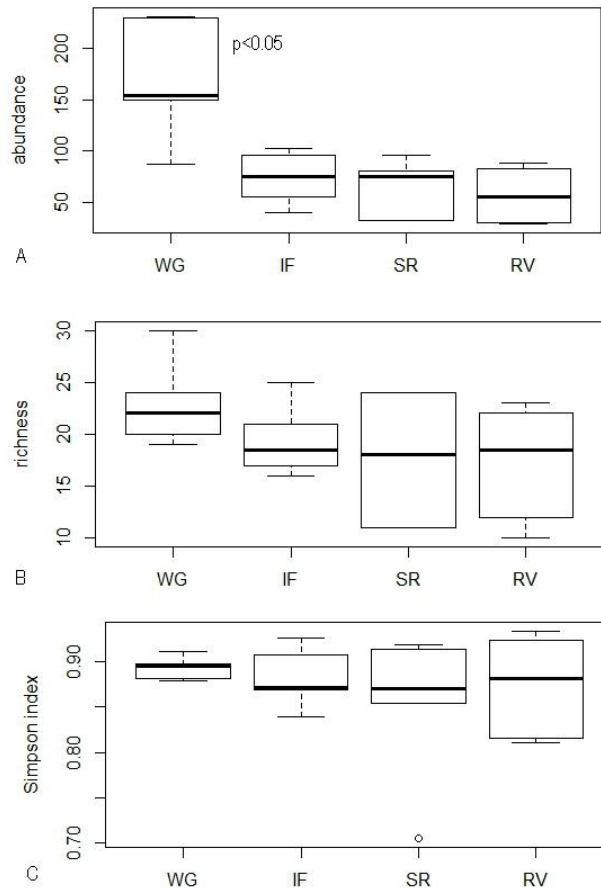


Fig. 1 Comparison between ecological variables of aquatic insect assemblages associated with invasive white ginger lily bank and other native bank vegetations in the littoral zone of a tropical reservoir in the Brazilian Savanna. **A**- abundance, **B** - richness species, **C** – Simpson diversity, WG – white ginger lily, IF – invaded forest, SR – spike-rush, RV – riparian vegetation.

The nMDS analyses showed that the aquatic insect assemblage associated with ginger lily banks differed from other bank vegetations. The axis1 accounted for 59% of the cluster analyses (stress= 0.22) (Figure 2). The ANOSIM analyses showed that aquatic insect assemblages associated with invasive macrophytes exhibited a lower dissimilarity index compared with other profiles ($p < 0.05$) (Figure 3). The dissimilarity distances of white ginger lily bank assemblages were lower especially when compared to banks without invasion

(partially invaded forest [$R= 0.43$, $p= 0.004$], native macrophyte [$R= 0.83$, $p= 0.002$], riparian vegetation [$R= 0.70$, $p= 0.002$]). These results supported the nMDS analyses.

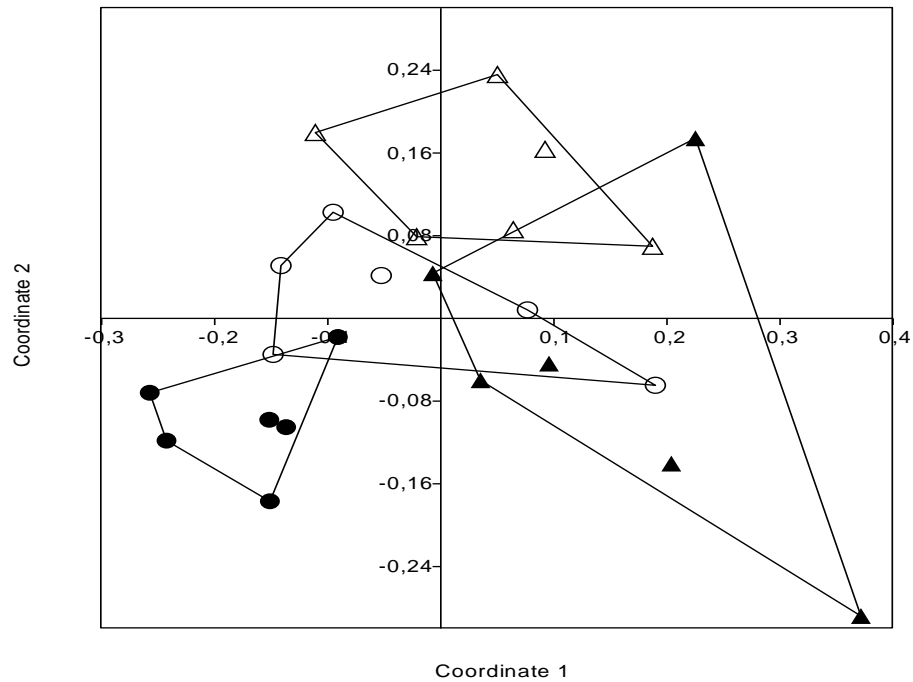


Fig. 2 Analyses of nMDS of aquatic insect assemblages associated with white ginger lily banks and native vegetation profiles in the littoral zone of a tropical reservoir in the Brazilian Savanna. Filled circle -white ginger lily; unfilled circle - invaded forest unfilled triangle - spike-rush, filled triangle - riparian vegetation.

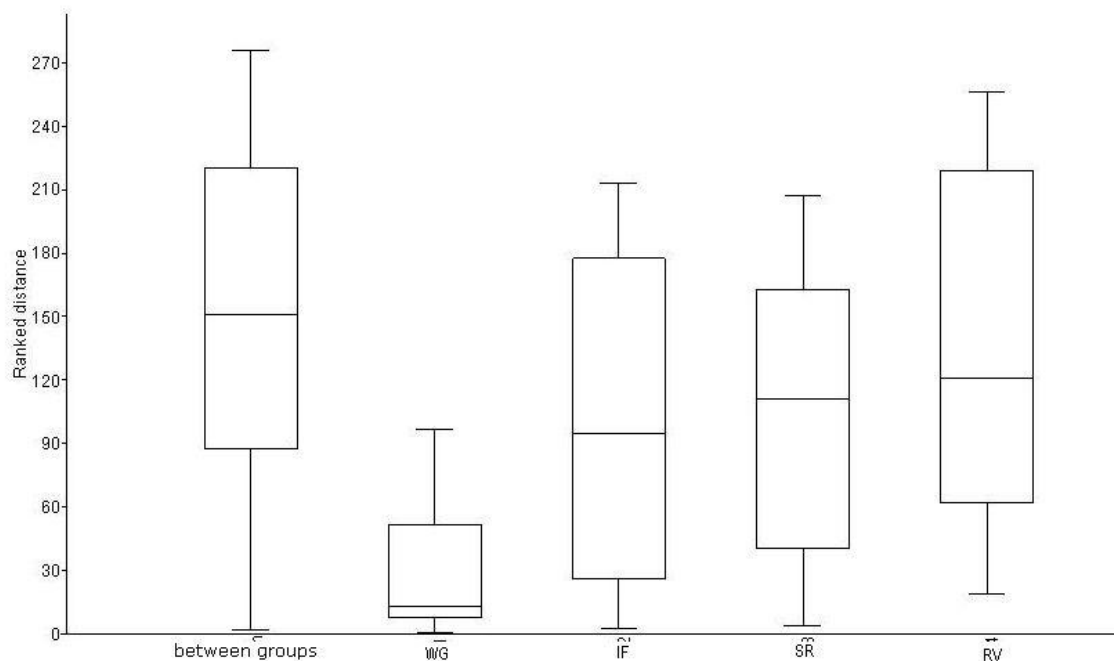


Fig. 3 Analyses of dissimilarity (ANOSIM) among aquatic insect assemblages associated with white ginger lily banks and native vegetation profile in the littoral zone of a tropical reservoir in the Brazilian Savanna. WG – white ginger lily, IF – invaded forest, SR - native macrophyte, RV – riparian vegetation.

The results of the analyses of indicator species (IndVal index) classified eight aquatic insect species as indicator species of vegetation profiles (Table 3). We observed that three species presented a strong association with white ginger lily banks ($A > 0.70$). *Tenagobia* sp. (Corixidae, Hemiptera) was most closely associated with white ginger lily ($A = 1.00$), but *Labrundinia unicolor* (Tanypodinae - Diptera) was the species that showed exclusive association ($B = 1.00$) with restricted distribution on this bank. Additionally, *Labrundinia paulae* (Tanypodinae - Diptera) was strongly associated with partially invaded forest banks ($A = 0.85$). We observed similar results with *Diastatops* sp. (Libellulidae – Odonata) ($A = 0.92$) and *Ablabesmyia depaulai* (Tanypodinae – Diptera) ($A = 0.85$) when we combined the invasive macrophyte areas with partially invaded forest banks (WG+IF). Regarding all bank vegetations on the reservoir, we observed that *Caladomyia kapilei* (Chironominae – Diptera)

($A= 0.94$, $B= 0.94$) and *Ablabesmyia strixinoae* (Tanypodinae – Diptera) ($A= 0.91$, $B=1.00$) were generally distributed in both invaded and non-invaded bank vegetations.

Table 3. Analysis of aquatic insect species indicators on bank vegetations in the littoral zone of a tropical reservoir in the Brazilian Savanna. WG– white ginger lily, IF – invaded forest, SR – spike-rush, RV – riparian vegetation

Vegetation profile	A	B	r	p-value
WG				
<i>Labrundinia unicolor</i>	0.72	1.00	0.85	0.049
<i>sLabrundinia</i> sp	0.80	0.67	0.73	0.009
<i>Tenagobia</i>	1.00	0.50	0.71	0.039
IF				
<i>Labrundinia paulae</i>	0.85	0.67	0.77	0.009
RV				
<i>Fissimentum</i> sp2	0.91	0.83	0.87	0.005
WG + IF				
<i>Ablabesmyia depaulai</i>	0.87	0.83	0.85	0.012
<i>Diastatops</i>	0.92	0.75	0.84	0.013
WG + IF + SR				
<i>Caladomyia kapilei</i>	0.94	0.94	0.94	0.018
WG + IF + RV				
<i>Ablabesmyia strixinoae</i>	0.91	1.00	0.95	0.019

4. Discussion

As many other invasive plant species (*e.g. Hydrilla verticillata*) (Theel et al., 2008) the invasion of white ginger lily shifted the aquatic insect assemblage composition. Our results showed that white ginger lily shifted aquatic insect assemblages causing a decrease in the dissimilarity distance when compared to other native vegetation on profiles. These results could be related to habitat changes caused by high plant biomass. Faster vegetative growth of white ginger lily could alter the littoral habitat by the occupation of shallow areas. The white ginger lily banks are formed by the high density of individuals (de Castro et al., 2016). We observed in white ginger lily monospecific banks that there was high accumulation of

biomass in shallower zones. Probably, this fact enables other individuals to move forward to open water areas of the reservoir.

Although the white ginger lily monospecific bank presented a lower dissimilarity of aquatic insect assemblage, in our study, the richness and Simpson diversity associated with invasive macrophytes were similar to native bank vegetations. We could infer that this pattern was due to the low spatial scale among bank vegetation of the studied reservoir. The short distances among the vegetation profiles were not long enough to disrupt aquatic insect assemblages. Nevertheless, the higher abundance of specimens on white ginger lily banks was the responsible variable that results in low dissimilarity diversity patterns. This could indicate a specific condition of habitat promoted by this macrophyte in the littoral zone. Such a habitat condition favoured aquatic insect taxa which presents adapted lifestyles to dwelling on these monospecific banks.

Aquatic insects have been considered good bio indicators of impacted habitats by invasive plants. Indicator species have been used especially in studies that analysed the influence of monoculture plants such as banana and sugar cane crops (Corbi et al., 2013; Corbi and Trivinho-Strixino, 2017). In our study, the ecological variables of richness and Simpson diversity did not demonstrate differences between white ginger lily banks and native bank vegetation. Nonetheless, the IndVal index provided good information about the composition of aquatic insect assemblages associated with this invasive macrophyte. As demonstrated through this index, the distribution of *Labrundinia unicolor* was restricted to white ginger lily banks (GM), and *Labrundinia paulae* was strongly associated with partially invaded forest (IF). This genus has been described as an aquatic insect commonly associated with dominant macrophyte species, especially *Salvinia* (da Silva et al., 2011). It is believed that this macrophyte with thin and ramified roots provides shelter against predators, and the algae attached to it serves as a main food resource for macrofauna (Trivinho-Strixino, 2000).

Additionally, it was demonstrated that the habitat characteristics provided by *Salvinia* provide a differential aquatic insect assemblage in lentic systems, which used host small taxa as *Labrundinia* (Peiró et al., 2016).

Although the biology and ecology of *L. unicolor* and *L. paulae* is unknown, the association with monospecific banks of white ginger lily and invaded banks could be related to specific conditions of habitat. The fast growth of white ginger lily results in banks formed by an entanglement of rhizomes, branches and leaves leading to the overlapping of many branches. These characteristics of the bank probably resulted in increased spatial complexity, which promoted higher microhabitat availability. Aquatic insect predators (e.g. *Labrundinia*, *Ablabesmyia* and *Diastatops*) are described as being associated with various invasive macrophyte species (e.g. *Ceratophyllum demersum*) (Tóth et al., 2012). Their presence in freshwater systems increase the habitat complexity and shift aquatic insect assemblages (Kuehne et al., 2016). We concluded that the different composition of indicator species among invaded and partially invaded banks could be used as aquatic insect indicator species to monitor the initial stage of invasion by white ginger lily in the littoral zone of the Fazzari reservoir.

In the present study, we demonstrated that invasive white ginger lily can shift aquatic insect assemblages, which identify species that can be considered indicators of changes in the littoral zone habitat. Recently, the interest in the invasion of white ginger lilies in freshwater systems in Brazil has increased and the analysis of indicator species proved to be a good tool for monitoring changes in freshwater systems caused by invasive macrophyte species. We emphasize the need to expand the analyses of the impacts of white ginger lily to other freshwater systems. The composition of aquatic insect indicators will contribute to a more comprehensive body of information regarding its influence on freshwater biodiversity.

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References

- Arimoro, F.O., Ikomi, R.B., 2009. Ecological integrity of upper Warri River, Niger Delta using aquatic insects as bioindicators. *Ecol. Indic.*, 9, 455-461.
- Blakely, T.J., Harding, J.S., Mcintosh, A.R., Winterbourn, M.J., 2006. Barriers to the recovery of aquatic insect communities in urban streams. *Freshw. Biol.*, 51, 1634-1645.
- Boyero, L., Barmuta, L.A., Ratnarajah, L., Schmidt, K., Pearson, R.G., 2012. Effects of exotic riparian vegetation on leaf breakdown by shredders: a tropical–temperate comparison. *Freshw. Sci.* 2, 296–303
- Cáceres, M.D., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566-3574.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, 18, 117-143.
- Corbi, J.J., Kleine, P., Trivinho-Strixino, S., 2013. Are aquatic insect species sensitive to banana plant cultivation? *Ecol. Indic.*, 25, 156-161
- Corbi, J.J., Trivinho-Strixino, S., 2017. Chironomid species are sensitive to sugarcane cultivation. *Hydrobiologia*, 785, 91-99.
- Da Silva, F.L., Oliveira, H.R.N., Escarpinati, S.C., Fonseca-Gessner, A.A., de Paula, M.C., 2011. Colonization of leaf litter of two aquatic macrophytes, *Mayaca fluviatilis* Aublet and *Salvinia auriculata* Aublet by aquatic macroinvertebrates in a tropical reservoir. *Rev. Ambient. Água*, 6, 30-39.
- De Cáceres, M., 2013. How to use the indicpecies package (ver. 1.7. 1). Catalonia, Centre Tecnològic Forestal de Catalunya.
- De Cáceres, M., Jansen, F., De Cáceres, M.M., 2015. Package ‘indicpecies’.

de Castro, W.A.C., Almeida, R.V., Leite, M.B., Marrs, R.H. & Matos, D.M.S. 2016. Invasion strategies of white ginger lily (*Hedychium coronarium*) J. König (Zingiberaceae) under different competitive and environmental conditions. *Environ. Exp. Bot.*, 127, 55-62.

Dominguez, E., Fernandez, H.R., 2009. Macroinvertebrados bentónicos sudamericanos: sistemática y biología. Tucuman, Argentina.

Dundgeon, D., 2010. Prospects for sustaining freshwater biodiversity in the 21 st century: linking ecosystem structure and function. *Sciencedirect*, 2, 422-430

Kovalenko, K.E., Dibble, E.D., Slade, J. G. 2010. Community effects of invasive macrophyte control: role of invasive plant abundance and habitat complexity. *J. Appl. Ecol.*, 47, 318-328.

Kovalenko, K.E., Dibble, E.D., 2011. Effects of invasive macrophyte on trophic diversity and position of secondary consumers. *Hydrobiologia*, 663, 167-173.

Kuehne, L.M., Olden, J.D., Rubenson, E.S., 2016. Multi-trophic impacts of an invasive aquatic plant. *Freshw. Biol.*, 61, 1846-1861.

Leite-Rossi, L.A., Saito, V.S., Cunha-Santino, M.B., Trivinho-Strixino, S., 2016. How does leaf litter chemistry influence its decomposition and colonization by shredder Chironomidae (Diptera) larvae in a tropical stream? *Hydrobiologia*, 771, 119-130

Navarro-Llácer, C., Baeza, D., de las Heras, J., 2010. Assessment of regulated rivers with indices based on macroinvertebrates, fish and riparian forest in the southeast of Spain. *Ecol. Indic.*, 10, 935-942.

Oliveira, C.S.N., da Silva, M.A., Fonseca-Gessner, A.A., 2013. Neotropical *Ablabesmyia* Johannsen (Diptera: Chironomidae, Tanypodinae). Part I. *Zootaxa*, 3733, 1–123.

Peiró, D.F., do Amaral, G.F., Saulino, H.H. Structure community of aquatic insects associated with different macrophytes in ornamental lakes in a savanna region, Southeastern Brazil. *Panam. J. Aquat. Sci.*, 10, 273-282

Rosenberg, D.M., Resh, V.H., 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman & Hall.

Saulino, H.H., Leite-Rossi, L.A., Trivinho-Strixino, S., 2016 The effect of small reservoirs on chironomid diversity and trait composition in Savanna streams: evidence for Serial Discontinuity Concept. *Hydrobiologia*, 782, 1-11.

Schultz, R., Dibble, E., 2012. Effects of invasive macrophytes on freshwater fish and macroinvertebrates communities: the role of invasive plants traits. *Hydrobiologia*, 684, 1-14

Silva, F.L., Fonseca-Gessner, A.A., Ekrem, T., 2014. A taxonomic revision of genus *Labrundinia* Fittkau, 1962 (Diptera: Chironomidae: Tanypodinae). *Zootaxa* 3769, 1–185.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at: <http://www.R-project.org> (accessed 26.10.16).

Theel, H.J., Dibble, E.D., Madsen, J.D., 2008. Differential influence of a monospecific and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. *Hydrobiologia*, 600, 77-87.

Thomaz, S.M.; Cunha, E.R., 2010 The role of macrophytes in habitat structuring ins aquatic ecosystem: methods of measurements, causes and consequences on animal assemblages's composition and biodiversity. *Acta Limnol. Brasi.*, 22, 218-236

Tóth, M., Móra, A., Kiss, B., Dévai, G., Specziár, A., 2012. Are macrophyte-dwelling Chironomidae (Diptera) largely opportunistic in selecting plant species? *Eur. J. Entomol.*, 109, 247.

Trivinho-Strixino, S., Correia, L.C.S., Sonoda, K., 2000. Phytophilous Chironomidae (Diptera) and other macroinvertebrates in the ox-bow Infernão Lake (Jataí Ecological Station, Luiz Antônio, SP, Brazil). *Rev. Bras. Biol.*, 60, 527-535.

Trivinho-Strixino, S., 2011. Larvas de Chironomidae: guia de identificação. Departamento de Hidrobiologia/Lab. De Entomologia Aquática, São Carlos.

Trivinho-Strixino, S., 2012. A systematic review of Neotropical *Caladomyia* Säwedal (Diptera: Chironomidae). *Zootaxa*, 3495, 1–41.

Trivinho-Strixino, S., Pepinelli, M., 2015. A systematic study on *Endotribelos* Grodhaus (Diptera: Chironomidae) from Brazil including DNA barcoding to link males and females. *Zootaxa*, 3936, 1–41.

Vander Zanden, M.J., Casselman, J.M., Rasmussen, J.B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401, 464-467.

Warfe, D.M., Barmuta, L.A., 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia*, 150, 141-154

Capítulo II

The invasive white ginger lily (*Hedichium coronarium*) simplifies the trait composition of an insect assemblage in the littoral zone of a Savanna reservoir

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Abstract

The invasive white ginger lily (*Hedichium coronarium* – J. Koenig, 1783) simplifies the trait composition of an insect assemblage in the littoral zone of a Savanna reservoir. Invasive plants are believed to shift the trait composition of aquatic insects dwelling in banks of lentic ecosystems. In this study, we analyzed the relationship between the presence of the invasive white ginger lily (*H. coronarium*) and the functional trait indices of the aquatic insect assemblage in the littoral zone of a tropical reservoir. We sampled aquatic insects on the invaded and non-invaded banks of the reservoir and then analyzed the insect trait indices by estimating the Functional Dispersion (FDis), Functional Evenness (FEve) and the Functional Divergence (FDiv), as well as the Community level Weight-Mean traits (CWM). Finally, we compared these indices between invaded and non-invaded banks as well as their relationship with the abiotic variables, such as dissolved oxygen, pH, depth and water temperature. The result confirmed that the invaded banks had lower values of functional indices as well as dissolved oxygen. However, this abiotic variable was found to have no effect on the functional indices. In addition, the white ginger lily bank presented higher contribution of collector-gathering to predator-piercer groups. We suggest that the invasion of white ginger lily promotes low heterogeneity habitat resulting in simplification on functional traits of aquatic insect assemblage.

Keywords

Biodiversity

Biological invasions

Functional diversity

Lentic system

1. Introduction

The littoral zone of lentic system contains highly diversified community (Heino 2000, 2008); this biodiversity of this ecosystem have been seriously disturbed and threatened by human activities and is on the verge of losing its characteristic features (e.g. nutrient storage, water supply, recreation) (Brauns et al., 2007; McGoff et al., 2013). The invasive species plants are among the main stressors agents that shift the diversity and structure of many assemblages in freshwater systems (Kelly and Hawes, 2005), especially of the aquatic insects (Kovalenko et al., 2010). With respect to this, it research has shown that alteration of structure of aquatic insect assemblage by invasive plants has important implications to their diversity maintenance. This is justified by the ecological relationships observed between these representative communities, especially those involving the changes caused by decomposition and habitat structure (Vannote et al., 1980; Graça, 2001).

For instance, the growth of macrophytes in the littoral zones provides habitat (Cheruvilil et al., 2000; Becerra-Muñoz and Schramm Jr., 2007) and food resource that promote high diversity of aquatic insects (Cronin et al., 1998; Clapcott and Bunn, 2003; Stenberg and Stenberg, 2012). Nevertheless, the consumption of invasive macrophyte plants such as Eurasian watermill foil (*Myriophyllum spicatum*), which contains high concentrations of secondary compounds (e.g., polyphenols), can interfere with the growth rate of some aquatic insect species (Choi et al., 2002). This could results to changes of the structural assemblage due to the removal of some functional feeding group especially shredders (Boyero et al., 2012) this change would have a negative impact in the bioconversion of Coarse Particulate Organic Matter CPOM to Fine Particulate Organic Matter (FPOM) which is the major food resource to collector-gather and filtering-feeders groups. Another important aspect is related to changes in habitat structure, the change in the habitat structure is to verify the absence of which invasive macrophyte species have caused the changes in the freshwater systems. In respect to this, invasive submerged macrophyte species such as *Hydrilla* (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*) with high morphological complexity host great abundance of aquatic insects, especially those that present high vulnerability to fish predators (e.g. Odonata) (Theel et al., 2008; Kovalenko and Dibble, 2011). This occurs because macrophytes with higher morphological complexity impair to

predators identify their preys, which present adaptive ability to blend with their intrinsic spaces. The dominance of these invasive macrophytes have been reported as the major factor that disrupts food webs through decoupling of predator-prey interactions due to the homogenization of habitat (Kovalenko and Dibble, 2011).

Considering the role of ecological processes previously mentioned and the biological invasions causing the decrease biodiversity (Dundgeon, 2010), our aim in this study was to investigate the influence of the invasive plant, white ginger lily (*Hedychium coronarium* – J. Köenig, 1783) in the aquatic insect assemblage's traits composition in the littoral zone of a tropical reservoir. In Brazil, this invasive plant is widely distributed with high predominance in marshy areas, mainly in coastal regions, as well as in transition regions between the Atlantic Forest and the Cerrado (Zenin and Ziller, 2011). These invasive emergent plants species (e.g. *Urocloa* sp.), the white ginger lily presents strong competitive strategies such as fast growth and rapid dispersal that enable them to become dominant in wetlands, riparian zones, lake banks, where it forms dense populations (De Castro et al., 2016). Additional information regarding the influence of these invasive plants species in aquatic insects assemblages have been attempted to explain the change in the functional feeding group's (FFG) and the claim about whether invasive macrophyte species can alter other aquatic insect's functional structures such as body length and habit, which are directly related to habitat modification. Here, we explored the Functional Diversity (FD) using a multimetric dissimilarity index approach, which we explored as aquatic insect's combination traits (FFG, body length, strategy feed and habitat) to analyze the influence of invasive plant in the aquatic insect trait assemblage composition. To do this, we utilized three FD indices, which explore different ecological traits aspect of niche assemblages: (i) Functional dispersion (FDis) – which measure how composition traits differ among species within assemblages; (ii) Functional evenness (FEve) – which measure how niche space is occupy by traits composition assemblages, and (iii) Functional divergence (FDiv) – which measure the level of niche differentiation by functional traits within the assemblages.

It was expected that the dominance of the invasive white ginger lily would modify some of the environmental conditions such as abiotic variables and the habitat structure of this invaded bank and consequently would lead to a simplification of the trait composition of the aquatic insect assemblage resulting to a decrease of the FD indices. This resultant would be a

niche constrain of aquatic insect assemblages, once specified the aquatic species traits selection would mirror the habitat and the resource food modification caused by the invasive dominance of macrophyte.

2. Material and methods

2.1 Study area

This study was performed in a tropical reservoir located in a preserved area of Brazilian Savanna vegetation (Cerrado Biome) in the central region of São Paulo State (Brazil) (Fig. 1). The Fazzari reservoir presents chemical characteristics such as high levels of dissolved oxygen, slightly acidic pH, low ammonium and nitrite concentrations (Table 1), and diverse vegetation on its banks. Its total area is 11,370 m², 220 meters long, an average width of 51.5 m and average depth of 1.10 m and maximum 4 m. According to the Koeppen classification, this region is characterized with hot and wet summers and dry winters (Cwa), with average annual temperatures ranges of 18–22°C and an average annual rainfall of approximately 1,450 mm.

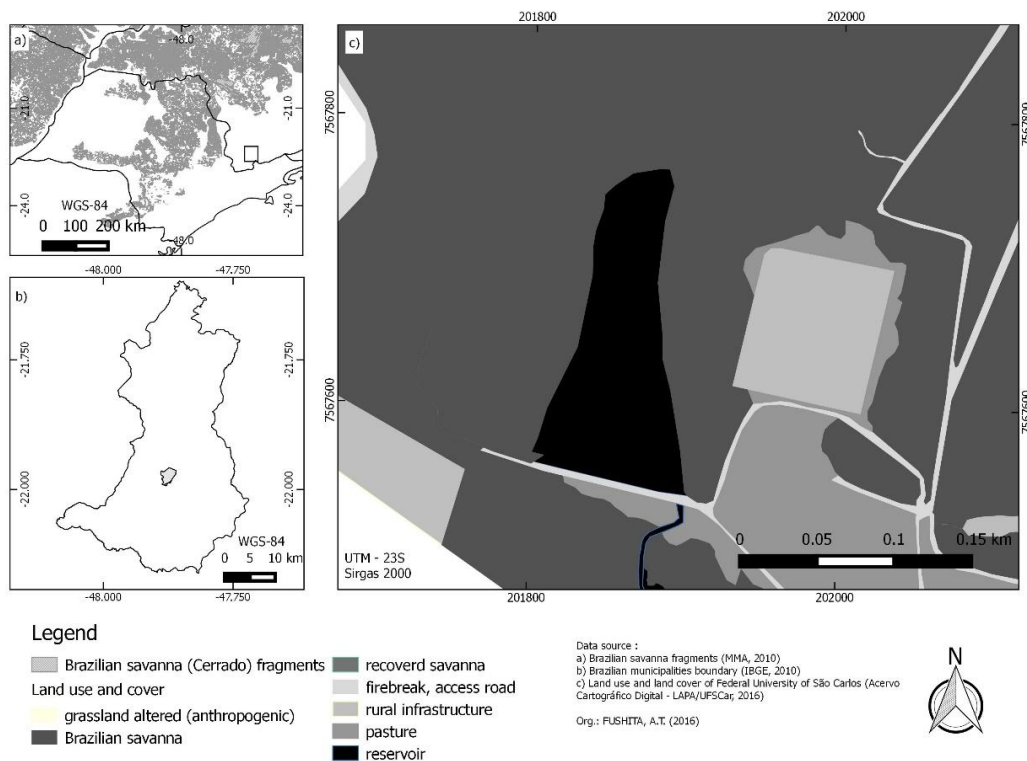


Fig. 1. Location and characterization of plant composition banks of Fazzari reservoir in the Brazilian Savanna (Cerrado Biome, Brazil).

Table 1. Abiotic characterization of Fazzari reservoir localized in the Brazilian Savanna (Cerrado Biome) area.

abiotic variable	Reservoir banks	
	invaded bank	non-invaded
dissolved oxygen (mg/L ⁻¹)	7.67 ±0.61	8.29 ±0.26 *
pH	5.42 ±0.51	5.71 ±0.26
water temperature (°C)	19.25 ±1.54	18.60 ±0.51
litoral depth (cm)	0.42 ±0.13	0.37 ±0.14

(*) – p<0.05

The vegetation surrounding its banks consists of two main profiles. The right reservoir bank, which stretch about 80 meters is completely dominated by the invasive white ginger lily (*H. coronarium*) followed by a forest partially invaded by the same invasive plant. The left reservoir bank is surrounded by a native riparian forest (trees, shrubs and ferns) and with amphibian macrophyte *Eleocharis* R. Brown.

2.2 Sampling and identification of fauna

The aquatic insect from the invaded bank and non-invaded reservoir bank were sampled at the beginning of the dry season (May/June, 2014). Twelve stretches with 10 meters distance long were randomly sorted in each vegetation bank, totaling 48samples. At each stretch, we took one sample from the littoral zone using two collectors: the kick sampling method (“D” net - mesh 250 µm) was used in the 10 meters long stretches in areas nearer to the reservoir bank, and Ekman grab was used at 1.5 m away from the reservoir bank. In additional, we also measured the abiotic variables such as the dissolved oxygen, pH, and water temperature using a multisensory probe (HORIBA U010), the depth was obtained using a measuring tape.

The specimens were sorted live on transilluminated trays and conserved in 80% ethanol. We carried out the specimen identification to the lowest possible taxonomic level using identification taxonomic keys of aquatic insects of the Neotropical region (Domingues and Fernandes, 2009; Trivinho-Strixino, 2011; Trivinho-Strixino, 2012; Oliveira et al., 2013;

Silva et al., 2014; Trivinho-Strixino and Pepinelli, 2015) and with the help of specialists for Odonata.

Functional classification of aquatic insects

In order to obtain the FD indices, we attributed qualitative scores according to the classification trait as follow.

(i) Functional feeding groups (FFG): scrapers, shredders, collectors and predators. For these biological traits, we classified the FFG according to studies of the Neotropical region (see Table 2) and scored the values according to the Anderson and Cummins (1979) ranking of the organic material potentially available to aquatic insects on an increasing nutritive gradient as: (1) scrapers that consume the microbiota associated with senescence leaves and stems plants. (2) shredders that consume wood and leaf litter and live leaf tissue; (3) collectors that consume decomposing vascular plant and FPOM; (4) predators that usually consume animal tissues.

(ii) Feeding strategy – detritivore, filtering-feeder, gatherer, herbivore, engulfer and piercer. For this biological trait, we scored the aspects according to the organic particle size that are used by larvae: (1) detritivore (detritus), (2) filter-feeder (FPOM), (3) gatherer (medium detrital particles) and (4) herbivore (CPOM), (5) engulfer (planktonic and benthic algae) and piercer (generally invertebrates with high biomass).

(iii) Body length – (1) short (about 10 mm long), (2) mid (between 10 mm and 30 mm long) and (3) long (higher than 30 mm long).

(iv) Habit – (1) sprawler, (2) swimmers, (3) planktonic, (4) diver, (5) climber/clinger, (6) silk tube builder, (7) miner, (8) burrower. The classification of functional feeding groups of each taxon followed the diet studies of aquatic insects in the Neotropical regions (Table 2). In the cases, where we lacked the knowledge about feeding strategy and habit of some taxa, we utilized the information available in Merritt and Cummins (1996).

Table 2. Score and classification of aquatic insect's functional traits associated with an invaded and non invaded bank in littoral zone of Fazzari reservoir – Brazilian Savanna (Cerrado Biome).

taxa	Functional trait scores					References
	body	ffg	feed	habitat	bank	
<i>Campsurus</i> Walker, 1853	2	3	2	8	I N	Molineri and Emmerich (2010), Brasil et al. (2014)
<i>Caenis</i> Stephens, 1835	1	1	4	1	I N	Edmunds and Waltz (1996), Molineri and Malzacher (2007)
<i>Ulmeritus</i> Traver, 1956	1	3	3	2	I N	Cummins (2005), Sales and Dominguez (2012).
<i>Callibaetis</i> Eaton, 1875	1	1	4	2	- N	Salles et al. (2004), Da-Silva and Salles (2012), Tomanova et al. (2006)
<i>Aedomyia</i> Theobald, 1901	1	3	2	3	I N	Merritt and Cummins (1996)
<i>Dasyhelea</i> Kieffer, 1911	1	3	3	1	I N	Ferreira-Kelpler et al. (2014)
<i>Gyrinus</i> Latreille, 1810	2	4	5	2	I N	Archegelesky et al. (2009)
<i>Desmopachria</i> Babington, 1841	1	4	6	4	I N	Braga and Ferreira-Jr (2014)
<i>Andonectes</i> Guéorguiev, 1971	1	4	6	4	I -	Archegelesky et al. (2009)
<i>Laccophilus</i> Leach, 1815	1	4	6	4	I N	Archegelesky et al. (2009)
<i>Pronoterus</i> Sharp, 1882	1	4	5	2	I -	Archegelesky et al. (2009)
<i>Mesonoterus</i> Sharp, 1882	1	4	5	2	I N	Archegelesky et al. (2009)
<i>Hydrocanthus</i> Say, 1823	1	4	5	2	I N	Archegelesky et al. (2009)
Scirtidae	1	1	4	5	- N	Merritt and Cummins (1996)
<i>Macronema</i> Pictet, 1836	2	3	2	5	I N	Flint and Bueno-Soria (1982)
<i>Cynellus</i> Banks, 1913	1	3	2	5	I N	Pes et al. (2014)
<i>Oecetis</i> McLachlan, 1877	1	4	5	5	I N	Domingues et al. (2009)
<i>Protoneura</i> Selys, 1857	2	4	5	5	I N	Costa et al. (2004)
<i>Oxyagron</i> Selys, 1876	2	4	5	5	I -	Costa et al. (2004)
<i>Telebasis</i> Selys, 1865	2	4	5	5	I N	Costa et al. (2004)
<i>Acanthagrion</i> Selys, 1876	3	4	5	5	I N	Costa et al. (2004)
<i>Diastatops</i> Rambur, 1842	2	4	5	1	I N	Costa et al. (2004)
<i>Miathyria</i> Kirby, 1889	3	4	5	1	I N	Costa et al. (2004)
<i>Erythrodiplax</i> Brauer, 1842	3	4	5	1	I N	Costa et al. (2004)
<i>Macrothemis</i> Hagen, 1868	2	4	5	1	I -	Costa et al. (2004)
<i>Orthemis</i> Hagen, 1861	2	4	5	1	I -	Costa et al. (2004)
<i>Idiataphe</i> Cowley, 1934	2	4	5	1	I N	Costa et al. (2004)
<i>Gynothemis</i> Calvert, 1909	2	2	1	4	I N	Costa et al. (2004)
<i>Lestes</i> Leach, 1815	3	4	5	5	I -	Costa et al. (2004)
<i>Belostoma</i> Latreille, 1807	3	4	5	5	- N	Nieser and Melo (1997)
<i>Notonecta</i> Hungeford, 1933	1	4	5	5	I N	Nieser and Melo (1997)
<i>Limnocois</i> Stål, 1860	1	4	5	5	I N	Nieser and Melo (1997)
<i>Tenagobia</i> Bergroth, 1899	1	1	4	2	I -	Nieser and Melo (1997)
<i>Aedokritus coffeatus</i> Trivinho-Strixino, 1997	1	3	3	8	I N	Butakka et al. (2014)
<i>Asheum beckae</i> Sublette & Sublette 1964	1	3	3	8	I N	Butakka et al. (2014)
<i>Caladomyia kapilei</i> Trivinho-Strixino, 2012	1	3	3	5	I N	Butakka et al. (2014)
<i>Caladomyia riotarumensis</i> Reiff, 2000	1	3	3	5	I N	Butakka et al. (2014)
<i>Chironomus</i> Meigen	1	3	3	8	I N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Cladopelma forcipes</i> (Rempel, 1939)	1	3	3	8	N	Merritt and Cummins (1996)
<i>Endotribelos bicolor</i> Trivinho-Strixino & Pepinelli, 2015	1	2	2	8	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Goeldichironomus maculatus</i> Trivinho-Strixino & Strixino, 1991	1	3	3	8	I -	Merritt and Cummins (1996)
<i>Polypedium</i> sp5 cf Trivinho-Strixino, 2011	1	3	3	2	I N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Polypedium</i> (Tripodura) sp3 cf Trivinho-Strixino, 2011	1	3	3	2	I N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Polypedium</i> sp3 cf Trivinho-Strixino, 2011	1	3	3	2	I N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Polypedium</i> sp4 cf Trivinho-Strixino, 2011	1	3	3	2	- N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Stenochironomus</i> Kieffer, 1919	1	2	4	7	I N	Sanseverino and Nessimian (2008), Butakka et al. (2014)
<i>Ablabesmyia depaulai</i> Neubern, 2013	1	4	5	1	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Ablabesmyia laurindoi</i> Neubern, 2013	1	4	5	1	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Ablabesmyia metica</i> Roback, 1983	1	4	5	1	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Ablabesmyia strixinoae</i> Neubern, 2013	1	4	5	1	I -	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Clynotanytus</i> Kieffer, 1913	2	4	5	1	- N	Butakka et al. (2014)
<i>Coelotanytus</i> Kieffer, 1913	2	4	5	1	I N	Butakka et al. (2014)
<i>Labruninia carolae</i> Silva, 2014	1	4	5	1	I N	Butakka et al. (2014)
<i>Labrundinia paulae</i> Silva, 2014	1	4	5	1	- N	Butakka et al. (2014)
<i>Labrundinia</i> sp Fittkau, 1962	1	4	5	1	I N	Butakka et al. (2014)
<i>Labrundinia tenata</i> Silva, 2013	1	4	5	1	I N	Butakka et al. (2014)
<i>Labrundinia unicolor</i> Silva, 2013	1	4	5	1	I N	Butakka et al. (2014)
<i>Larsia</i> Fittkau, 1962	1	4	5	1	- N	Henriques-Oliveira et al. (2003)
<i>Monopelopia</i> Fittkau, 1962	1	4	5	1	I N	Butakka et al. (2014)
<i>Pentaneura</i> Philippi, 1865	1	4	5	1	- N	Henriques-Oliveira et al. (2003), Butakka et al. (2014)
<i>Procladius</i> Skuse, 1889	1	4	5	1	- N	Henriques-Oliveira et al. (2003), Butakka et al. (2014)
<i>Fissimentum desiccatum</i> Cranston & Nolte, 1996	1	3	3	1	I N	Butakka et al. (2014)
<i>Fissimentum</i> sp 3 cf Trivinho-Strixino, 2011	1	3	3	1	- N	Butakka et al. (2014)
<i>Fissimentum</i> sp 2 cf Trivinho-Strixino, 2011	1	3	3	1	- N	Butakka et al. (2014)
<i>Tanytarsus</i> sp v. d. Wulp, 1874	1	3	2	6	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)
<i>Tanytarsus obiriciae</i> Trivinho-Strixino & Sonoda, 2006	1	3	2	6	I N	Henriques-Oliveira et al. (2003), Sanseverino and Nessimian (2008)

2.3 FD analyses and fauna composition

The FD indexes were calculated by combining a matrix containing the abundances and trait classification of each taxon as cited above. The FD index is represented by the distance measured based on trait values, where the distance between the taxa is calculated using a PCoA matrix. The distances of aquatic insect's assemblage traits were calculated using the Gower dissimilarity distance "in a trait space", separating species with a cluster analysis based on their proximity in a trait distance matrix. To do so, we used the "FD-package" (Laliberté et al., 2014), which is available on the R platform (R Development Core Team, 2014).

In order to analyze the trait composition of aquatic insect assemblages, the following FD indices were considered: 1) Functional Dispersion (FDis) – it measures the mean weight mean distance of the individual species to their weight centroid, where the weights are their relative abundances. FDis has been considered as a functional index of biodiversity (Anderson et al., 2006; Laliberté and Legendre, 2010); 2) Functional Evenness (FEve) – it measures the niche space occupied by the community. This index analyses the effective use of all resource bands that are available for the community; 3) Functional divergence (FDiv) – it measures the level of niche differentiation occupied by the community (Manson et al., 2005); 4) Community-level Weight Means (CWM) – it measures the relevance of the traits found in the community. This measure of diversity is directly related to the hypothesis of Grime's mass ratio, which considers that the more abundant traits of the species determine the ecosystem processes (Lavorel et al., 2008).

2.4 Data analysis

We compared the estimated values of FDis, FEve, FDiv and CWM-traits between the invaded and non-invaded banks, as well as the abiotic variables, with a permutation test for independent samples (n=999), which is analogous to a nonparametric t-test. In addition, we analyzed whether there were some influence of abiotic variables in the FD indices. To do this, we used a multiple linear regression model, in which we modeled only the FD indices (dependent variable) and abiotic variables (independent variable) that presented significant differences between the invaded and non-invaded banks.

We complemented our study by comparing the assemblage composition throughout the analysis of the similarity percentage (SIMPER) using the abundances of FFG as well as aquatic insect taxa. It verifies the contribution of each FFG and taxon to the observed similarity between the vegetation banks. In addition, this analysis enables us to identify the FFG that are most important in creating the observed pattern of structural assemblage. The Bray-Curtis index was used to calculate the aquatic insect assemblage's FFG and the taxa dissimilarity on the invaded and non-invaded banks and the relative participation of the taxon to deduce the influence in the trait composition of aquatic insect assemblage.

3. Results

2,067 specimens were collected and analyzed for the trait composition of 66 taxa (Table2). The observed lower averages were FDis ($t = -6.08$, $p < 0.0001$), FEve ($t = -4.03$, $p < 0.001$) of aquatic insect assemblages in the invaded bank (Figure 2). CWM-trait of functional feeding groups ($t = 2.76$, $p = 0.01$) presented the same results, however the CWM-trait of strategic feed ($t = 4.06$, $p < 0.001$) was higher in the invaded bank (Figure3). For the abiotic variables, the observed lower dissolved oxygen was ($t = -3.24$, $p = 0.004$) in the invaded bank (Table 1).

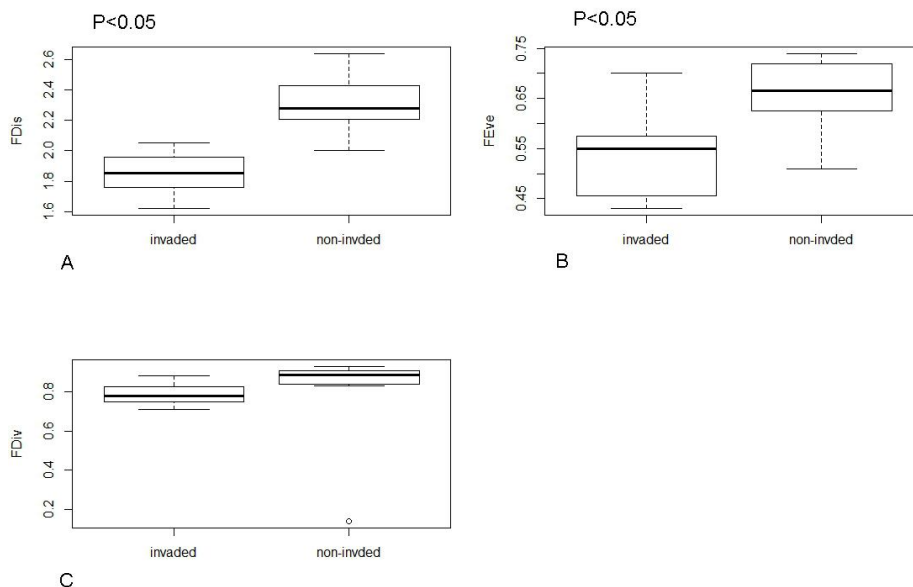


Fig. 2. The average values of FD indices of aquatic insect assemblages in invaded and non-invaded bank by white ginger lily of a reservoir in Brazilian Savanna (Cerrado Biome) – A – FDis, B – FEve, C – FDiv.

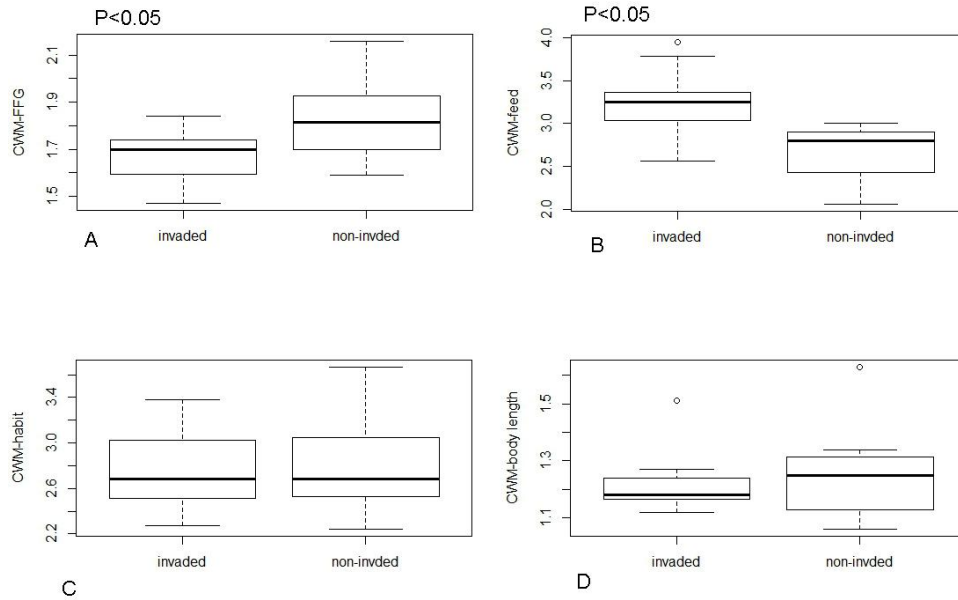


Fig. 3. The average values of CWM-trait values of aquatic insect assemblages in invaded and non-invaded banks by white ginger lily of a reservoir in Brazilian Savanna (Cerrado Biome). A- CWM-FFG, B-CWM-feed, C-CWM-habit, D-CWM body length.

With respect to the influence of the abiotic variables in the FD indices, we observed that the dissolved oxygen had no influence on the FDis ($b = -0.05$, $p = 0.53$, $R^2 = 0.22$), FEve ($b = -0.03$, $p = 0.34$, $R^2 = 0.08$), CWM-trait of functional feeding groups ($b = 0.05$, $p = 0.46$, $R^2 = 0.21$) or CWM-trait of strategy feeding ($b = -0.04$, $p = 0.81$, $R^2 = 0.22$).

The SIMPER analyses indicated an overall average dissimilarity of 45% between the functional feeding groups of aquatic insect assemblages. The collector-gathers contributed more than 30% of the assemblages, followed by predators-piercers (>20%) (Table 3). *Chironomus* (8%), *Asheum beckae* (8%), *Caladomyia kapilei* (5%) and *Ablabesmyia strixinoae* (7%), contributed the highest participation in the overall trait composition, as well as higher average abundance in the invaded bank. The other two groups, collector-filterers (>15%) and predator-engulfers (>10%) also contributed a high participation in the composition traits of aquatic insect assemblages. *Aedomyia* (9%) and *Telebasis* (5%)

contributed higher participation in the composition assemblages, as well as a higher average abundance in the invaded bank . In contrast, the non-invaded bank presented higher average abundance of the scrapers group, that presented low relative participation in the overall composition assemblage (<5%) (Table 4).

Table 3. Average dissimilarity and relative participation of aquatic insects' functional feeding groups in assemblages of invaded and non-invaded bank by white ginger lily of a reservoir in Brazilian Savanna (Cerrado Biome).

FFG/strategy feeding	Av. dissim	Contrib. %	Cumulative %	reservoir bank	
				invaded abund.	non-invaded abund.
coletor-gathering	14.06	31.38	31.38	41.20	15.30
predator-piercer	10.60	23.67	55.05	26.80	9.33
coletor-filtering	7.82	17.45	72.50	26.50	17.70
predator-engulfér	6.47	14.45	86.95	21.10	9.58
scrapers	3.33	7.42	94.37	2.75	6.25
predator-sucker	1.38	3.10	97.46	0.42	2.50
shredder-herbivore	0.76	1.71	99.17	1.58	0.25
shredder-minner	0.37	0.83	100.00	0.50	0.25

Table 4. Average dissimilarity and relative participation of aquatic insect taxa in assemblages of invaded and non-invaded bank by white ginger lily of a reservoir in Brazilian Savanna (Cerrado Biome).

Taxon	Average Dissimilarity	Contribution %	Cumulative %	reservoir bank	
				Invaded bank Mean abundance	Non-invaded bank Mean abundance
<i>Aedomyia</i>	6.40	9.10	9.10	19.30	10.50
<i>Chironomus</i>	5.72	8.13	17.23	13.60	3.50
<i>Asheum beckae</i>	5.59	7.94	25.17	11.80	2.25
<i>Ablabesmyia strixinoae</i>	5.29	7.53	32.70	12.30	3.33
<i>Caladomyia kapilei</i>	3.74	5.31	38.02	8.75	2.25
<i>Campsurus</i>	3.25	4.62	42.64	3.25	5.33
<i>Telebasis</i>	3.14	4.47	47.11	5.33	0.83
<i>Caenis</i>	2.90	4.12	51.23	1.92	5.25
<i>Ablabesmyia laurindoi</i>	2.24	3.19	54.42	5.00	1.25
<i>Diastatops</i>	2.00	2.86	57.29	5.67	0.25
<i>Ablabesmyia depaulai</i>	1.70	2.40	59.70	3.42	0.50
<i>Dasyhelea</i>	1.60	2.29	61.99	1.08	2.50
<i>Labrundinia unicolor</i>	1.49	2.11	64.00	3.17	0.67
<i>Protoneura</i>	1.41	2.01	66.11	2.58	0.42
<i>Fissimentum</i> sp2	1.34	1.91	68.00	0.00	1.92
<i>Erythrodiplax</i>	1.33	1.82	70.00	1.92	1.67
<i>Acanthagrion</i>	1.32	1.88	71.80	0.50	2.17
<i>Miathyria</i>	1.03	1.46	73.26	1.25	0.83
<i>Polypedilum</i> sp5	1.00	1.45	74.70	1.50	0.42
<i>Cyrnellus</i>	0.98	1.39	76.10	1.67	0.92
<i>Polypedilum</i> sp3	0.94	1.34	77.44	1.58	0.25
<i>Notonecta</i>	0.91	1.29	78.22	0.33	1.58
<i>Labrundinia paulae</i>	0.89	1.27	80.00	0.00	1.58
<i>Macronema</i>	0.81	1.16	81.15	1.25	0.50
<i>Endotribelos bicolor</i>	0.76	1.09	84.24	1.58	0.25
<i>Tanytarsus obiriciae</i>	0.69	0.99	83.23	1.00	0.00
<i>Oecetis</i>	0.64	0.90	84.13	0.42	0.92
<i>Monopelopia</i>	0.62	0.88	85.00	0.92	0.50
<i>Polypedilum (Tripodura)</i> sp3	0.61	0.87	85.90	0.25	0.92
<i>Gyrinus</i>	0.61	0.86	86.74	1.17	0.33
<i>Pentaneura</i>	0.52	0.74	87.48	0.00	1.00
<i>Aedokritus coffeatus</i>	0.48	0.69	88.17	0.83	0.08
<i>Labrundinia carolae</i>	0.44	0.62	88.79	0.92	0.08
<i>Caladomyia riotarumensis</i>	0.42	0.59	89.39	0.67	0.17
<i>Labrundinia</i> sp	0.39	0.56	89.94	0.75	0.08
Scirtidae	0.38	0.54	90.49	0.00	0.67
<i>Stenochironomus</i>	0.37	0.53	91.02	0.50	0.25
<i>Orthemis</i>	0.35	0.50	91.52	0.50	0.00
<i>Tenagobia</i>	0.34	0.48	92.00	0.83	0.00
<i>Mesonoterus</i>	0.33	0.48	92.48	0.08	0.50
<i>Coelotanypus</i>	0.33	0.47	92.95	0.08	0.50
<i>Pronoterus</i>	0.30	0.42	93.38	0.42	0.00
<i>Limnocoris</i>	0.29	0.42	93.80	0.08	0.50
<i>Labrundinia tenata</i>	0.28	0.39	94.19	0.58	0.08
<i>Laccophilus</i>	0.27	0.38	94.58	0.42	0.17
<i>Ulmeritus</i>	0.26	0.37	94.95	0.42	0.08
<i>Tanytarsus</i> sp	0.26	0.37	95.33	0.08	0.42
<i>Desmopachria</i>	0.26	0.37	95.70	0.42	0.08
<i>Belostoma</i>	0.24	0.34	96.04	0.00	0.42
<i>Ablabesmyia metica</i>	0.22	0.31	96.36	0.58	0.00
<i>Cladopelma forcipes</i>	0.22	0.31	96.67	0.08	0.33
<i>Goeldichironomus maculatus</i>	0.21	0.30	96.97	0.50	0.00
<i>Macrothemis</i>	0.21	0.29	97.27	0.33	0.00
<i>Idiataphe</i>	0.19	0.27	97.54	0.17	0.08
<i>Fissimentum desiccatum</i>	0.19	0.27	97.81	0.17	0.17
<i>Lestes</i>	0.19	0.26	98.07	0.33	0.00
<i>Polypedilum</i> sp4	0.18	0.25	98.32	0.00	0.33
<i>Gynothemis</i>	0.17	0.24	98.56	0.08	0.25
<i>Callibaetis</i>	0.16	0.23	98.80	0.00	0.33
<i>Oxyagron</i>	0.16	0.23	99.03	0.25	0.00
<i>Hydrocanthus</i>	0.16	0.22	99.25	0.17	0.17
<i>Clynotanypus</i>	0.13	0.19	99.44	0.00	0.25
<i>Procladius</i>	0.13	0.19	99.63	0.00	0.25
<i>Fissimentum</i> sp3	0.11	0.19	99.79	0.00	0.17
<i>Larsia</i>	0.08	0.13	99.92	0.00	0.17
<i>Andonectes</i>	0.06	0.08	100	0.17	0.00

4. Discussion

As we expected, the invasive white ginger lily shifted the composition traits of the aquatic insect assemblage in the littoral zone especially by the decreasing especially the dissimilarity distance (FDis) and niche space occupation (FEve). The abundance distribution of the Functional Feeding Groups (FFG) seemed to be the main variable that influenced the trait composition of the assemblages.

It could be inferred throughout result that the presence of the monotypic banks formed by the white ginger lily, is likely to result into low habitat spatial heterogeneity in comparison to native vegetation banks. Some studies have already showed that the presence of riparian vegetation which is composed of different species plants, promotes higher diversity of aquatic insects associated (Voelz and McArthur 2000; Nessimian et al. 2008) with monotypic plant species banks (Kovalenko *et al.* 2010). This occurs because high diversity species plants can provide high substrate heterogeneity, interstitial space habitat and food resource (CPOM and FPOM) (Merritt and Cummins 1996; Heino 2000), which promote variety types of niche to aquatic insect species (Townsend et al. 1994). Throughout FFG composition, we observed that native vegetation banks, consisting of especially trunks, leaf litter increased the participation of aquatic insects groups such as scrapers and shredders, leading to the increase of functional traits diversity. On the other hand, the dominance of the invasive species plants which generally formed the monotypic banks seemed to host low diversity of aquatic insect species due to low spatial heterogeneity habitat and resource. This probably occurs due to the rapid vegetative growth of invasive species plants that lead to reduction of substrate heterogeneity, interstitial space and food resource on freshwater ecosystem (Theel et al., 2008; Hladyz et al., 2011; McNeish et al., 2012).

Generally, the rapid vegetative growth of invasive species plants promotes high biomass and it is reported as the main cause of habitat alteration by changing abiotic variables such as oxygen concentration that exclude sensitive species of aquatic insects such as Ephemeroptera nymphs (Sanways et al., 2011; Stiers et al., 2011; Coetzee et al., 2014). Although this variable had no effect on the functional trait composition on the aquatic insect. The main cause of the disrupting structural assemblage occurred through the higher

participation of chironomids. In fact, some chironomids larvae can tolerate very low level of dissolved oxygen (Whatley et al. 2014), however, they have been reported to have higher participation in aquatic insects dwelling and invade banks by invasive macrophytes species (Theel et al., 2008). As observed in such studies, the high participation of the larvae of this family probably is due to the habitat quality and high availability of food resource (FPOM), which corroborate with our inferences about the negative impact of white ginger in the littoral zone. In respect to habitat heterogeneity, the fast growth of white ginger lily results in banks formed by an entanglement of rhizomes, branches and leaves leading to the overlapping of many branches that probably reduced habitat spatial heterogeneity. Therefore, based on the results we suggested that the invasion by white ginger lily probably promoted low spatial heterogeneity habitat especially when we observed it in a narrow niche band occupation resulting in lower FEve and lower dissimilarity composition traits (FDIs). In additional, we also could consider that the availability of resource was the main factor that selected specific traits especially CWM-FFG composition, with the higher abundance of chironomid collector-gathering groups seemed strongly influence by the lower FD indices.

According to Wellnitz and Poff (2001), the increase in the assemblage similarity traits is one of the main causes of extinctions of diversity functions. In addition, the availability of resource acts as filter that selects species trait determining the width of the ranges of niche occupation of assemblages on ecosystems (Southwood, 1977; Korfiatis and Stamou, 1999). In this respect, the invasion by white ginger lily in the littoral zone had important implication for the conservation of the biodiversity (Samways et al., 2011; McNeish et al., 2012), The decrease of habitat heterogeneity and low availability resource display important role in the maintenance of aquatic insect's composition trait leading to simplification of structure assemblages. Furthermore, the resource availability could be considered an important variable that would influence the composition of FFG assemblage, once the low resource heterogeneity decreases the participation of scrapers. The low participation of this functional feeding group in the assemblage composition traits was an indication that the white ginger lily invasion along time could lead to homogenization of aquatic insect's structure assemblage in the reservoir banks.

Finally, we highlighted that the predominance of these invasive plant species in the littoral zone as we expected it shifted the functional structure of aquatic insect assemblages,

acting as a selective filter that benefits only few species, whose functional feeding groups reflect the low variety of resources used by the aquatic insect assemblages. This finding has important implications for the maintenance of ecological processes such as exchange of energy flow in the system, as well as for the biological diversity of aquatic insect assemblages in the littoral zones. Similar to other diverse stressor agents found in freshwater environments (e.g. eutrophication, agriculture and urbanization expansion), the invasion of white ginger lily has a negative impact on the aquatic insects assemblage composition traits resulting in the loss of the functional diversity. Similar to other invasive species, the occupation of this plant in surrounding freshwater ecosystems resulted in the loss of the functional traits structures of the native assemblages (Olden et al., 2004). Considering that due to the wide propagation of white ginger lily in many Brazilian biomes, interest related to aspects of its invasion has increased (Zenni and Ziller, 2011; Sampaio and Schimidit, 2013). We highlight the importance of the role of control of invasive plant species, as they contribute to decreasing the aquatic biodiversity and ecosystem services in the Neotropical region.

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References

- Anderson, N.H., Cummins, K.W., 1979. Influences of diet on the life histories of aquatic insects. *J. Fish. Res. Board. Can.* 36, 335–342.
- Anderson, M.J.K., Ellingsen, E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693.
- Archengelsky, M., Manzo, V., Michat, M.C., Torres, P.L.M., 2009 , p. 411–468. Coleoptera. In: Dominguez E., Fernandez H.R. Macroinvertebrados bentónicos sudamericanos: sistemática y biología. Tucuman, Argentina.
- Becerra-Muñoz, S., Schramm, H.L.Jr., 2007. On the influence of substrate morphology and surface area on phytofauna. *Hydrobiologia* 575, 117–128.
- Boyero, L., Barmuta, L.A., Ratnarajah, L., Schimist, K., Pearson, R.G., 2012. Effects of riparian vegetation on leaf breakdown by shredders: a tropical-temperate comparison. *Freshw. Sci.* 2, 296–303.
- Braga, R.B., Ferreira-Jr, N., 2014. Carnivorous diving beetles of the genus *Desmospachria* (Coleoptera: Dytiscidae) from Brazil: New species, new records and a checklist. *J. Insect. Sci.* 14, 1–26.
- Brasil, L.S., Juen, L., Batista, J.D., Pavan, M.G., Cabette, H.S.R., 2014. Longitudinal distribution of the functional feeding groups of Aquatic Insect in streams of the Brazilian Cerrado Savanna. *Neotrop. Entomol.* 43, 421–428.
- Brauns, M., Garcia, X-F., Walz, N., Pusch, M.T., 2007. Effects of human shoreline development on littoral macroinvertebrates in lowlands lakes. *J. Appl. Ecol.* 44, 1138–1144.
- Butakka, C.M.M., Grybkowska, M., Pinha, G.D., Takeda, A.M., 2014. Habitat and trophic relationship of Chironomidae insect larvae from the Sepotuba River Basin, Pantanal of Mato Grosso, Brazil. *Braz. J. Biol.* 74, 395–407.
- Carreira, B.M., Dias, M.P., Rebelo, R., 2014. How consumption and fragmentation macrophytes by the invasive crayfish *Procambarus clarkia* shape the macrophyte communities of temporary ponds. *Hydrobiologia* 72, 89–98.

- Cheruvilil, K.S., Soranno, P.A., Serbin, S.D., 2000. Macroinvertebrates associated with submerged macrophytes: sample size and power to detect effects. *Hydrobiologia* 441, 133–139.
- Choi, C., Bareiss, C., Walenciak, O., Gross, E.M., 2002. Impact of polyphenols on growth of the aquatic herbivore *Acentria ephemerella*. *J. Chem. Ecol.* 28, 2245–2256.
- Clapcott, J.E. & Bunn, S., 2003. Can C4 plants contribute to aquatic food webs of subtropical streams. *Freshw. Biol.* 48, 1105–1116.
- Coetze, J.A., Jones, R.W., Hill, M.P., 2014. Water hyacinth, *Eichornia crassipes* (Pontederiaceae), reduce macroinvertebrates diversity in a protected subtropical lake in South Africa. *Biol. Cons.* 23, 1319–1330.
- Costa, J.M., Machado, A.B.M., Lecioni, F.A.A., Santos, T.C., 2004. Diversidade e distribuição dos Odonata (Insecta) no Estado de São Paulo, Brasil: Parte I – Lista das espécies e registros bibliográficos. *Publicações Avulsas do Museu Nacional Rio de Janeiro* 80, 1–27.
- Cronin, G., Wissing, K.D., Lodge, D.M., 1998. Comparative feeding selectivity of herbivorous insects on water lilies: aquatic vs. semi-terrestrial insects and submersed vs. floating leaves. *Fresh. Biol.* 39, 243–257.
- Cummins, K.W., Merritt, R.W., Andrade, P.C., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Stud. Neotrop. Fauna Environ.* 40, 69–89.
- Da-Silva, E.R., Salles, F.F., 2012. Ephemeroptera Hyatt, Arms, 1891 In: Rafael, J.A.L., Melo, G.A.R., de Carvalho, C.J.B., Casari, S.A., Constantino, R. (Eds.), *Insetos do Brasil: Diversidade e taxonomia*. Ribeirão Preto, São Paulo.
- De Castro, W.A.C., Almeida, R.V., Leite, M.B., Marrs, R.H., Matos, D.M.S., 2016. Invasion strategies of white ginger lily (*Hedychium coronarium*) J. König (Zingiberaceae) under different competitive and environmental conditions. *Enviro. Exp. Bot.* 127, 55–62.
- Dominguez, E., Fernandez, H.R., 2009. *Macroinvertebrados bentónicos sudamericanos: sistemática y biología*. Tucuman, Argentina.
- Dundgeon, D., 2010. Prospect for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Enviro. Sustain.* 2, 422–430.

- Edmunds, G.F. Jr., Waltz, R.D., 1996. Ephemeroptera. In: Merritt, R.W., Cummins K.W. (Eds.), An introduction to the Aquat Insect of North America. 3rd Ed. Kendall Hunt Publishing Co., Dubuque, Iowa.
- Ferreira-Kepler, R.L., Rondero, M.M., Díaz, F., Spinelli, G.R., Torreiras, S.R., 2014 Ordem Diptera: Familia Ceratopogonidae In: Namada, N., Nessimian, J.L. & Querino, R.B. (Eds.), Insetos aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia. Instituto Nacional de Pesquisa na Amazônia, Manaus.
- Flint, O.S. Jr., Bueno-Soria, J., 1982. Studies of Neotropical Caddisflies, XXXII: The immature stages of *Macronema viriipenne* Flint & Bueno, with the division *Macronema* by the resurrection of *Macrostemum* (Trichoptera: Hydropsychidae). P. Bio. Soc. Wash. 95, 358–370.
- Graça, M.A.S., 2001. The role of invertebrates on leaf litter decomposition in streams – review. Int. Rev. Hydrobiol. 86, 383–393.
- Heino, J., 2000. Lentic macroinvertebrates assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. Hydrobiologia 418, 229–242.
- Heino, J., 2008. Patterns of biodiversity and function environment relationships in lake littoral macroinvertebrates. Limnol. Oceanogr. 53, 1446–1455.
- Henriques-Oliveira, A.L., Nessimian, J.L., Dorvillé, L.F.M., 2003. Feeding habits of Chironomidae larvae (Insecta, Diptera) from a stream in the Floresta da Tijuca, Rio de Janeiro, Brazil. Braz. J. Biol. 63, 269–281.
- Hlyladz, S., Åbjörnsson, K., Giller, P.S., Woodward, G., 2011. Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. J. Appl. Ecol. 48, 443–452.
- Kelly, D.J., Hawes, I., 2005. Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high-country lake. J. N. Am. Benthol. Soc. 24, 300–320.
- Korfiatis, K.J., Stamou, G.P., 1999. Habitat templets and the changing worldview of ecology. Biol. Phil. 14, 375–393.
- Kovalenko, K.E., Dibble, E.D., Slade, J.G., 2010. Community effects of invasive macrophyte control: role of invasive plant abundance and habitat complexity. J. Appl. Ecol. 47, 318–328.

- Kovalenko, K.E., Dibble, E.D., 2011. Effects of invasive macrophyte on trophic diversity and position of secondary consumers. *Hydrobiologia* 663, 167–173.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Laliberté, E., Legendre, P., and Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonniss, A., 2008. Assessing functional diversity in the field – methodology matters! *Funct. Ecol.* 22, 134–147.
- Manson, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118.
- McGoff, E., Solimini, A.G., Pusch, M.T., Jurca, T., Sandin, L., 2013. Does lake habitat alterations and land pressure homogenize European littoral macroinvertebrate communities. *J. Appl. Ecol.* 50, 1010–1018.
- McNeish, R.E., Benbow, M.E., McEwan, R.W., 2012. Riparian forest invasion by a terrestrial shrub (*Lonicera maackii*) impacts aquatic biota and organic matter processing in headwater streams. *Biol. Invasions* 14, 1881–1893.
- Merritt, R.W., Cumins, K.W., 1996. An introduction to the Aquatic Insect of North America, 3rd Ed. Kendall Hunt Publishing Co., Dubuque, Iowa.
- Molineri, C., Emmerich, D., 2010. New specie and new stage description of *Campsurus major* species groups (Polymitarcidae: Campsurinae), with first report of silk-case construction in mayfly nimphs. *Aqua. Insects* 32, 265–280.
- Molineri, C., Malzacher, P., 2007. South American *Caenis* Stephens (Ephemeroptera, Canenidae), new species and stage descriptions. *Zootaxa* 1660, 1–31.
- Nessimian, J.L., Venticinque, E.M., Zuanon, J., De Marco Jr., P., Gordo, M., Fidelis, L., Batista, J.D., Juen, L., 2008. Land use, habitat integrity, and aquatic insect assemblages in Central Amazonian streams. *Hydrobiologia* 614, 117–131.

- Nieser, N., Melo, A.L., 1997. Os heterópteros aquáticos de Minas Gerais: guia introdutório com chave de indentificação para as espécies de Neomorpha; Gerromorpha. UFMG, Belo Horizonte.
- Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24.
- Oliveira, C.S.N., Da Silva, M.A., Fonseca-Gessner, A.A., 2013. Neotropical Ablabesmyia Johannsen (Diptera: Chironomidae, Tanypodinae). Part I. *Zootaxa* 3733, 1–123.
- Pes, A.M., Santos, A.P.M., Barcelos-Silva, P., Camargos, De L.M., 2014. Ordem Trichoptera (*tricho*= cerda; *pteron* = asa) In: Namada, N., Nessimian, J.L., Querino, R.B. (Eds.). Insetos aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia. Instituto Nacional de Pesquisa na Amazônia, Manaus.
- R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at: <http://www.R-project.org> (accessed 26.10.16).
- Salles, F.F., Da-Silva, E.R., Serrão, J.E., Francischetti, C.N., 2004. Systematics, morphology and physiology Baetidae (Ephemeroptera) na região Sudeste do Brasil: Novos Registros e Chave para os gêneros no estágio ninfal. *Neotrop. Entomol.* 33, 725–735.
- Salles, F.F., Domínguez, E., 2012. Systematics and phylogeny of *Ulmeritruz-Ulmeritroides* revisited (Ephemeroptera: Leptoplebeiidae). *Zootaxa* 3571: 49–65.
- Sampaio, A.B. & Schimidt, I.B., 2013. Espécies exóticas invasoras em Unidades de Conservação Federais do Brasil. *Biodiversidade Brasileira* 3, 32, 49.
- Sanseverino, A.M., Nessimian, J.L., 2008. The food of larval Chironomidae (Insecta, Diptera) in submerged litter in a forest stream of the Atlantic Forest (Rio de Janeiro, Brazil). *Act. Limnol. Brasil.* 20, 15-20.
- Samways, M.J., Sharratt, N.J., Simaika, J.P., 2011. Effect of riparian vegetation and its removal on a highly endemic river macroinvertebrate community. *Biol. Invasions* 13, 1305–1324.
- Silva, F.L., Fonseca-Gessner, A.A., Ekrem, T., 2014. A taxonomic revision of genus *Labrundinia* Fittkau, 1962 (Diptera: Chironomidae: Tanypodinae). *Zootaxa* 3769, 1–185.

- Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46, 337–365.
- Stenberg, J.A., Stenberg, J.E., 2012. Herbivory limits the yellow water lily in an overgrown lake and in flowing water. *Hydrobiologia* 691, 81–88.
- Stiers, I., Crohaín, N., Josens, G., Triest, L., 2011. Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. *Biol. Invasions* 13, 2715–2726.
- Theel, H.J., Dibble, E.D., Madsen, J.D., 2008. Differential of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. *Hydrobiologia* 600, 77–87.
- Tomanova, S., Goitia, E., Helešic, J., 2006. Trophic levels and functional feedings groups of macroinvertebrates in neotropical streams. *Hydrobiologia* 556, 251–264.
- Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biol.* 31, 265–275.
- Trivinho-Strixino, S., 2011. Larvas de Chironomidae: guia de identificação. Departamento de Hidrobiologia/Lab. De Entomologia Aquática, São Carlos.
- Trivinho-Strixino, S., 2012. A systematic review of Neotropical *Caladomyia* Sæwedal (Diptera: Chironomidae). *Zootaxa* 3495, 1–41.
- Trivinho-Strixino, S., Pepinelli, M., 2015. A systematic study on *Endotribelos* Grodhaus (Diptera: Chironomidae) from Brazil including DNA barcoding to link males and females. *Zootaxa* 3936, 1–41.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. *C. J. Fish. Aquat. Sci.* 30, 130–137.
- Voelz, N.J., Vaun McArthur, J., 2000. An exploration of factors influencing lotic insect species richness. *Biodivers. Conserv.* 9, 1543–1570.
- Zenni, R.D., Ziller, S.R., 2011. An overview of invasive plants in Brazil. *Revista Brasileira de Botanica* 34, 431–446.
- Wellnitz, T., Poff, N.L.R., 2001. Functional redundancy in heterogeneous environments: implications for conservation. *Ecol. Lett.* 4, 177–179.

Whatley, M.H., van Loon, E.E., Vonk, J.A., van der Geest, H.G., Admiraal, W., 2014. The role of emergent vegetation in structuring aquatic insect communities in peatland drainage ditches. *Aquat. Ecol.* 48, 267–283.

Capítulo III

Native macrophyte leaves influence more specialisation of Neotropical shredder chironomids than invasive macrophyte leaves

O artigo será submetido à revista Oecologia

Abstract

Freshwater herbivores have different adaptive feeding due to plant leaf chemical compounds. We investigated the composition and specialisation of shredder chironomids in an invasive white ginger lily (*Hedychium coronarium*) and in native pickerelweed (*Pontederia cordata*) leaves. We assumed that the difference of the chemical compound in macrophyte leaves would influence the shredder chironomid specialisation. A colonisation experiment was performed in eight periods over three years (2013-2015) using 40 bags for each macrophyte species. The main macrophyte leaf chemical compounds (organic matter, nitrogen, phosphorus, cellulose, lignin, soluble polyphenols and soluble carbohydrates) were measured. The shredder chironomid assemblages were analysed using total abundance, richness and dissimilarity distances. The herbivore specialisation was estimated using the individual specialisation index (d') and community specialisation index (H_2'). White ginger lily had higher nitrogen and organic matter. Shredder chironomid assemblages differed from the composition between invasive and native macrophytes. Invasive macrophytes presented a higher abundance of shredder specimens and a lower dissimilarity distance index of shredder assemblage than in native leaves. All shredder chironomid taxa had low specialisation in the invasive macrophyte. The *Polypedilum fallax* group, *Stenochironomus* and *Endotribelos calophylli* presented high individual specialisation (d') in pickerelweed leaves, resulting in high community specialisation (H_2'). The heterotrophic facilitation hypothesis explained the herbivores thriving in pickerelweed leaves due to their lower nutritional value. The intake-efficiency hypothesis explained the higher consumption of invasive plant tissue by *Stenochironomus*, due to its mining habit. We found evidence of evolutionary adaptation of freshwater herbivore eating habits. Additionally, our result added an important characteristic to shredder chironomid assemblages.

Key words: freshwater herbivory; *Hedychium coronarium*; herbivore adaptations; macroinvertebrates; *Stenochironomus*

1. Introduction

Previously, ecologists believed that the herbivory process was of minor importance in aquatic ecosystems (Wetzel 1983). However, recent research has emerged reporting various examples of interactions between herbivores and primary producers in aquatic systems, including freshwater lakes, rivers, estuaries, wetlands and shallow seas (Bakker et al. 2016). They found that in freshwater ecosystems the interaction between plant and herbivores are an important ecological process, especially interactions concerning the exchange of energy and nutrient flow, shaping herbivore communities (Carlsson and Lacoursière 2005; Morrison and Hay 2011a).

Aquatic macrophytes are one of the major primary producers in freshwater systems. Their physiologies determine their niche (Tiner 1991), which in turn influence the structuring of associated assemblages (Theel et al. 2008; Matsuda et al. 2015). Additionally, macrophytes are the basal food resource of many herbivores, which include a wide range of taxonomic groups (Wood et al. 2016). The nutritional value provided by macrophyte tissues influences the life history of herbivore species (*e.g.* fitness, reproduction) (Choi et al. 2002), which in turn can lead to the structuring of many macrophyte communities (Carreira and Rebelo 2014). Studies related to herbivores and macrophytes in freshwater systems have countered the opinion that herbivory is of minor importance in aquatic systems, broadening the understanding about the relationships between aquatic herbivores and macrophyte species (Lodge 1991; Bakker et al. 2016).

Invasive macrophytes pose a challenge for herbivores, a challenge that is increasing over time (Wong et al. 2010). It is reported that leaves of invasive macrophytes, especially

those with high secondary compounds (*e.g.* polyphenols and tanins) and high C: N ratio are a low nutritional value and, therefore a low preference by herbivores (Kubaneck et al. 2001; Morrison and Hay 2012). These characteristics have been justified as a favourable advantage to invasive plant species to gain success in foreign areas as defence behaviour to native herbivores (Morrison and Hay, 2011b). Nonetheless, invasive plants whose leaves have high nutritional value *i.e.* low concentration of secondary compounds and low carbon to nitrogen ratio) are more attractive (Leite-Rossi et al. 2016). This preference for macrophyte species with high nutritional value could be related to the adaptive evolution of herbivore species (*e.g.* mouth parts and physiology) (Sanches and Trexler 2016), which enable them to explore or compete for resources in a more effective manner (Lodge 1991).

Aquatic shredder insects play an important role in freshwater ecosystem process, contributing especially by accelerating litter plant decomposition rates (Leite-Rossi et al., 2016). The chemical compounds of invasive leaf plants (*e.g.* cellulose and lignin) are important variables that can interfere in aquatic shredder insect colonisation (Leite-Rossi and Trivinho-Strxino, 2012). For instance, tissue plant species with higher cellulose, poliphenol and lignin concentration are generally described as unpalatable to shredders (König et al., 2014). Nonetheless, freshwater shredders are able to consume plant tissues with low nutritional value, especially after the periphyton colonisation stage and during the senescence stage, which improves the palatability of the plant tissues (Cornut et al., 2015). Concerning this issue, the evolutionary adaptation hypothesis of freshwater herbivores emerged to explain their different feeding habits in plant species (Sanches and Trexler, 2016).

In this study, we compared Neotropical shredder chironomid larvae consumption of invasive macrophyte white ginger lily (*Hedychium coronarium* - J. Köenig, 1783) leaves with native macrophyte pickerelweed leaves (*Pontederia cordata* – L.). Chironomid larvae presents wide distribution in freshwater ecosystems, whose taxa represent more than 70% of

aquatic insect assemblages (Biasi et al, 2013). Additionally, shredder chironomid larvae have been described as an important component in freshwater conservation studies (Saulino et al., 2014; Corbi and Trivinho-Strxino, 2016). It is also recognized that the shredder chironomid community contributes to accelerating decomposition rates of litter plants (Leite-Rossi et al., 2016). Nonetheless, there is a lack of knowledge regarding their relationships of plant litter selection.

In Brazil, the white ginger lily, an exotic macrophyte introduced from Asia, is considered an invasive plant due to its strong competitive strategies (de Castro et al., 2016). Pickerelweed, a native macrophyte which has a wide distribution in the American continent, presents similar life form characteristics. Both macrophyte species are monocots and exhibit adaptive habits such as amphibious and emergent types with a wide distribution in freshwater ecosystems (Lorenzi 1991; Lorenzi and Souza 2001). Their leaves have different chemical compounds in cellulose percentage, lignin, polyphenols, phosphorus and nitrogen content. Their similar lifestyle characteristics enabled us to test if the shredder chironomid larvae composition assemblages differ in invasive and native macrophyte leaves in the littoral zone of a tropical reservoir. Our main hypothesis was that the difference in chemical compounds of macrophyte leaves would influence the shredder chironomid specialisation.

Based on shredder chironomid composition species, we investigated their preference throughout the adaptive evolution hypotheses of herbivores in freshwater systems suggested by Sanches and Trexler (2016), which proposed: (i) heterotrophic facilitation— herbivores consume microbes associated with producers and (ii) intake-efficiency –herbivores use part of their food source as a habitat, thus minimizing the energy/time spent searching for food and avoiding predators. Based on these two adaptive evolution hypotheses, we investigated the results of invasive macrophytes concerning the conservation of freshwater systems.

2. Material and Methods

2.1 Study area

This study was carried out in the littoral zone of the Fazzari reservoir located in a preserved area of the Cerrado biome (645 ha) at the Universidade Federal de São Carlos (UFSCar, Brazil). The Fazzari reservoir (21°58'S, 47°53'W) has chemical characteristics such as high levels of dissolved oxygen (> 7mgL), acidic pH (\pm 5.5) and diverse vegetation on its banks. Its total area is 11,370 m², 220 meters long, an average width of 51.5 m and an average depth of 1.10 m and maximum 4 m.

2.2 Chironomid larvae species colonisation on macrophyte leaves

Leaf colonisation experiments were performed in the littoral zone of the reservoir using fresh leaves of the invasive macrophyte white ginger lily (*H. coronarium*) and the native macrophyte pickerelweed (*P. cordata*). Fresh leaves of each macrophyte were picked from adult plants without injuries and initial senescence signs. Six leaves from each macrophyte were put separately into five bags (0.20x0.40, 01mm) (Figure 1). The colonisation experiment was carried out over three years in eight periods of 45 days: May-June/August-September/2013, June-July/August-September/2014, November-December/2013, February-March/2014, January-February/March-April/2015, totaling 40 bags of samples for each treatment.

Leaf bags were randomly submersed in littoral zone points and then carefully collected with a dip net (mesh 250 μ m) after 40-45 days of colonisation. The colonisation period of leaf bags in the littoral zone was determined according to studies regarding macroinvertebrate colonisation (Leite-Rossi and Trivinho-Strixino, 2012; Leite-Rossi et al., 2016). They demonstrated an optimal density of macroinvertebrates reaching colonisation in 35-45 days.

The chironomid specimens were picked alive, using illuminated trays, and identified using the taxonomic level of species or morphotypes according to Trivinho-Strixino (2014).

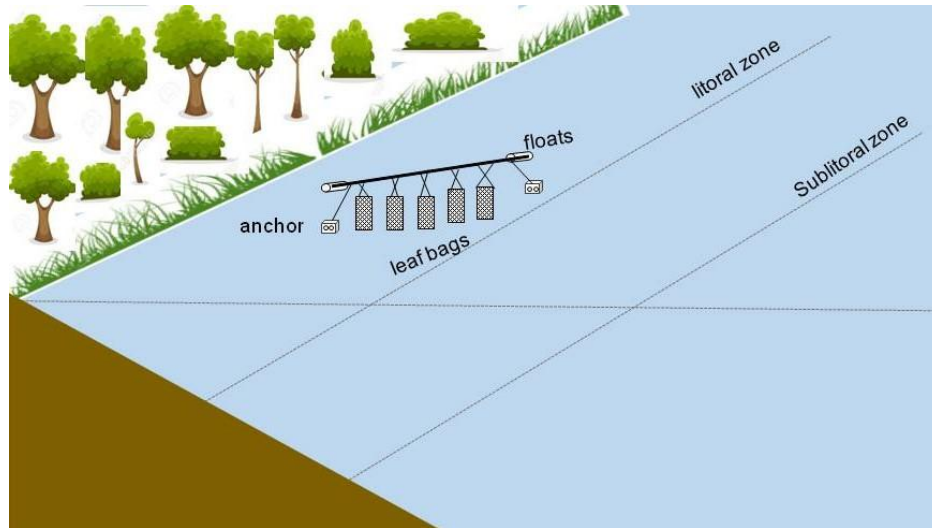


Figure 1. Scheme of colonisation experiment with invasive white ginger lily and native pickerelweed macrophyte leaves in the littoral zone

2.3 Quantification of consumption of macrophyte leaves by herbivore species

Shredder chironomid taxa were quantified for each macrophyte leaf. Analysis of the gut content was performed in 3-10 specimens of each chironomid taxa to quantify the average macrophyte leaf consumption. The gut content of each shredder taxon was classified into four categories: CPOM, FPOM, plant tissues and algae. The specimens were analysed on slides using an ocular micrometer (Carl Zeiss WH10X) and examined at a magnification of 400 xs. The consumption of macrophytes was obtained using a ratio of the number of squares filled by plant tissue to the total square completed by all food items in the chironomid guts. The values obtained are expressed as the average percentage of total squares of the micrometer grid.

2.4 Macrophyte leaf chemical compounds

Fresh leaves from each macrophyte were collected from adult plants, washed in running water to remove any materials that could interfere with the determination of initial leaf litter mass (e.g., inorganic material, small animals and animal feces) and oven-dried at 45°C to a constant mass. The leaf chemical compounds total phosphorous (P %), nitrogen (N %), organic matter, cellulose (%), lignin (%), soluble carbohydrates (%) and soluble polyphenols (%) were determined to characterize macrophyte leaf chemical compounds.

Oven-dried macrophyte leaves (three leaves per macrophyte) were ground to 1 mm in a knife grinder for chemical analysis. The P (%) and N (%) concentrations were determined using Vanadato-Molibdato (Sarruge and Haag 1974) and micro-Kjeldahl methods (Coelho-Silva 1967; Association of Official Agricultural Chemists 1995). The organic matter was determined by using the percentage of ash free dry mass (AFDM %) by the gravimetric method. The soluble carbohydrate concentration was determined by using the colorimetric method (Dubois et al. 1956). The total lignin concentrations were determined by a sequential analysis of neutral and acidic detergents (Robertson and Van Soest 1981; Mertens 2002). Polyphenol concentrations were determined by using the gravimetric method (Makkar et al. 1993).

2.5 Data analyses

The macrophyte leaf chemical compounds AFDM (%), N (%), P (%), cellulose, lignin, total soluble polyphenols and total soluble carbohydrates were compared in macrophytes using the nonparametric Mann-Whitney test.

Shredder larvae specimens presented low abundance of in most samples. At least three specimens of each taxon of shredder chironomid larvae were counted in the macrophyte leaves. Due to this, the 40 bags of samples were reduced to 10 samples. The total abundances (N) and richness (S) of herbivore assemblages were compared using the nonparametric

Mood's median test. In this test, the data in each sample are assigned to two groups: one consisting of data whose values are higher than the median value in the two groups combined, and the other consisting of data whose values are at the median or below. A Pearson's chi-squared test is then used to determine whether the observed frequencies in each sample differ from the expected frequencies derived from a distribution combining the two groups (Friedlin and Gastwirth, 2000).

The composition of herbivore species in each macrophyte leaf bag was analysed using a non-metric multidimensional scale (nMDS). The clustering among samples was determined by the dissimilarity distance measured using the Bray-Curtis index. In addition, significant differences between dissimilarity distances of the herbivore assemblages were compared using an analysis of similarity test (ANOSIM). To do this, the total abundance of chironomid larvae on macrophyte leaf bags was used to measure the dissimilarity distances. They were calculated using the Bray-Curtis index. The significant differences between assemblages were analysed using statistic tests (R) and descriptive level sampling ($p < 0.05$) (Clarke 1993).

The average consumed plant tissue by each shredder chironomid species in the invasive and native macrophytes were compared using the nonparametric Mood's median test. The preference of shredder chironomid species to chemical compounds of invasive and native macrophyte leaves was analysed using the Pearson's correlation analyses. The correlation coefficients were used as a measure of the strength of the interaction between shredder chironomid species preferences and the chemical compounds of macrophyte leaves.

The shredder specialisation was estimated in each leaf macrophyte treatment using the degree of specialisation index (d'). This index estimates the individual degree of specialisation species. The d' index is derived from Kulback-Leibler distance (as is Shannon's diversity index). It calculates how strongly a species deviates from a random sampling of the

interacting partners, ranging from 0 (no specialisation) to 1 (perfect specialist). Furthermore, the specialisation of shredder assemblages were estimated using the degree of community specialisation index (H_2'). H_2' is an index that describes the level of “complementarity specialisation” of an entire bipartite network. It describes to which extent observed interactions deviate from those that would be expected given the species marginal totals. The more selective a species is, the larger the H_2' is for the web (Blüthgen et al. 2006; Dorman et al. 2016). Matrices for each macrophyte species were built to obtain these indices, with columns representing shredders according to their respective average consumption of plant tissue and rows representing each macrophyte leaf sample. The d' and H_2' were calculated using the “bipartite” package (Dorman et al. 2016) available in the R platform program (R Development Core Team 2014).

3. Results

The white ginger lily leaves had a higher average of AFDM % and N%, but lower P(%), cellulose, lignin total polyphenols and carbohydrates when compared with pickerelweed leaves ($p < 0.05$) (Table 1). Seven shredder chironomid larvae were identified (Table 2). *Endotribelos calophyllii* and *Stenochironomus* presented a high frequency in the invasive macrophyte leaf samples. *Polypedilum (Tripodura)* sp3 presented a high frequency in native macrophyte leaves (Figure 2). The abundance of specimens in white ginger lily leaves ($N = 4.3$) was higher than in the pickerelweed leaves ($N = 3.2$) ($\chi^2 = 5.05$, $p = 0.02$). There was no difference in herbivore richness between them (white ginger [$S = 2$], pickerelweed [$S = 1.7$], $\chi^2 = 2.20$, $p = 0.14$).

Table 1 Chemical composition of white ginger lily and pickerelweed leaves. AFDM - Ash free dry mass, N - nitrogen, P - phosphorous.

Leaf chemical compound	White ginger lily	Pickerelweed	U	p
AFDM%	93.78 ±0.10	92.78 ±0.30	0	0.0001*
nitrogen (%)	2.18 ±0.01	1.35 ±0.04	0	0.0002*
phosphorus (%)	0.08 ±0.01	0.16 ±0.01	0	0.0001*
cellulose	11.46 ±2.80	29.95 ±4.10	0	0.0002*
Lignin	23.27 ±2.70	26.36 ±2.10	0	0.0002*
total polyphenol	1.77 ±2.50	4.27 ±0.90	0	0.0001*
total carbohydrates	5.66 ±0.70	7.87 ±1.30	0	0.0002*

p<0.05, ±Std.

Table 2. Percentage consumption of macrophyte leaves by shredder chironomid and individual specialisation index (d') during the leaf macrophyte colonisation experiment.

Taxa	Invasive tissue (%)	leaf consumed d'	Native tissue (%)	leaf consumed d'
<i>Endotribelos calophylli</i> Roque et Trivinho-Strixino 2008	32.00±4.00	0.39	22.00 ±4.50	0.70
<i>Fissimentum</i> sp2 cf Trivinho-Strixino 2014	11.00±2.00	0.44	-	-
<i>Phaenopsectra</i> Kieffer 1921	-	-	3.00 ±2.00	0.56
<i>Polypedilum fallax</i> group cf Trivinho-Strixino 2014	-	-	17.00 ±12.00	1.00
<i>Polypedilum (Polypedilum)</i> sp.4 cf Trivinho-Strixino 2014	25.00 ±0.00	-	-	-
<i>Polypedilum (Tripodura)</i> sp. 3 cf Trivinho-Strixino 2014	14.00 ±3.40*	0.40	23.00 ±4.00	0.26
<i>Stenochironomus</i> Kieffer 1919	84.00 ±1.70*	0.43	80.00 ±0.00	0.69

p<0.05, ±Std.

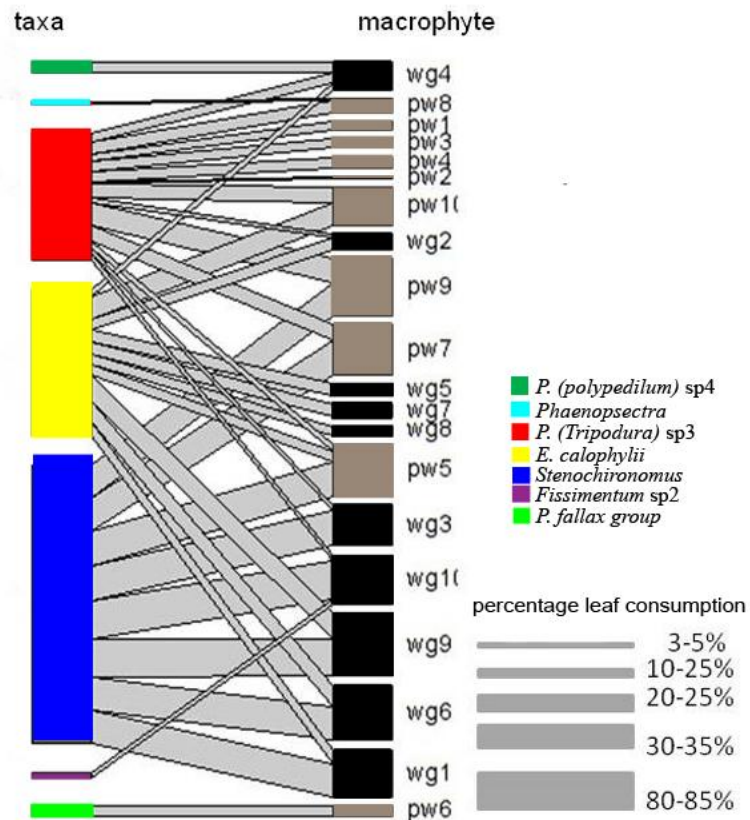


Figure 2 Distribution of shredder chironomid species and percentage of macrophyte leaves consumption in white ginger lily and pickerelweed leaves during colonisation experiment. wg – white ginger lily, pw – pickerelweed.

The nMDS analyses indicated that shredder composition associated with white ginger lily differed from pickerelweed leaves (Figure 3). Axis 1 responded to 73% of the analysis results (stress= 0.24). The ANOSIM showed that shredder assemblage associated with white ginger presented a lower dissimilarity distance than pickerelweed assemblage ($R= 0.98$, $p= 0.0002$) which corroborated with the nMDS analyses (Figure 4).

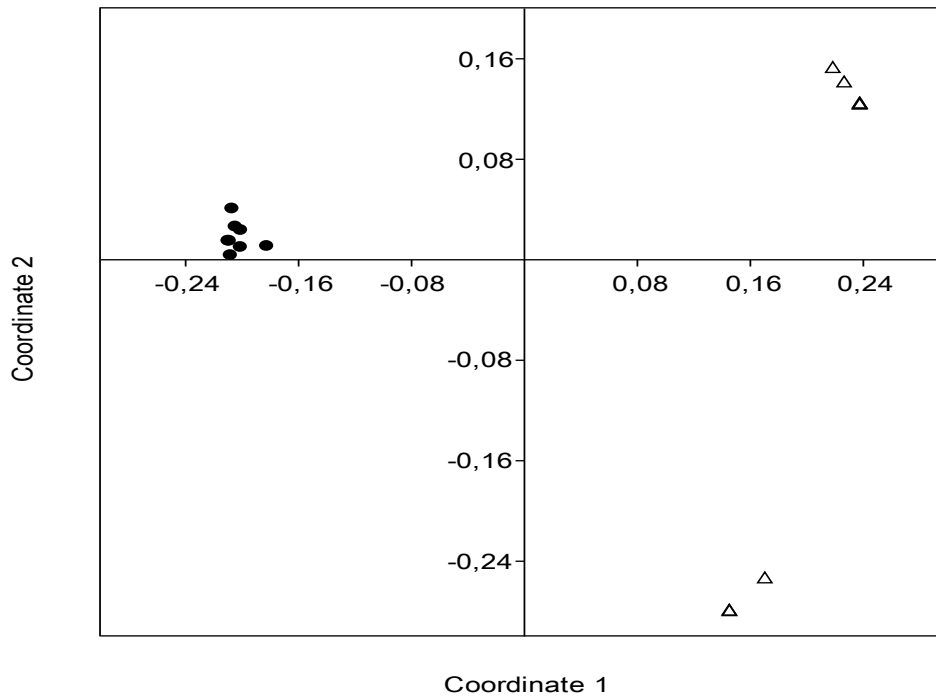


Figure 3 Results of Analyses of non-metric multidimensional scale (NMDS) of shredder chironomid assemblages associated with white ginger lily and pickerelweed leaves during the colonisation experiment (filled circle – white ginger lily, triangle – pickerelweed)

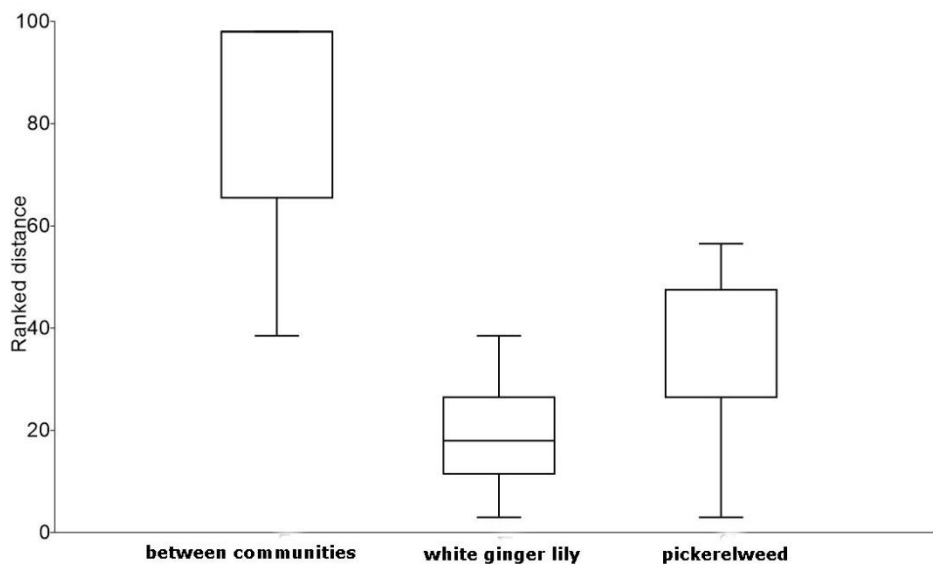


Figure 4. Results of ANOSIM (dissimilarity index) between shredder chironomid assemblages associated with white ginger lily and pickerelweed leaves during a colonisation experiment.

P. (Tripodura) sp3 consumed less white ginger lily leaf tissues than pickerelweed leaves ($\chi^2 = 4.95$, $p = 0.02$). *Stenochironomus* sp larvae consumed more white ginger leaf tissues ($\chi^2 = 4.80$, $p = 0.03$) (Table 2). The analysis of the preference for shredders by the chemical compounds of macrophyte leaves showed that *P. (Tripodura)* sp3 showed a positive relation with P (%) ($r = 0.61$, $p = 0.004$), lignin ($r = 0.64$, $p = 0.002$), cellulose ($r = 0.60$, $p = 0.005$) and soluble carbohydrates ($r = 0.60$, $p = 0.006$). *E. calophyllii* showed a positive relation with N% ($r = 0.45$, $p = 0.04$) and a negative relation with P% ($r = -0.51$, $p = 0.02$), cellulose ($r = -0.46$, $p = 0.04$) and soluble carbohydrates ($r = -0.46$, $p = 0.04$). Similar results were observed for *Stenochironomus* larvae (N (%) [$r = 0.46$, $p = 0.04$], cellulose [$r = -0.46$, $p = 0.04$], carbohydrates [$r = -0.46$, $p = 0.04$]).

The shredder individual specialisation index (d') ranged between the two macrophyte leaves. Most of the shredder chironomid taxa presented high individual specialisation ($d' > 0.69$) in the native macrophyte leaves (Table 2). This occurred due to their low distribution in native pickerelweed leaves. All shredder larvae had a low specialisation index for the invasive white ginger lily. This result indicated a generalist habit. Only *P. (Tripodura)* sp3 presented a low specialisation index for native pickerelweed leaves. The shredder assemblage in the invasive macrophyte leaves presented a low community specialisation index ($H_2' = 0.47$) when compared with native macrophyte leaves ($H_2' = 0.64$).

4. Discussion

Macrophyte leaf chemical compounds influenced the shredder chironomid specialisation, as well as the preference for composition due to their different nutritional value leaves. Due to higher nitrogen (N%) and organic matter (AFDM %) ,the invasive white ginger lily leaves could consider a higher quality resource than the native pickerelweed species. Its

leaves seemed more attractive to shredder chironomid species. On the other hand, the native pickerelweed leaves could be considered as low nutritional value due to the higher concentration of cellulose and polyphenol. Its leaves showed less attractiveness to shredder larvae, influencing a higher specialisation of the shredder species and community. Based on these observations, the different compositions of shredder species could be explained by adaptive evolution traits of herbivores species in freshwater systems (Sanches and Trexler 2016).

Diet selectivity has been proposed as a mechanism to permit subsistence on the relatively poor-quality herbivorous diet. Such herbivore species consuming chemically defended resources may consume other items of high qualities in order to “dilute” the toxin concentration (Provenza et al. 2003). *P. (Tripodura) sp3* and *E. calophylli* could be related to this diet selectivity mechanism, as they consumed only around 20% of native macrophyte tissue. This mechanism could fit into the heterotrophic facilitation hypothesis (Sanches and Trexler 2016). This hypothesis states that herbivores indirectly consume heterotrophic microbes (bacteria, fungi, protozoan), which are associated to primary producer communities. Heterotroph organisms, in general, incorporate nutrients (*e.g.* phosphorus) into their cell walls which serve as rich nutrients for herbivores (Martin-Creuzburg et al. 2011).

Higher phosphorus percentages observed in pickerelweed leaves could be an important source of nutrients for heterotrophic associated fauna which showed a positive relation with *P. (Tripodura) sp3*. The heterotrophic facilitation hypothesis could explain their predominance, explaining the generalist habit observed by this taxon in the pickerelweed leaves. Nonetheless, the higher specialisation index observed in other taxa such as the *P. fallax* group, *Stenochironomus* and *E. calophylli* was related to their low frequency in the native macrophyte leaves. We infer that the low frequency of these taxa indicated that they appeared in the pickerelweed leaves in the late stages of decomposition, where chemical

compounds such as polyphenols are quickly leached (Leite-Rossi et al. 2016). The reduction of the labile fraction component of the plant would make pickerelweed leaves more palatable to shredder chironomid species (Boyero et al. 2012).

In our study, it is clear that some shredder chironomids preferred invasive macrophyte tissue due to their higher resource quality (e.g. N%, lower polyphenol and cellulose). The lower dissimilarity diversity of shredder chironomid assemblages observed in white ginger occurred due to the higher abundance of *E. calophylli*, as well as of *Stenochironomus*. These taxa presented a positive relation with N% and organic matter. In a study with shredder chironomid assemblage in a tropical stream, it was found that the abundance of *Endotribelos* larvae was lower in white ginger lily when compared with native three leaves (*Magnolia ovata*). This occurred due to the native three species having lower cellulose when compared with the invasive white ginger lily (Leite-Rossi et al. 2016). Such results show that resource quality provided by leaf plant species influence herbivore species assemblages.

Concerning the lower dissimilarity index of shredder larvae in white ginger lily leaves, this was especially influenced by higher abundance of *Stenochironomus*. This chironomid taxon is a typical shredder, which consumes a higher percentage of plant tissue than other shredder chironomids (Borkent 1984). The intake-efficiency hypothesis has proven how robust this herbivore species is. This hypothesis states that intake-efficiency mechanism favours herbivory, because the herbivore maximizes energy intake by minimizing the energy and time spend searching for and subduing prey (Sanches and Trexler 2016). The habit of mining in plant species tissues enables *Stenochironomus* to use plants as habitats and also obtain its food resource, which supports this hypothesis. This adaptive evolution demonstrated effectiveness to *Stenochironomus*, which consumed a high percentage of invasive macrophyte leaves than pickerelweed leaves. The leaf chemical composition of invasive white ginger lily leaves seemed to be an important diet component for this shredder chironomid.

Despite the high impact of invasive macrophyte species in freshwater ecosystems, interest in their management has increased due to the necessity of freshwater conservation practices (Kuehne et al. 2016). In our study, we showed that invasive white ginger lily was considered as a higher quality resource. Its leaf characteristics became more attractive to shredder species than the native pickerelweed. Additionally, the resource quality provided by macrophyte leaves may be important in terms of selecting evolutionary adaptation traits of associated herbivores. These results added knowledge to the ecological relationships between Neotropical chironomids and plant species. We highlighted the importance of selecting native macrophyte species with higher resource quality to conservation practices in the littoral zone of lentic systems.

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Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Association of Official Agricultural Chemists (1995) *Official methods of analysis of the AOAC*. Arlington, AOAC International, 1, 1–30.

Bakker ES, Wood KA, Pagès, JF, Veen GC, Christianen MJ, Santamaría L, Nolet BA, Hilt S (2016) Herbivory on freshwater and marine macrophytes: A review and perspective. *Aquatic Botany*, 135:18-36.

- Biasi, C., Tonin, A. M., Restello, R. M., & Hepp, L. U. (2013). The colonisation of leaf litter by Chironomidae (Diptera): the influence of chemical quality and exposure duration in a subtropical stream. *Limnologica-Ecology and Management of Inland Waters*, 43(6), 427-433.
- Borkent A (1984) The systematics and phylogeny of the *Stenochironomus* complex (*Xestochironomus*, *Harrisius*, and *Stenochironomus*) (Diptera: Chironomidae). *Memoirs of the Entomological Society of Canada*, 116:5-270.
- Boyero L, Barmuta LA, Ratnarajah L, Schmidt K, Pearson RG (2012) Effects of exotic riparian vegetation on leaf breakdown by shredders: a tropical–temperate comparison. *Freshwater Science*, 31:296-303
- Blüthgen N, Menzel F, Blüthgen, N (2006) Measuring specialization in species interaction networks. *BMC ecology*, 6:1-12.
- Carlsson, NO, Lacoursiere JO (2005) Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. *Biological Invasions*, 7: 233-241.
- Carreira BM, Dias MP, Rebelo R (2014) How consumption and fragmentation of macrophytes by the invasive crayfish *Procambarus clarkii* shape the macrophyte communities of temporary ponds. *Hydrobiologia*, 721:89-98.
- Choi C, Bareiss C, Walenciak O, Gross EM (2002) Impact of polyphenols on growth of the aquatic herbivore *Acentria ephemerella*. *Journal of Chemical Ecology*, 28: 2245-2256.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Journal of Ecology*, 18:117-143.
- Coelho-Silva JF (1967) *Noções Sobre Análise de Alimentos*. Imprensa Universitária da Universidade Rural do Estado de Minas Gerais, Viçosa.

Corbi, J. J., & Trivinho-Strixino, S. (2017). Chironomid species are sensitive to sugarcane cultivation. *Hydrobiologia*, 785(1), 91-99.

Cornut, J., Ferreira, V., Gonçalves, A. L., Chauvet, E., & Canhoto, C. (2015). Fungal alteration of the elemental composition of leaf litter affects shredder feeding activity. *Freshwater Biology*, 60(9), 1755-1771.

de Castro, WAC, Almeida, RV, Leite, MB, Marrs, RH, Matos, DMS. 2016. Invasion strategies of white ginger lily (*Hedychium coronarium*) J. König (Zingiberaceae) under different competitive and environmental conditions. *Environment and Experimental Botany*, 127: 55-62.

Dormann CF, Fruend J, Gruber B, Dormann MCF, LazyData TRUE (2016) Package 'bipartite'.

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956) Colorimetric method for determination of sugars and related substances. *Analytical Chemistry*, 28:350–356.

Friedlin, B., Gastwirth, J.L. (2000). Should the median test be retired from general use? *The American Statistician*, 54:161–164.

König, R., Hepp, L. U., & Santos, S. (2014). Colonisation of low-and high-quality detritus by benthic macroinvertebrates during leaf breakdown in a subtropical stream. *Limnological Ecology and Management of Inland Waters*, 45, 61-68.

Kubanek J, Hay ME, Brown PJ, Lindquist N, Fenical W (2001) Lignoid chemical defenses in the freshwater macrophyte *Saururus cernuus*. *Chemoecology*, 11:1-8.

Kuehne LM, Olden JD, Rubenson ES (2016) Multi-trophic impacts of an invasive aquatic plant. *Freshwater Biology*, 61:1846-1861.

- Leite-Rossi, LA, Trivinho-Strixino, S. (2012). Are sugarcane leaf-detritus well colonized by aquatic macroinvertebrates?. *Acta Limnologica Brasiliensia*, 24:303-313.
- Leite-Rossi LA, Saito VS, Cunha-Santino MB, Trivinho-Strixino S (2016) How does leaf litter chemistry influence its decomposition and colonization by shredder Chironomidae (Diptera) larvae in a tropical stream? *Hydrobiologia*, 77:119-130.
- Lodge DM (1991) Herbivory on freshwater macrophytes. *Aquatic botany*, 41: 195-224.
- Lorenzi H (1991) Plantas daninhas do Brasil: terrestres, aquáticas, parasitas, tóxicas e medicinais. Instituto Plantarum, Nova Odessa.
- Lorenzi H, Souza H (2001) Plantas ornamentais. Plantarum, São Paulo.
- Makkar HP, Blümmel M, Borowy NK, Becker K (1993) Gravimetric determination of tannins and their correlations with chemical and protein precipitation methods. *Journal of the Science of Food and Agriculture*, 61:161-165.
- Martin-Creuzburg D, Beck B, Freese HM (2011) Food quality of heterotrophic bacteria for *Daphnia magna*: evidence for a limitation by sterols. *FEMS Microbiology Ecology*, 76:592-601.
- Matsuda JT, Lansac-Tôha FA, Martens K, Velho LFM, Mormul RP, Higuti J (2015) Association of body size and behavior of freshwater ostracods (Crustacea, Ostracoda) with aquatic macrophytes. *Aquatic Ecology*, 49:321-331.
- Mertens DR (2002) Gravimetric determination of amylase treated neutral detergent fiber in feeds with refluxing in beaker or crucibles: collaborative study. *Journal of AOAC International* 85:1217–1240

Morrison WE, Hay ME (2011a) Induced chemical defenses in a freshwater macrophyte suppress herbivore fitness and the growth of associated microbes. *Oecologia*, 165:427-436.

Morrison, W. E., & Hay, M. E. (2011b). Herbivore preference for native vs. exotic plants: generalist herbivores from multiple continents prefer exotic plants that are evolutionarily naïve. *PLoS One*, 6(3), e17227.

Morrison WE, Hay ME (2012) Are lower-latitude plants better defended? Palatability of freshwater macrophytes. *Ecology*, 93:65-74.

Provenza FD, Villalba JJ, Dziba LE, Atwood SB, Banner RE (2003). Linking herbivore experience, varied diets, and plant biochemical diversity. *Small ruminant research*, 49:257-274.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at: <http://www.R-project.org> (accessed 26.10.16).

Robertson JB, Van Soest PJ (1981). The detergent system of analysis and its application to human foods. In James WPT, Theander O (eds), *The Analysis of Dietary Fiber in Food*. Marcel Deller, New York, pp 123–158

Sanchez JL, Trexler JC (2016). The adaptive evolution of herbivory in freshwater systems. *Ecosphere*, 7(7). DOI: 01414. 10.1002/ecs2.1414

Sarruge JR, Haag HP (1974) *Análises Químicas em Plantas*. Escola Superior de Agricultura Luiz de Queiroz. Universidade de São Paulo, Piracicaba

Saulino, H. H. L., Corbi, J. J., & Trivinho-Strixino, S. (2014). Aquatic insect community structure under the influence of small dams in a stream of the Mogi-Guaçu river basin, state of São Paulo. *Brazilian Journal of Biology*, 74(1), 79-88.

Theel HJ, Dibble ED, Madsen JD (2008). Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. *Hydrobiologia*, 600:77-87

Tiner RW (1991) The concept of a hydrophyte for wetland identification. *Bioscience*, 41:236-247.

Trivinho-Strixino S (2014) Ordem Diptera. Família Chironomidae. Guia de identificação de larvas,. In Hamada N, Nessimian JL, RB Querino (orgs). *Insetos Aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia*. Editora do INPA, Manaus, BR, pp. 457-660

Wetzel RG (1983) *Limnology*. Second Edition. W. B. Saunders, Philadelphia.

Wong PK, Liang YAN, Liu NY, QIU JW (2010) Palatability of macrophytes to the invasive freshwater snail *Pomacea canaliculata*: differential effects of multiple plant traits. *Freshwater Biology*, 55:2023-2031.

Wood KA, O'Hare MT, McDonald C, Searle KR, Daunt F, Stillman RA (2016) Herbivore regulation of plant abundance in aquatic ecosystems. *Biological Reviews*. doi: 10.1111/brv.12272

Capítulo IV

Can herbivore functional traits influence food web complexity? - Implications for an invasive macrophyte species.

Abbreviated title: *Herbivore macroinvertebrate traits in food webs: implications for an
invasive macrophyte*

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Summary

1. Invasive macrophyte species have implied changes in the composition of functional traits of herbivorous macroinvertebrates in freshwater systems. These changes in trait composition could have important implications for food web structures. We compared macroinvertebrate herbivore trait compositions with food web structures in parts of the littoral zone of a tropical reservoir with and without the presence of the invasive white ginger lily (*Hedichium coronarium*- Zingiberaceae).
2. We conducted macroinvertebrate leaf colonisation experiments during the dry and rainy seasons for two years (2013-2015). These experiments compared the colonisation of invasive white ginger to that of the native pickerelweed (*Pontederia cordata* - Pontederiaceae) in a total of 40 sample leaf bags of each macrophyte species.
3. We estimated the functionally singular species (sing.sp) and functional richness (FRic) trait indices to represent herbivore functional trait compositions. To analyse macroinvertebrate food webs, we calculated the total links (L), link density (L/S), connectance (C) and predator-prey ratio indices using a predator-prey matrix. Furthermore, we analysed the influence of the chemical traits of invasive and native macrophyte species' leaves, such as, P, N, AFDM, total polyphenols, total carbohydrates and associated periphyton, on herbivore traits and food web indices.
4. White ginger leaves had higher quality resources (N and AFDM), which resulted in higher herbivore trait indices than pickerelweed. The lower quality resources of native macrophyte leaves, such as higher P and carbohydrates, negatively influenced sing.sp, FRic, L and L/S, and resulted in lower N and predator-prey ratios. C, which represents food web complexity, was similar between macroinvertebrate assemblages due to the participation of omnivorous intermediate trophic levels. Nonetheless, a decrease in predator-prey interactions

due to lower N indicated that lower resource quality influences the food web through a bottom-up effect.

5. Our study demonstrated that the resource quality of macrophyte leaves had an important influence on the herbivores' macroinvertebrate traits, which in turn can affect food web structures. Additionally, our study indicated the importance of selecting native macrophyte species with higher resource quality for restoration practices in freshwater conservation programs.

Key words: herbivory, scrapers, shredders, biological invasions, littoral zone.

1. Introduction

The influence of invasive plant species in herbivore assemblages has received significant attention in ecological studies of terrestrial systems. Nowadays, the number of studies that focus on herbivory in freshwater systems has increased, especially those involving macroinvertebrate communities (Morrison & Ray, 2011; Leite-Rossi *et al.*, 2016). Concerning this issue, some studies have reported the problematic influence of invasive macrophytes (*e.g.*, *Ceratophyllum*) with high concentrations of secondary compounds (*e.g.*, polyphenols and tannins). These affect macroinvertebrate herbivores and biological traits, such as fitness and growth rates (Choi *et al.*, 2002; Boiché *et al.*, 2011).

The negative impact of such chemical compounds from invasive macrophytes can be minimized when they decompose faster. This process accelerates the leaching of such secondary compounds (Elger *et al.*, 2005). Concerning the macroinvertebrate herbivore shredders, such changes in the chemical compounds of invasive macrophyte species seem to be an important factor. These chemical compound changes make invasive macrophyte tissues more palatable, resulting in increased consumption (Newman *et al.*, 1996; Leite-Rossi *et al.*,

2015). In the macroinvertebrate food webs of species other than shredders, the scraper feeding groups consist of herbivores (Gregory, 1983). During the colonisation of leaf plant species, the periphyton (composed of algae, bacteria, fungi and detritus) and leaf litter represent their main food resources. Shredders and scrapers explore food resources in different ways (Cummins, 2016), depending on the availability of food. For instance, some chironomid larvae differ from shredders by their traits, such as low biomass, body shape and mouthparts, that enable them to utilize the leaf plant tissues as food (e.g., *Stenochironomus*, *Xestoschironomus*) (Borkent, 1984). Some mayfly nymphs, such as *Americanbaetis* (Baetidae) and *Miroculis* (Leptophlebeiidae), known as scrapers, differ in the composition of their diets (periphytic algae or algae/detritus) due to their different mouthpieces. These different traits enable these herbivores to utilize different resources in different niches in freshwater systems, such as shallow and deeper depths (Baptista *et al.*, 2006).

Concerning the importance of herbivory to the freshwater ecosystem, analysing the relationships between herbivores and invasive macrophyte species is crucial to understand if the resource quality provided by these plant species can affect herbivore assemblages. Dominance of an invasive plant could severely change the food resource quality in freshwater systems, which could lead to the loss of various ecological functions (Claeson *et al.*, 2014; Correa-Araneda *et al.*, 2015). Additionally, because herbivores are the basal level of food webs, alterations in their composition assemblages would affect the exchange of energy flow to the higher trophic levels, altering the food web structure through a bottom-up effect.

In the present study, we analysed the influence of the invasive macrophyte white ginger lily (*Hedychium coronarium* J. König, Zingiberaceae) on the herbivore functional trait compositions of freshwater herbivore species and the macroinvertebrate food web structure. To do this, we conducted leaf colonisation experiments in the littoral zone of a tropical reservoir to compare the invasive white ginger lily to the native pickerelweed species

(*Pontederia cordata*, L. - Pontederiaceae). These two macrophyte species present similar characteristics of life forms, white ginger lily is amphibious and pickerelweed is an emergent macrophyte species. Both macrophyte species are monocotyledons with a wide distribution in freshwater ecosystems, such as the littoral zone of lakes and riparian and marsh areas (Lorenzi, 1991; Lorenzi & Souza, 2001). Additionally, these macrophytes differ in their chemical compounds (*e.g.*, cellulose, lignin, and nitrogen concentrations) and decomposition rates; pickerelweed decomposes faster than white ginger lily (Odum & Heywood, 1978; Leite-Rossi *et al.*, 2015).

Our main hypothesis was that macroinvertebrate herbivore trait diversity decreases according to the available macrophyte species; such an effect would mirror a negative impact on entire food webs, affecting the ecological process of energy flow exchange.

2. Material and Methods

2.1 Study area

We carried out a macroinvertebrate colonisation experiment of macrophyte leaves in the littoral zone of the Fazzari Reservoir, which is located in the preserved area of the Cerrado biome (645 ha) at the Universidade Federal São Carlos (UFSCar, Brazil) (21°58'S, 47°53'W). This reservoir has a total area of 13 ha, with an average depth of 1.1 m and a maximum depth of 4.0 m. The abiotic characteristics of its littoral zone are high dissolved oxygen concentrations, acid pH and average water temperatures ranging from 18°C to 21°C (Table 1).

Table 1. Abiotic characterization of colonisation points in different macrophyte leaf species in the littoral zone of the Fazzari Reservoir – Cerrado biome, Brazil.

Abiotic variables	Leaf bag			
	White-ginger lily	Pickerelweed	t	p
Water temperature (°C)	19.77 ±0.24	19.76 ±0.26	0.13	0.89
pH	6.37 ±0.15	5.49 ±0.09	5.00	<0001*
Dissolved oxygen (mg/L)	8.65 ±0.15	8.00 ±0.20	2.58	0.01*
Depth	0.40 ±0.03	0.41 ±0.02	-0.15	0.87

* - <0.05, ± Std.

The vegetation surrounding the Fazzari Reservoir banks consists of two main profiles: the right reservoir bank has an 80-meter stretch that is completely dominated by the invasive white ginger lily (*H. coronarium*) followed by forest that is partially invaded by the same invasive plant; the left reservoir bank is surrounded by a native riparian forest (trees, shrubs, and ferns) and the amphibian spike-rush macrophyte (*Eleocharis*).

2.2 Macroinvertebrate leaf colonisation treatments

We performed macroinvertebrate leaf colonisation experiments in the littoral zone of the reservoir, using fresh leaves from the invasive macrophyte white ginger lily and the native macrophyte pickerelweed. The white ginger lily has recently received attention in freshwater studies in Brazil. As an invasive species, it has strong competitive strategies, which have a negative impact on freshwater biodiversity. As well as other invasive plant species (*e.g.*, *Urocloa* sp), the white ginger lily presents strong competitive strategies, such as fast growth and rapid dispersal, that enable it to become dominant in wetlands, riparian zones and lake banks, where it forms dense populations (De Castro *et al.*, 2016).

We collected leaves from each macrophyte species from adult plants without injuries and signals or initial senescence signs. Six leaves from each macrophyte species were stocked in each colonisation bag (0.20x0.40, 01mm). We utilized five sample bags for each plant treatment, which we sampled from 2013 to 2015 over eight periods: May-June/August-September/November-December/2013, February-March/June-July/August-September/20142014, and January-February/March-April/2015, totaling 40 samples for each

treatment. We submersed leaf colonisation bags in randomly-chosen littoral zone points, which we collected carefully with a dip net (mesh 250 μm) after 40-45 days of colonisation. We picked the macroinvertebrate specimens alive, utilizing illuminated trays and identifying them to the lowest taxonomic level possible by using identification keys for macroinvertebrates of the Neotropical region.

We measured the abiotic variables, such as water temperature, pH, dissolved oxygen and depth for each littoral colonisation point (Table 1). Dissolved oxygen concentrations were measured using the Winkler method and pH by the colorimetric method. Additionally, we measured biotic variables, such as periphyton biomass during colonisation. To estimate the periphyton, we used chlorophyll *a* content associated with macrophyte species' leaves, which we gathered by scraping the leaf species with a soft toothbrush. Afterwards, we filtered a volume of 150 ml of leaf scrapings through a nitrate membrane (47 mm, $\theta = 0.45 \mu\text{m}$) using a vacuum pump. For each leaf treatment, we used five replicates. The chlorophyll *a* content of each treatment was extracted using acetone (90%) for a 24-h incubation period and quantified via spectrophotometry (665 and 750 nm wavelengths) (Creitz & Richards, 1955). We expressed the periphyton values as the relationship between the chlorophyll *a* content ($\mu\text{g/L}$) and total leaf plant area (m^2).

2.3 Characterization of macrophyte species' leaf chemical compounds

In order to analyse the influence of the chemical compounds of macrophyte leaf species on the herbivores' functional traits and macroinvertebrate food webs, we determined the macrophyte leaf percentage of chemical compounds, such as total phosphorous (P%), nitrogen (N%), organic matter, cellulose, lignin, soluble carbohydrates and soluble polyphenols. To do this, we collected fresh leaves from adult macrophyte species; these leaves were washed in running water to remove any materials that could interfere with the

determination of initial leaf litter mass (*e.g.*, inorganic material, small animals and animal feces). Then, we oven-dried them at 45°C to a constant mass.

We used the oven-dried macrophyte species' leaves (triplicates per leaf macrophyte species), which were ground to a thickness of 1 mm in a knife grinder for chemical analysis. We determined the P% and N% by the Vanadato-Molibdato (Sarruge & Haag, 1974) and micro-Kjeldahl methods (Coelho-Silva, 1967; Association of Official Agricultural Chemists, 1995), respectively. The organic matter content was determined using the percentage of ash-free dry mass (AFDM %) by the gravimetric method and the soluble carbohydrate concentration was determined using the colorimetric method (Dubois *et al.*, 1956). The total lignin concentration was determined by a sequential analysis of neutral and acid detergents (Robertson & Van Soest, 1981; Mertens, 2002) and the polyphenol concentration was determined using the gravimetric method (Makkar *et al.*, 1993).

2.4 Herbivore macroinvertebrate functional traits and food web structure

We classified the macroinvertebrate specimens into functional feeding groups (FFG), such as scrapers, shredders, collectors, filterers, and predators, according to studies that were conducted in the Neotropical region (Motta & Ueda, 2004; Reynaga & Martin, 2013; Brasil *et al.*, 2014; Butaka *et al.*, 2014). Within this FFG classification, we selected the scrapers (S= 5) and shredders (S= 10) to analyse the functional composition of herbivore traits. To compose the herbivore trait community, we measured and scored five functional trait categories: body length, herbivore habits, lifestyle, shelter and respiration. We measured the body length - (1) – small (<5mm), (2) – medium (5-10 mm) and (3) – large (>10 mm) – by measuring 10 specimens of each taxa found in each colonisation bag treatment throughout the different season periods. We considered the herbivore habit as (1) facultative when an organism presents two or more feeding habit preferences (*e.g.*, algae + detritus, CPOM + FPOM) or (2)

restrictive when an herbivore presents an exclusive feeding habit preference (*e.g.*, algae or CPOM); we follow these classifications according to FFG studies that were conducted in the Neotropical region and analysed the percentage of organic matter particles found in the digestive tract of each herbivore taxon (Motta & Ueda, 2004; Baptista *et al.*, 2006; Reynaga & Martin, 2013; Butaka *et al.*, 2014; Leite- Rossi *et al.*, 2015). Lifestyle was classified by whether the species was (1) free living, (2) silk tube building, (3) cocoon building, or (4) a miner. Habit was classified by whether the species was a (1) sprawler, (2) burrower or (3) climber, and we classified the respiration system as (1) osmotic or (2) branchial. Concerning the lack of information regarding these classification traits, and especially the herbivore community consisting of aquatic insect larvae, we classified these categories according to the information available in Merritt & Cummins (1996) (Table 2).

Table 2. Herbivore functional traits score associated with the invasive (white ginger lily) and native (pickerelweed) macrophyte leaf species in the littoral zone of the Fazzari Reservoir, Cerrado biome, Brazil. Shr – shredder, sc – scraper, cg – collector-gathering, pr - predator

Taxa	FFG	Functionaltrait score					Reference
		herbivory	length	shelter	habit	respiration	
<i>Beardius phytophilus</i>	shr	2	1	2	2	1	Leite-Rossi et al., 2015
<i>Caenis caenis</i>	sc	2	2	1	3	2	Baptista et al., 2006
<i>Cleaodes</i>	scr	2	2	1	3	2	Baptista et al., 2006
<i>Endotribelos bicolor</i>	shr	2	2	2	2	1	Leite-Rossi et al., 2015
<i>Endotribelos calophylli</i>	shr	2	2	2	2	1	Leite-Rossi et al., 2015
<i>Endotribelos sublettei</i>	shr	2	2	2	2	1	Leite-Rossi et al., 2015
<i>Marilia</i>	shr/cg/pr	1	3	3	1	2	Reynaga& Martin, 2013
<i>Miroculis</i>	scr/cg	1	2	1	3	2	Baptista et al., 2006
<i>Phaenopsectra</i>	shr/cg	1	2	2	2	1	Leite-Rossi et al., 2015
<i>Polypedilum fallax</i> group	shr/cg	1	1	2	3	1	Leite-Rossi et al., 2015
<i>Polypedilum (Polypedilum)</i>	shr/cg	1	1	2	3	1	Leite-Rossi et al., 2015
<i>Polypedilum (Tripodura)</i>	shr/cg	1	1	2	3	1	Buttaka et al., 2014
Scirtidae	sc	2	3	1	1	2	Merritt& Cummins, 1996
<i>Stenochironomus</i>	shr	2	2	4	2	1	Leite-Rossi et al., 2015
<i>Ulmeritrus</i>	sc	2	2	1	3	2	Baptista et al., 2006

We obtained the herbivore macroinvertebrates' functional trait compositions using a multimeric functional diversity (FD) approach, which is represented by the distance measured based on trait values where the distance between taxa is calculated by using a principal component analysis matrix. The distances between the herbivore community traits were

calculated by using the Gower dissimilarity distance “in a trait space,” separating species with a cluster analysis based on their proximity in a trait distance matrix (Laliberté *et al.*, 2014). In order to represent herbivore macroinvertebrate composition traits associated with different macrophyte species in the littoral zone, we utilized the functionally singular species (sing.sp) and functional richness (FRic) indices; FRic estimates the dispersion of species’ traits in an area with the volume of the minimum convex hull that includes all species (Villéger *et al.*, 2008; Laliberté & Legendre, 2010). To do this, we utilized the FD-package (Laliberté *et al.*, 2014) available in the R platform (R Development Core Team, 2014).

We built the food web network based on the FFG classification and body length of specimens using predator-prey matrices, which contain all taxa found in the community associated with different macrophyte leaf treatments and season periods. The taxa were distributed in columns and rows, and linkages between taxa were indicated in a binary manner, in which 0 indicated no linkage and 1 was a linkage between two macroinvertebrate taxa. We determined the food web structures using: the number of trophic links (L) and number of links (edges) among the taxa; the C, an indicator of the degree of inter-connectivity in a food web; link density (L/S index), the number of links that species establish with other nodes, weighed by their magnitude within the food webs; and predator-prey ratio, a measure of food web shape (values <1 may indicate instability) (Scotti *et al.*, 2009). To do this, we utilized the “foodweb-package” (Perdomo *et al.*, 2015) which is available on the R platform (R Development Core Team, 2014).

2.5 Data analyses

2.5.1 Chemical traits of macrophyte species’ leaves

We analysed the significance of the differences between the periphyton and chemical traits of different macrophyte species’ leaves (P%, N%, AFDM, cellulose, lignin, polyphenols

and carbohydrates) using the Student's T-test, considering a 95% confidence interval (P<0.05).

2.5.2 Macroinvertebrate herbivore traits and food web measures

We also used the Student's T-test to analyse the significance of differences in macroinvertebrate herbivores' functional trait indices, *sing.sp* and *FRic*, as well as food web measures (*L*, *C*, *L/S* and predator-prey ratio) among the different macrophyte leaf treatments using a 95% confidence interval (P<0.05). In addition, we analysed the influence of leaf chemical traits on functional herbivore traits, as well as the macroinvertebrate food web measures by using a multivariate linear regression model. Furthermore, in order to estimate the contribution of significant variables to this model, we used a *post hoc* Pearson's correlation model. The correlation coefficients were used as a measure of the relationship between the chemical traits of the leaves of the macrophyte species and periphyton that significantly influenced the functional traits and food web measure indices.

3. Results

3.1 Chemical traits of macrophyte species' leaves

The leaf traits of the invasive white ginger lily presented better quality resources than the pickerelweed leaves due to higher N% and AFDM, as well as lower P%, cellulose, total polyphenols and carbohydrates. However, white ginger lily leaves presented lower concentrations of associated periphyton than the native pickerelweed (Table 3).

Table 3. Chemical traits of the invasive and native macrophytes' leaves and associated periphyton in colonisation experiments in the littoral zone of the Fazzari Reservoir – Cerrado biome, Brazil. P – phosphorous, N – nitrogen, AFDM – ash free dry mass

Leafchemical compound	Leaf bag			
	Wite ginger lily	Pickerelweed	T	p
P (%)	0.08 ±0.01	0.16 ±0.01	-10.14	<0001*

N (%)	2.18 ±0.01	1.35 ±0.04	4.22	<0001*
AFDM%	93.78 ±0.10	92.78 ±0.30	20.76	<0001*
cellulose %	11.46 ±2.80	29.95 ±4.10	183.58	<0001*
lignin %	23.27 ±2.70	26.36 ±2.10	-423.32	<0001*
total polyphenol %	1.77 ±2.50	4.27 ±0.90	-51.11	<0001*
total carbohydrates %	5.66 ±0.70	7.87 ±1.30	-18.38	<0001*
periphyton (mg/m ²)	29.18 ±4.26	68.47 ±9.67	-3.81	<0001*

(*) – p<0.05

3.2 Macroinvertebrate herbivore traits and food web measures

We collected 3,730 specimens. Herbivores represented 18% of the assemblage (n=662). White ginger lily leaf colonisation bags presented higher functionally singular species (sing.sp= 3.6, SE ±0.19, t= 2.13, p= 0.03) and functional richness (FRic= 2.83, SE ±0.43, t= 2.07, p= 0.04) indices than pickerelweed leaves ([sing.sp= 3.05, SE ±0.17], [FRic= 1.70, SE ±0.29]) (Figure 2). Concerning macroinvertebrate food web measures, the indices of L, L/S, C and predator-prey ratio were very similar between the macroinvertebrate assemblages for the two macrophyte species' leaves (p>0.05) (Figure 3).

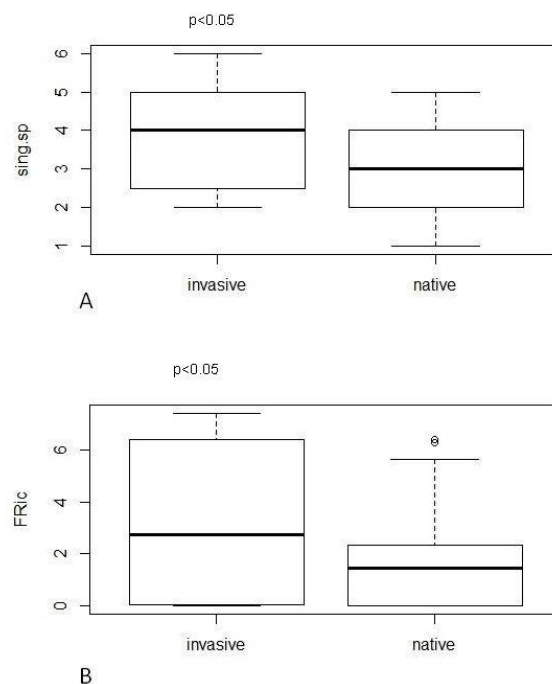


Figure 2. Herbivore functional trait indices associated with the invasive white ginger lily and native pickerelweed macrophyte leaves in the Fazzari Reservoir, Cerrado biome, Brazil. A – Functionally singular species (sing.sp); B – Functional richness (FRic).

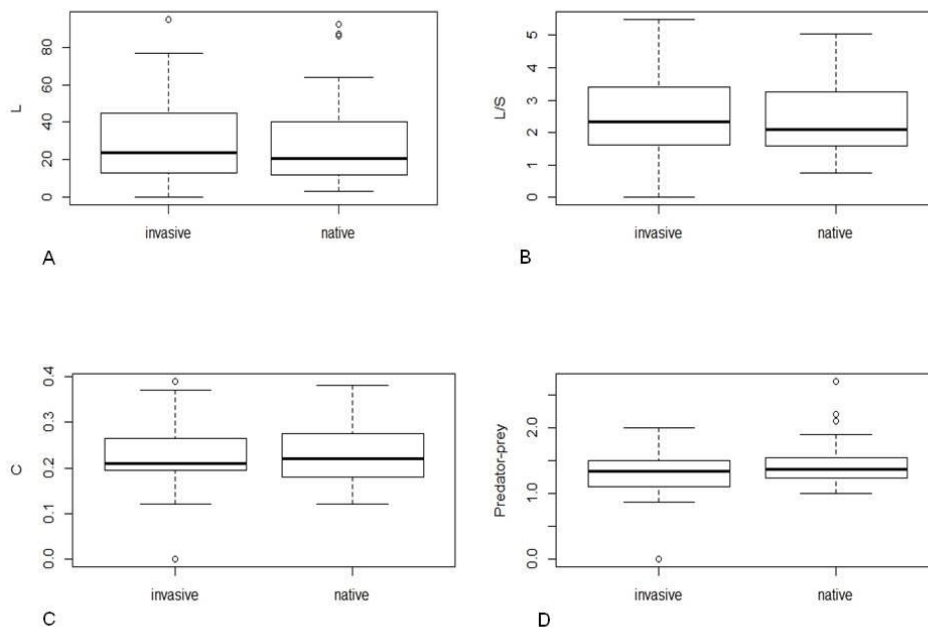


Figure 3. Macroinvertebrate food web indices associated with the invasive white ginger lily and native pickerelweed macrophyte leaves in the Fazzari Reservoir. A) L - Total Links; B) L/S - Link density; C) C - Connectance; D) Predator-prey ratio.

The analyses of the influence of chemical leaf traits on herbivore traits showed that the higher percentage of phosphorous of pickerelweed leaves negatively influenced the functionally singular species (sing.sp) and functional richness (FRic) indices of herbivore traits. For food web indices, this same chemical compound negatively influenced total links (L) and link density (L/S). We observed that link density (L/S) and the predator-prey ratio were negatively influenced by a lower percentage of nitrogen and a higher percentage of total carbohydrates. The lower associated periphyton in the white ginger lily negatively influenced the total links (L) and link density (L/S) of macroinvertebrate food web indices (Table 4). The *post hoc* test of Pearson's correlation corroborated all the results indicated by the multivariate linear regression model (Table 5).

Table 4. Analysis of the influence of leaf chemical traits of the invasive white ginger lily and native pickerelweed species and associated periphyton on herbivore functional traits and the macroinvertebrate food web in the littoral zone of the Fazzari Reservoir – Cerrado biome, Brazil. P – phosphorous, N – nitrogen, sing.sp – functionally singular species, FRic – functional richness, L – total links, L/S – link density

Chemical leaf trait	Indices	Coeff.	Std.err.	t	p	R²
pickerelweed						
P (%)	sing.sp	-2.96	1.15	-2.56	0.020*	0.13
	FRic	-3.48	1.61	-2.16	0.040*	0.15
	L	-4.24	2.07	-2.05	0.040*	0.16
	L/S	-2.57	1.05	-2.44	0.020*	0.15
total carbohydrates (%)	L/S	-2.73	0.84	-3.21	0.003*	0.15
N (%)	predator-prey	-0.46	0.22	-2.08	0.045*	0.24
white ginger lily						
periphyton (mg/m ²)	L	-0.43	0.16	-2.70	0.011*	0.16
	L/S	-0.16	0.08	-2.04	0.049*	0.10

(*) p<0.05

Table 5. Results of Pearson’s correlation analyses of the influence of the chemical traits of the leaves of the macrophyte species on the functional traits of herbivore species and macroinvertebrate food web structures during the colonisation experiment in the littoral zone of Fazzari Reservoir – Cerrado biome, Brazil. P – phosphorous, N – nitrogen, sing.sp – functionally singular species, FRic – functional richness, L – total links, L/S – link density

Chemical leaf trait	Indices	r	p
pickerelweed			
P (%)	sing.sp	-0.35	0.028*
	FRic	-0.42	0.007*
	L	-0.40	0.008*
	L/S	-0.36	0.018*
total carbohydrates (%)	L/S	-0.37	0.018*
N (%)	predator-prey	-0.42	0.002*
white ginger lily			
periphyton (mg/m)	L	-0.41	0.007*
	L/S	-0.38	0.008*

(*) p<0.05

4. Discussion

Herbivore macroinvertebrates are considered one of the main components of freshwater ecosystems. They have an important ecological role by exchanging nutrient cycles and energy flow throughout food webs (Wallace & Webster, 1996). In our study, the functional traits of herbivore species changed with the lower quality of food resources (higher lignin and cellulose) provided by leaves of the native pickerelweed. Additionally, our results showed that the lower-quality resources provided by the leaves of this macrophyte species affected the macroinvertebrates' food web. We observed this by the decrease in the trophic level (L) and link density (L/S). These results could negatively influence the predator-prey ratio, which decreased due to lower N concentration.

Some studies have reported that invasive macrophytes with higher C:N ratios present disadvantageous characteristics, which negatively affect herbivore macroinvertebrates' traits (Wong *et al.*, 2010; Morrison & Hay, 2011). Our results contradicted these findings. The invasive white ginger lily leaves were a high-quality resource and the pickerelweed leaves presented higher concentrations of secondary compounds (especially polyphenols). Additionally, fresh leaves of white ginger lily presented advantageous chemical characteristics, such as higher AFDM and higher N% than the native leaf species, which had higher *sing.sp* and *FRic* values than those of the native pickerelweed. Hence, the results observed here indicate that herbivore macroinvertebrate functional trait assemblages depend on the chemical traits of the leaves of macrophyte species. Furthermore, changes in their composition can affect food web structures via a bottom-up effect.

We observed that the lower periphyton content in the white ginger lily had a negative influence on the L and L/S of macroinvertebrate food webs. This result could be explained by the exclusion of some scraper species, such as *Cleodes* (Batidae) and *Miroculis*

(Leptophlebeidae), which predominantly consume algae (Baptista *et al.*, 2006). On the other hand, the higher periphyton concentrations in pickerelweed could be related to higher P%. It is well known that autotrophic organisms, such as algae are generally dependent on P%, which is incorporated into their cells (Martin-Creuzburg *et al.*, 2011). The higher availability of this resource could explain the lower sing.sp and FRic values obtained from pickerelweed, probably due to the predominance of scraper species. In general, algae are an important resource for generalist macroinvertebrates, such as *Ablabesmyia* larvae (Tanypodinae – Diptera), which have omnivorous habits (Motta & Uieda, 2004). Furthermore, replacing herbivores for these omnivorous species could contribute to lower herbivore functional trait indices, as well as the similar patterns of the macroinvertebrate food webs in the two macrophyte species.

Regarding macrophyte leaf tissues, shredder larvae usually process vascular plants (Sinsabaugh *et al.*, 1985; Wallace & Webster, 1996). Their feeding habit trait, especially those with facultative habits, explains their presence in the native macrophyte tissues. Facultative herbivores ingested fine particle organic matter (FPOM) and associated periphyton instead of leaf tissues with lower-quality resources. Some authors consider that the habit of ingesting other resources is a variation of adaptive evolution for aquatic herbivores. This habit would have emerged because herbivores sought to improve the digestibility of plant tissues with high concentrations of secondary compounds. (Sanches & Trexler, 2016). In our study, chironomid shredder taxa *Endotribelos calophylli* and *Polypedilum (Tripodura)* larvae particularly predominated. However, the invasive macrophyte presented higher N% and AFDM and kept a positive relationship with restrictive shredders, such as *Stenochironomus* larvae, that have miner habits (Borkent, 1984). The presence and feeding preference of this taxon could be considered an important variable that led to the higher sing.sp and FRic values that we observed in the white ginger lily leaves.

Concerning the food web structures, we observed that there were similar patterns between associated communities. This result could be related to the predominance of intermediate trophic-level species, which could maintain strong relationships with top predators. The predator-prey biomass displays important implications for the link of prey species (Boukal, 2014). Dragonflies have high feeding rates, especially with smaller prey such as omnivorous chironomids. These contributed to the similar patterns of prey density bindings in leaf colonisation bags. Furthermore, the contribution of omnivore species includes entire macroinvertebrate food webs (Hall *et al.*, 2000). In addition, aquatic insect cannibalism has been reported as ubiquitous in standing freshwater systems (Klecka & Boukal, 2013). These could be considered the main reasons for the similar food web structures observed in our study. The macrophyte leaf species aspects did not have a strong influence on the food web structures. The many macroinvertebrate relationships seemed to occur regardless of the aquatic plant tissue present.

Concerning the results discussed above, we conclude that the interaction among intermediate (omnivorous species) and high trophic species (large predators) explains the non-differences between the macroinvertebrate food webs associated with the leaves of the macrophyte species studied. Nonetheless, the relationship between herbivore functional traits and the resource quality of the macrophyte species' leaves seemed an important factor for the herbivore assemblage composition in the littoral zone. Although generalist aspects of macroinvertebrates can maintain the food web structures, we observed evidence that changes in the herbivore functional traits can affect food web structures (L, L/S, and predator-prey ratio) due to the native macrophyte's lower resource quality. Additionally, our study pointed out the importance of selecting native macrophyte species with higher resource quality for restoration practices in freshwater conservation programs.

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References

- Association of Official Agricultural Chemists (1995) *Official methods of analysis of the AOAC*. Arlington, AOAC International, 1, 1–30.
- Baptista D. F., Buss D. F., Dias L. G., Nessimian J. L., Da Silva E. R., Neto A. D. M., & Andrade L. R. (2006) Functional feeding groups of Brazilian Ephemeroptera nymphs: ultrastructure of mouthparts. *International Journal of Limnology*, 42, 87-96.
- Boiché A., Lemoine D. G., Barrat-Segretain M. H. & Thiébaud, G. (2011) Resistance to herbivory of two populations of *Elodea canadensis* Michaux and *Elodea nuttallii* Planchon St. John. *Plant Ecology*, 212, 1723-1731.
- Borkent A. (1984). The systematic and phylogeny of the *Stenochironomus* complex (Diptera: Chironomidae). *Memories of Entomological Society of Canada*, 128, 1-269.
- Boukal D. S. (2014) Trait-and size-based descriptions of trophic links in freshwater food webs: current status and perspectives. *Journal of Limnology*, 73(s1).
- Brasil L. S., Juen L., Batista J. D., Pavan M. G. & Cabette H. S. R. (2014) Longitudinal Distribution of the Functional Feeding Groups of Aquatic Insects in Streams of the Brazilian Cerrado Savanna. *Neotropical entomology*, 43, 421-428.
- Buttakka C. M. M., Grybkowska M., Pinha G. D. & Takeda A. M. (2014) Habitat and trophic relationship of Chironomidae insect larvae from the Sepotuba River Basin, Pantanal of Mato Grosso, Brazil. *Brazilian Journal of Biology*, 74, 395-407.
- Choi C., Bareiss C., Walenciak O. & Gross E. M. (2002) Impact of polyphenols on growth of the aquatic herbivore *Acentria ephemerella*. *Journal of Chemical Ecology*, 28, 2245-2256.
- Claeson S. M., LeRoy C. J., Barry J. R. & Kuehn K. A. (2014) Impacts of invasive riparian knotweed on litter decomposition, aquatic fungi, and macroinvertebrates. *Biological invasions*, 16, 1531-1544.

- Coelho-Silva J. F. (1967) *Noções Sobre Análise de Alimentos*. Imprensa Universitária da Universidade Rural do Estado de Minas Gerais, Viçosa.
- Correa-Araneda F., Boyero L., Figueroa R., Sánchez C., Abdala R., Ruiz-García A. & Graça M. A. (2015) Joint effects of climate warming and exotic litter (*Eucalyptus globulus* Labill.) on stream detritivore fitness and litter breakdown. *Aquatic Sciences*, 77, 197-205.
- Creitz, G. I., Richards F. A. (1955) The estimation and characterization of plankton populations by pigment analysis: III a note on the use of “Millipore” membrane filters in the estimation of plankton pigments. *Journal of Marine Research*, 14, 211-216.
- Cummins K. W. (2016). Combining taxonomy and function in the study of stream macroinvertebrates. *Journal of Limnology*, 75(s1).
- De Castro W. A. C., Almeida R. V., Leite M. B., Marrs R. H. & Matos D. M. S. (2016) Invasion strategies of white ginger lily (*Hedychium coronarium*) J. König (Zingiberaceae) under different competitive and environmental conditions. *Environmental and Experimental Botany*, 127, 55-62.
- Dubois M., Gilles K. A., Hamilton J. K., Rebers P. A. & Smith F. (1956) Colorimetric method for determination of sugars and related substances. *Analytical Chemistry*, 28, 350–356.
- Elger A., Barrat-Segretain M. H. & Willby N. J. (2005) Seasonal variability in the palatability of freshwater macrophytes: a case study. In *Macrophytes in Aquatic Ecosystems: From Biology to Management*, pp. 89-93. Springer, Netherlands.
- Gregory S. V. (1983) Plant-herbivore interactions in stream systems. In Barnes, J. M.; Minshall, G. W. *Stream ecology*, pp. 157-189. Springer, US.
- Hall R. O., Wallace J. B. & Eggert S. L. (2000) Organic matter flow in stream food webs with reduced detrital resource base. *Ecology*, 81, 3445-3463.

- Klecka J. & Boukal D. S. (2013) Foraging and vulnerability traits modify predator–prey body mass allometry: freshwater macroinvertebrates as a case study. *Journal of Animal Ecology*, 82, 1031-1041.
- Laliberté E. & Legendre P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299-305
- Laliberté E., Legendre P. & Shipley B. (2014) FD: measuring functional diversity from multiple traits, and other tools for Funct. Ecol. R package version, 1-12.
- Leite-Rossi L. A., Saito V. S., Cunha-Santino M. B. & Trivinho-Strixino S. (2016) How does leaf litter chemistry influence its decomposition and colonization by shredder Chironomidae (Diptera) larvae in a tropical stream? *Hydrobiologia*, 77, 119-130.
- Lorenzi, H., 1991. *Plantas daninhas do Brasil: terrestres, aquáticas, parasitas, tóxicas e medicinais*. Instituto Plantarum, Nova Odessa.
- Lorenzi H. & Souza H. (2001) *Plantas ornamentais*. Plantarum, São Paulo.
- Makkar H. P., Blümmel M., Borowy N. K. & Becker K. (1993). Gravimetric determination of tannins and their correlations with chemical and protein precipitation methods. *Journal of the Science of Food and Agriculture*, 61, 161-165.
- Martin-Creuzburg D., Beck B., Freese H. M. (2011) Food quality of heterotrophic bacteria for *Daphnia magna*: evidence for a limitation by sterols. *FEMS Microbiology Ecology*, 76:592-601.
- Merritt R. W. & Cumins K. W. (1996) *An introduction to the Aquatic Insect of North America*. Kendall Hunt Publishing Co., Dubuque, Iowa.

- Mertens D. R. (2002) Gravimetric determination of amylase treated neutral detergent fiber in feeds with refluxing in beaker or crucibles: collaborative study. *Journal of AOAC International* 85, 1217–1240
- Morrison W. E. & Hay, M. E. (2011) Induced chemical defenses in a freshwater macrophyte suppress herbivore fitness and the growth of associated microbes. *Oecologia*, 165, 427-436.
- Motta R. L. & Uieda V. S. (2004) Diet and trophic groups of an aquatic insect community in a tropical stream. *Brazilian Journal of Biology*, 64, 809-817.
- Newman R. M., Kerfoot W. C. & Hanscom Z. (1996) Watercress Allelochemical Defends High-Nitrogen Foliage Against Consumption: Effects on Freshwater Invertebrate Herbivores. *Ecology*, 77, 2312-2323.
- Odum W. E. & Heywood M. A. (1978) *Decomposition of intertidal freshwater marsh plants. Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York, 89-97.
- Perdomo G., Sunnucks P. & Thompson R. M. (submitted). *Food web: an open-source program for the visualisation and analysis of compilations of complex food webs*. Environmental Modelling and Software.
- R Development Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria, Available at: <http://www.R-project.org> (accessed 26.10.16)
- Reynaga M. C. & Rueda M., Paola A. (2014) Análisis trófico de três espécies de *Marilia* (Trichoptera: Odontoceridae) del neotrópico. *Revista de Biología Tropical*, 62, 543-550.

Robertson J. B. & Van Soest P. J. (1981). The detergent system of analysis and its application to human foods. In James W. P. T. & Theander O. (eds). *The Analysis of Dietary Fiber in Food*. Marcel Deller, pp. 123–158. New York.

Sanchez J. L. & Trexler J. C. (2016). The adaptive evolution of herbivory in freshwater systems. *Ecosphere*, 7 (7). DOI: 01414. 10.1002/ecs2.1414

Sarruge J. R. & Haag H. P. (1974) *Análises Químicas em Plantas*. Escola Superior de Agricultura Luiz de Queiroz. Universidade de São Paulo, Piracicaba

Scotti M., Bondavalli C., Bodini A. & Allesina, S. (2009) Using trophic hierarchy to understand food web structure. *Oikos*, 118, 1695-1702.

Sinsabaugh R. L., Linkins A. E. & Benfield E. F. (1985) Cellulose Digestion and Assimilation by Three Leaf-shredding Aquatic Insects. *Ecology*, 66, 1464-1471.

Villéger S., Mason N. W. & Mouillot D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290-2301.

Wallace J. B. & Webster J. R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual review of entomology*, 41, 115-139.

Wong P. K., Liang Y. A. N., Liu N. Y. & QIU J. W. (2010) Palatability of macrophytes to the invasive freshwater snail *Pomacea canaliculata*: differential effects of multiple plant traits. *Freshwater Biology*, 55, 2023-2031.

Considerações finais

No Brasil, o bioma Cerrado é um dos *hot spot* de interesse conservacionista. Assim como os biomas Mata Atlântica e a Amazônia. O Cerrado abriga grande diversidade vegetal, a qual está suscetível às influências de diversas espécies de plantas invasoras. Recentemente as informações dos possíveis impactos causados por essas espécies invasoras a biodiversidade têm recebido maior atenção, uma vez que as mesmas contribuem para as tomadas das diretrizes de manejo e gestão conservacionista (ZENNI; ZILLER, 2011). Neste contexto, as análises dos caracteres funcionais das comunidades têm grande importância a manutenção da integridade dos processos ecossistêmicos. Através da análise de diversidade funcional e de suas implicações na estrutura das redes tróficas de macroinvertebrados, os seguintes aspectos da influência da macrófita invasora lírio-do-brejo sobre a comunidade de macroinvertebrados aquáticos na zona litoral de um reservatório tropical foram destacados:

a) A presença da macrófita invasora lírio-do-brejo alterou a estrutura funcional da comunidade de macroinvertebrados aquáticos, em vista da menor diversidade funcional de insetos aquáticos. Provavelmente este resultado esteve relacionado a maior complexidade de habitat, a qual foi promovida pela rápida propagação desse vegetal. Em especial para as larvas de insetos aquáticos predadores a maior complexidade de habitat promovida pela macrófita invasora no ecossistema lêntico parece ter sido um importante fator na estruturação de sua comunidade associada. Fato já relatado por outros autores (KOVALENKO; DIBBLE, 2011). Habitats mais complexos podem proporcionar maior disponibilidade de espaços, promovendo mais micro-habitats que resultam numa melhor proteção das larvas de insetos aquáticos contra grandes predadores (*e.g.* peixes), e até mesmo locais para oviposição. Em vista dessa relação ecológica com larvas predadoras na margem do reservatório estudado, pode-se deduzir que a modificação de qualidade de habitat promovida pela rápida propagação do lírio-do-brejo direciona a estruturação funcional e taxonômica da comunidade de forma determinística. Sendo assim, estratégias de conservação direcionadas ao controle populacional dessa espécie vegetal invasora são indicadas, uma vez que sua rápida propagação pode levar a um processo de homogeneização faunística.

b) Quanto à sua influência como recurso alóctone, pode-se afirmar que suas folhas demonstraram melhor qualidade de recurso alimentar para as larvas de

Chironomidae fragmentadoras do que a espécie nativa (*P. cordata*). Este foi um importante fator que influenciou na seleção taxonômica de larvas de insetos aquáticos herbívoros devido as suas diferentes adaptações alimentares. Alguns estudos, como, por exemplo, os desenvolvidos por Boyero et al. (2012) têm demonstrado que invasão por espécies vegetais podem alterar as comunidades de macroinvertebrados, através da modificação da qualidade de recurso alimentar. No entanto isto somente ocorreu quando as espécies vegetais invasoras apresentaram baixa qualidade de recurso alimentar quando comparadas às espécies nativas (KÖNING et al., 2014; LEITE-ROSSI et al., 2015). Destacamos, através dos resultados apresentados no Capítulo III, os herbívoros em razão das suas adaptações de hábitos alimentares podem selecionar a qualidade nutricional das plantas diferentes comunidades de. Tais diferenças em composição refletem a história evolutiva das espécies herbívoras, as quais foram condicionadas as diferentes qualidades nutricionais dos vegetais.

c) A qualidade nutricional das folhas das espécies de macrófitas aqui analisadas desempenhou um importante papel na estruturação dos traços funcionais das comunidades de herbívoros. Estes por sua vez, demonstraram alterar as redes tróficas. Os padrões de redes tróficas foram similares em ambas as espécies de macrófitas. Isso ocorreu devido a predominância de táxons onívoros e suas relações com os predadores, os quais foram suficiente para manter a estrutura da comunidade estável (NAMBA et al., 2008, KATRINA et al., 2012). No entanto, a estrutura das redes tróficas dos macroinvertebrados decresceu em razão da baixa concentração de nitrogênio das folhas da espécie nativa. Tal característica nutricional influenciou no decréscimo da relação predador-presa. Ta resultado nos possibilitou inferir que essa relação decresceu em razão da redução de herbívoros na estrutura comunitária. Em vista da crescente preocupação da conservação e restauração de áreas impactadas por essas espécies de plantas e suas implicações para a conservação da biodiversidade aquática, faz-se importante selecionar espécies nativas com qualidade nutricionais superiores às das espécies vegetais invasoras. Tais medidas poderão auxiliar na recuperação da flora nativa, bem como na manutenção e conservação das comunidades associadas que manterão os processos ecológicos.

Referências

- BOYERO, L., BARMUTA, L. A., RATNARAJAH, L., SCHIMIST, K., PEARSON, R. G.. Effects of riparian vegetation on leaf breakdown by shredders: a tropical-temperate comparison. **Freshwater Science**, v. 2, p. 296–303, 2012.
- KRATINA, P., LECRAW, R. M., INGRAM, T., ANHOLT, B. R. Stability and persistence of food webs with omnivory: is there a general pattern?. **Ecosphere**, v. 3., p. 1-18, 2012.
- KÖNIG, R., HEPP, L. U., SANTOS, S. Colonisation of low-and high-quality detritus by benthic macroinvertebrates during leaf breakdown in a subtropical stream. **Limnological Ecology and Management of Inland Waters**, v. 45, p. 61-68, 2014.
- KOVALENKO, K. E., DIBBLE, E. D. Effects of invasive macrophyte on trophic diversity and position of secondary consumers. **Hydrobiologia**, v. 663, p. 167-173, 2011.
- LEITE-ROSSI, L. A., SAITO, V. S., CUNHA-SANTINO, M. B., TRIVINHO-STRIXINO, S.. How does leaf litter chemistry influence its decomposition and colonization by shredder Chironomidae (Diptera) larvae in a tropical stream?. **Hydrobiologia**, v. 771, p. 119-130, 2015
- NAMBA, T., TANABE, K., MAEDA, N. Omnivory and stability of food webs. **Ecological Complexity**, v. 5, p. 73-85, 2008.
- ZENNI, R. D., ZILLER, S. R. An overview of invasive plants in Brazil. **Revista Brasileira de Botanica**, v. 34, p. 431–446, 2011.