

Programa de Pós Graduação em Ecologia e Conservação Centro de Ciências Biológicas e da Saúde Universidade Federal de Mato Grosso do Sul

Odonates as indicators of landscape change in a region of the Cerrado Marciel Elio Rodrigues



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Marciel Elio Rodrigues

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Orientador: Dr. Fábio de Oliveira Roque

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Banca avaliadora

Dr. Daniel Forsin Buss
Fundação Osvaldo Cruz – FIOCRUZ/RJ
Dr. Gustavo Graciolli
Universidade Federal de Mato Grosso do Sul - UFMS
Dr. Leandro Juen
Universidade Federal do Pará - UFPA
Dra. Marina Schmidt Dalzochio
Unidade Integrada Vale do Taquari de Ensino Superior - UNIVATES
Dra. Sheyla Regina Marques Couceiro
Universidade Federal do Oeste do Pará - UFOPA

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Abstract

The knowledge about which factors determine current biodiversity trends given recent conditions of habitat loss and fragmentation is essential to design and carry out strategies for species conservation. Identifying and describing the consequences of current anthropogenic threats and their effects on patterns and processes of species assemblages is central to community ecology. In this study, we investigate how anthropogenic land use changes on natural landscapes affect Odonata communities. We divided this study in three chapters. In the first chapter we assessed whether a damselfly community (Odonata) demonstrates non-linear responses in relation to the decline of native vegetation remnants around streams following a threshold approach analysis. In the second chapter, we evaluated how different traits following a deconstruction approach related to oviposition behavior in the communities respond to native to native vegetation loss. In the third chapter, we consider the community in traits related to dispersal ability emphasizing the role of landscape resistance as an important predictor in the structuring Odonata communities. The data for this study were obtained from samples of 116 streams in the state of Mato Grosso do Sul. Our results emphasizes that the loss of native vegetation and landscape modifications are key variables influencing Odonata communities. The two approaches used here, nonlinear responses considering the total community or the deconstructed community in traits related to dispersal ability and oviposition, are essential to evaluate the effect of changes in natural landscapes on the Odonata communities. These approaches are proven to be relevant tools in ecology studies, assisting in the decision-making in conservation of species and especially of aquatic environments that are essential for maintaining a large part of the planet's biodiversity.

Resumo

O conhecimento sobre quais fatores determinam as tendências atuais da biodiversidade considerando às condições recentes de perda e fragmentação de habitats é essencial para projetar e executar estratégias para conservação das espécies. Identificar e descrever as consequências das ameaças antropogênicas atuais e seus efeitos sobre os padrões e processos das assembleias de espécies são fundamentais para a ecologia de comunidades. Neste estudo, investigamos como mudanças antropogênicas do uso do solo em paisagens naturais afetam as comunidades de Odonata. Nós dividimos este estudo em três capítulos. No primeiro capítulo, nós avaliamos se a comunidade de Zygoptera (Odonata) demonstra respostas não lineares em relação ao declínio de remanescentes de vegetação nativa em torno de córregos seguindo uma abordagem de limiares. No segundo capítulo, considerando a desconstrução da comunidade em "traits", nós avaliamos como os diferentes comportamentos de oviposição das espécies respondem a perda de vegetação nativa. No terceiro capítulo, nós consideramos a comunidade desconstruída em "traits" relacionados à capacidade de dispersão enfatizando o papel da resistência da paisagem como um importante preditor na estruturação dessas comunidades de Odonata. Os dados para este estudo foram obtidos a partir de coletas em 116 córregos no estado de Mato Grosso do Sul. Nossos resultados enfatizaram que a perda e ou modificações na vegetação nativa são variáveis chaves que influenciam as comunidades de Odonata. As duas abordagens usadas nesse trabalho, respostas não lineares, considerando a comunidade como um todo ou a comunidade desconstruído em características relacionados à capacidade de dispersão e oviposição, são essenciais para avaliar o efeito das mudanças em paisagens naturais nas comunidades de Odonata. Essas abordagens provaram ser ferramentas relevantes em estudos de ecologia, auxiliando na tomada de decisões na conservação de espécies e

especialmente dos ambientes aquáticos que são essenciais para a manutenção de grande parte da biodiversidade do planeta.

Presentation

One of the great challenges facing humanity is to define best strategies to protect biodiversity, not only by the difficulties of reconciling the rational use of natural resources and development, but also by the complexity of this challenge which involves different scales, and includes local, regional and global factors (Millennium Ecosystem Assessment 2005). Currently the conversion of terrestrial ecosystems to agricultural, urban systems or other highly human dominated systems, also referred as "habitat loss" is one the main driver of changes in species abundance and decline globally (Foley 2005, Vörösmarty et al. 2010). Changes in coverage and configuration of remaining native vegetation alter the composition of species and ecological processes and are among the factors that best explain the ecological responses related to changes in ecosystem functions (Fahrig 2003, Pardini et al. 2010, Fahrig 2013).

Considering that fragmentation process and loss of natural habitats can lead to irreversible changes in biodiversity and species interactions (Chapin et al. 2000), researches have showed that the modification of natural landscapes can produce nonlinear responses or thresholds in different species communities (Baker & King 2010, Pardini et al. 2010). Thresholds are regions or a points (also called breaking point) when a sudden change on a particular trend occur generating the transformation of one condition to another (Hugget 2005). In other words the thresholds can be described as "small changes in an environmental driver produce large responses in the ecosystem" and can be a key point to support conservation initiatives (Groffman et al. 2006). Many studies have used this approach for evaluating the response of communities, especially those affected by anthropogenic land use change (Pardini et al. 2010, Hanski 2011, Estavillo et al. 2013, Rigueira et al. 2013, Lima & Mariano-Neto 2014, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015).

Another approach used to predict the effect of changes in landscapes on biodiversity it is related to deconstruction of the communities in traits. This approach holds higher potential for predicting changes of both species and species assemblages along environmental gradients given differential trait's sensitivity to local environmental conditions (Poff et al. 2006, Webb et al. 2010, Heino & Peckarsky 2014). Strategy of deconstructing communities reveals important patterns usually masked when pooling all species together (Marquet et al. 2004). Mainly in lotic systems, given the difficulties with predicting species composition, researchers have advanced in the functional classifications of species into groups with similar biological and ecological traits that are expected to respond consistently along specific environmental gradients (Poff et al. 2006, Webb et al. 2010).

Insects as bioindicators of environmental changes

The use of indicators species that can evaluate these changes in the landscapes are extremely important for studies in ecology and conservation. Species with good performance as bio-indicators will provide better information about the magnitude and direction of the effects considering the changes environments on biodiversity (McGeoch 1998, McGeoch 2007). Among insects, aquatic insects are considered good environmental indicators as they exhibit complex life histories and often shift habitats during their life cycles. Aquatic insects have a great diversity in number of species, life strategies, feeding, habitat requirements and adaptations with respect to several variables of aquatic environments. With a strong history in scientific studies, mainly in evaluation and monitoring programs considering the different environmental impacts (e.g. Bonada et al. 2006, Siqueira & Roque 2010, Monteiro-Júnior et al. 2013).

Odonates are good model for assessing the effects of environmental change, mainly in relation the landscape changes (Bried & Samways, 2015). This group of

aquatic insects has a complex life cycle that can experience niche shifts. The adults live in different types of habitats, exhibit widespread distributions. The larvae exhibit relatively limited dispersal ability and are susceptible to aquatic-and-terrestrial environmental change. Both adult and larvae exhibit rapid and congruent response to environmental change (Valente-Neto et al. 2016). Most of the species in this taxonomic group are sensible the changes on the environment, including the loss of native vegetation in riparian zone (Silva et al. 2010, Monteiro-Júnior et al. 2015, Rodrigues et al. 2016). They have certain specific ecological traits that are related the wide variation in behaviors of territoriality, reproduction, oviposition, requirements ecophysiological and dispersion capacity. These characteristics allow us to make predictions and test different scenarios of natural environments change trough the assessment of this taxonomic group (Monteiro-Junior et al. 2015, Dutra & De Marco 2015, De Marco et al. 2015, Bried & Samways 2015).

The knowledge about which factors determine the communities on the present conditions of habitat loss and landscape change is essential to develop strategies of species conservation (Gardner et al. 2009). Then, in this study, we investigated how the loss and or changes in natural landscapes configuration affects the Odonata communities. This work was divided into three chapters that are complementary and uses different approaches for evaluate the effects of changes and losses in natural environments with the loss of species in aquatic environments. We expect that if communities have nonlinear responses and if certain traits of communities (oviposition behavior and dispersion capacity) those communities will be more affected than others.

Structure of this thesis

In the first chapter, we use threshold approach as a tool to evaluate the change of the community over a vegetation loss gradient. In this study, our goal was to assess whether a damselfly community (Odonata) demonstrates non-linear responses in relation to the decline of native vegetation remnants around streams. This chapter was entitle Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. This chapter was recently published in Biological Conservation Journal (edition: February, 2016 doi:10.1016/j.biocon.2015.12.001).

In the second and third chapter, we consider the Odonata community deconstructed in traits related to the behavior of oviposition and dispersal ability of species. According to Heino & Peckarsky (2014), community deconstruction in traits allows a better understanding of the processes that keep communities in natural or altered places with different environmental characteristics. As one way to make sense of this diversity and its mechanistic underpinnings is to focus not on species but on the functional traits they possess. Because, a group of species with similar biological and ecological traits that are expected to respond consistently along specific environment gradients (Poff et al. 2006, Heino & Peckarsky 2014). In this sense, we use the oviposition behavior of the species of Odonata to answer the following question (chapter 2). Is the loss of native vegetation around streams influencing the maximum number of species with certain oviposition behavior in Odonata community? This chapter was entitled: Deconstructing odonata richness by oviposition behaviors reveals effects of riparian vegetation loss.

In the third chapter, we continue with the approach of traits, but now linking the ability of dispersion of species of Odonata with a newer approach within the landscape ecology, called landscape resistance (McRae 2006). Whereas that dispersal can be a crucial factor affecting the relative roles driving biodiversity patterns (Vellend et al. 2014). Many studies have shown that environmental and geographical distances are the main factors in driver of communities similarities (Nekola & White 1999, Soininen et

al. 2007, Heino et al. 2014, Kärnä et al. 2015, Saito et al. 2015). However, few studies have considered the role of landscape resistance, especially when dispersal efficiency is related to the quality and configuration of the elements involved in different route types (Heino et al. 2014, Canedo-Arguelles et al. 2015). So, in the third chapter, we deconstruct Odonata community on two traits that are strongly related to dispersal ability of species (body size and thermoregulation capacity), and classify the species in slow and high dispersion capacity, to answer the following question: What role of landscape resistance to determine dissimilarities of Odonata communities in forested streams immersed in pasture matrix in the Cerrado according to the different dispersion capacity. This chapter was entitled: Dispersal ability of Odonata unveils decay assemblage similarity patterns masked when pooling all species together.

Study area and data collection

All this studies were carried out in the Mato Grosso do Sul State in areas along the Pantanal plateau. We sampled 116 streams between the years of 2001 and 2013 (figure 1 and figure 2). We collected 82 species (see some species figure 3 and 4), with 30 new records for the state (Rodrigues & Roque *no prelo*) and a new species for description (*Acanthagrion* n. sp.). Currently, about 60 species and 200 specimens have their mitochondrial DNA (COI) sequenced (Koroiva et al. 2016). The state of Mato Grosso do Sul has about 200 species of Odonata registered in approximately 300 collection points (Souza & Costa 2006, Dalzochio et al. 2011, Rodrigues & Roque *no prelo*, Rodrigues et al. 2016). The specimens are deposited in the zoological collection of the Federal University of Mato Grosso do Sul, about 120 species and 5,000 specimens.

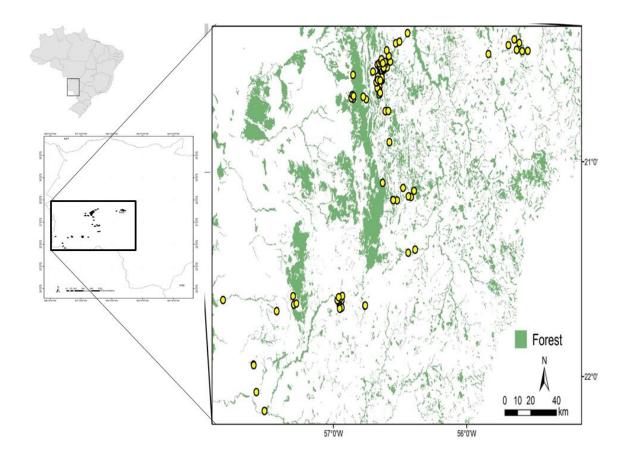


Figure 1: Map showing the region of the 116 sampling sites in Mato Grosso do Sul state, Brazil.

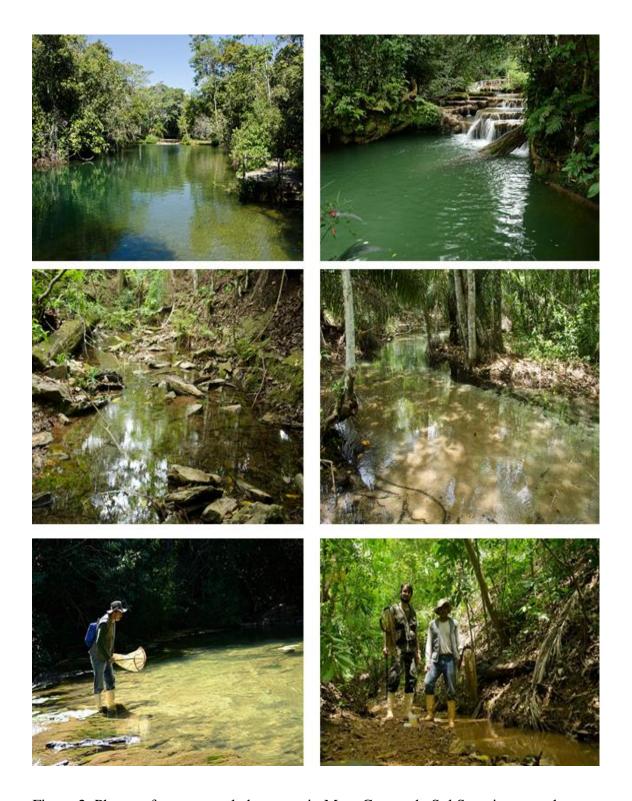


Figure 2: Photos of some sampled streams in Mato Grosso do Sul State in areas along the Pantanal plateau (Photos: Francisco Valente Neto).



Figure 3: Photos of some species collected in streams in Mato Grosso do Sul State in areas along the Pantanal plateau: A) *Peristicta aeneoviridis* Calvert, 1909, B) *Neoneura sylvatica* Hagen, 1886, C) *Neoneura ethela* Williamson, 1917, D) *Hetaerina rosea* Selys, 1853, E) *Mnesarete pudica** (Hagen, 1853) and F) *Argia reclusa* Selys, 1865. (Photos: Francisco Valente Neto, *photo: Dragonflies and Damselflies of the Neotropics-https://www.facebook.com/groups/NeoOdonata/)

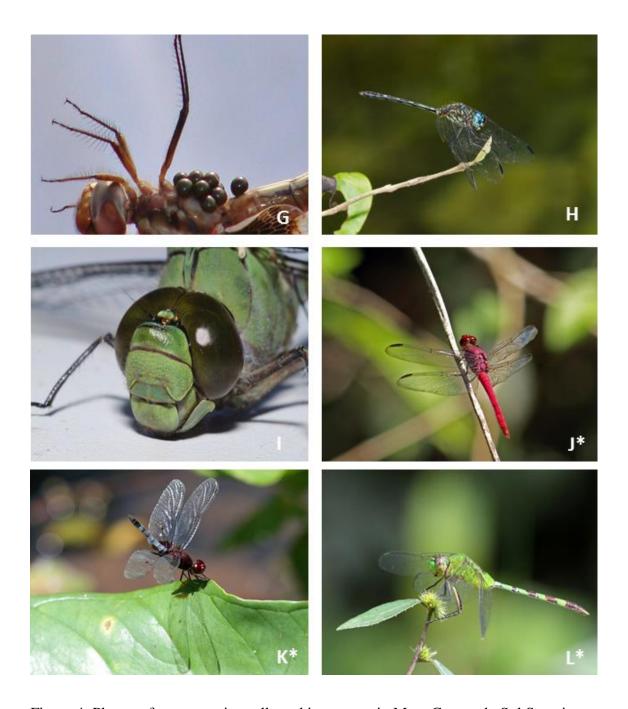


Figure 4: Photos of some species collected in streams in Mato Grosso do Sul State in areas along the Pantanal plateau: G) Acari in *Miathyria marcella* (Selys, 1857) (see Rodrigues et al. 2013), H) *Dythemis multipunctata* Kirby, 1894, I) *Staurophlebia reticulata* (Burmeister, 1839) J) *Orthemis discolor** (Burmeister, 1839), K) *Erythrodiplax fusca** (Rambur, 1842) and L) *Erythemis vesiculosa** Fabricius, 1775 (Photos: Francisco Valente Neto, *photos: Dragonflies and Damselflies of the Neotropics-https://www.facebook.com/groups/NeoOdonata/)

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Chapter 1

Nonlinear responses in damselfly community along a gradient of habitat loss in a $savanna\ landscape^*$



Neoneura sylvatica. Photo: Francisco Valente-Neto

Abstract

Riparian zones are among the most threatened natural ecosystems, being greatly affected by land use changes across the world. Working in a savanna landscape in the Central-West region of Brazil, we assessed the responses of damselflies (Odonata) communities to changes on native vegetation extent in riparian zones. We sampled damselflies around 98 streams in a continuous gradient of native vegetation loss (0 to 100%). We used the Threshold Indicator Taxa Analysis (TITAN) to test whether the damselfly community showed nonlinear responses related to native vegetation loss within buffers of 250m radius. We collected 1245 individuals of damselflies, representing 31 species. The TITAN identified 16 species with a significant response: 11 species with negative indicators (Z-) and five as positive indicators (Z+) in relation to native vegetation loss. Six species showed evidence of nonlinear response (Z-), at sites with native vegetation loss between 40% and 60%. We also used segmented regression analysis with species richness, which showed weak evidence of a threshold located at 54% of native vegetation loss. Differently of previous studies with other taxonomic groups in forested environments, our results indicate that the variability around the threshold is higher. Under a precaution perspective and given current levels of vegetation loss around streams where the risk of losing species is higher, we reinforce the importance of appropriate landscape management strategies. In order to effectively conserve biodiversity in aquatic-and-terrestrial environments, the native vegetation loss within pastures and agriculture landscapes, should be above the "zone of increasing risk of impact" level. According to the current Brazilian Forest Act, riparian forest of at least 30 m wide must be preserved along both sides of each watercourse. In our study 30 m vegetation wide represents only 10% of the 250 m buffer area. It implies that the current Brazilian Forest Act does not preserve the Cerrado's riparian vegetation

and its associated aquatic biodiversity, since the amount of native vegetation loss is below the "zone of increasing risk of impact" we detected for damselflies in evaluated landscapes.

Key words: Odonata; Threshold; TITAN; Native vegetation loss.

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Introduction

Human activities are the main cause of habitat loss and landscape changes around the world, resulting in modifications of biological communities, including species extinction (Barnosky et al. 2011). The conversion of native grasslands, forests, wetlands, and other natural land covers to human-modified landscapes (e.g. cultivated and urban landscapes), is one of the most prevalent drivers of biodiversity loss (Gardner et al. 2009). Moreover, freshwaters are among the most threatened ecosystems in the world (Vörösmarty et al. 2010). Land use changes are expected to have large impacts, especially on freshwater systems because humans tend to live disproportionately near waterways and extensively modify riparian zones. This leads to changes within the riparian ecosystems, including native vegetation loss and increased inputs of nutrients, sediments and contaminants. In addition, humans use waterways as transportation corridors, sewage disposal sites, and water sources. Consequently an important proportion of Earth's accessible freshwaters ecosystems are already co-opted by humans (Sala et al. 2000, Allan 2004).

Researches evaluating the effects of habitat fragmentation and species loss have recognized nonlinear responses in aquatic and terrestrial systems (Andrén 1994, Fahrig 2003, Pardini et al. 2010, Baker & King 2010). Studies have demonstrated changes in trends of biodiversity loss at a particular level of habitat loss as a result of changes on habitat configuration features (Pardini et al. 2010). Based on general percolation theory (Stauffer 1985), the "fragmentation threshold hypothesis" was proposed to explain nonlinear changes in species loss (Andrén 1994, Fahrig 2003). The hypothesis has been applied to understand the influences of aspects such as the landscape matrix and spatial arrangements of habitat patches on species persistence and dispersal (Pardini et al. 2010, Villard & Metzger 2014). Recently, theoretical and empirical studies have shown that

biodiversity typically declines proportionally with the amount of suitable habitat in a landscape up to certain level of habitat loss; below this point nonlinear changes emerge. These particular points have been identified as thresholds (Pardini et al. 2010, Hanski 2011, Estavillo et al. 2013, Rigueira et al. 2013, Lima & Mariano-Neto 2014, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015). It is considered that such changes occur as responses to shrinking patch size and increasing isolation (Pardini et al. 2010). The detection of thresholds is a key task for landscape ecology studies, as it may demonstrate the relevance of the linked effect of fragmentation per se on the known effects of habitat loss.

A number of studies have found that terrestrial landscape conversions can cause effects on stream biodiversity in riparian zones (Allan 2004, King et al. 2011, Monteiro Júnior et al. 2014, Monteiro Júnior et al. 2015). This is of great concern given the extensive conversion from native land cover to agricultural lands predicted to occur globally in the next few decades (Vörösmarty et al. 2010). Under such circumstances, the lack of information about biological consequences of land cover change in riparian communities is likely to reduce our ability to provide an integrative view of riverine systems from a landscape perspective. This knowledge could generate the basis for understanding how adjacent terrestrial habitat loss may affect aquatic communities, particularly for taxonomic groups strongly dependent on riparian zones.

Many organisms that live in riparian zones possess biological characteristics that make them sensitive to landscape change-induced habitat fragmentation. Those characteristics are related to their dispersion ability, habitat selection, habitat specificity, naturally low abundance, microhabitat requirements or the need of large natural areas to establish their populations, and the availability of key resources (Banks-Leite et al. 2012). Dispersal ability and movement behavior may have a special role in determining

the nature and extent of how landscape changes impact particular species. This may involve aspects such us distances between subpopulations, but also the physical characteristics of the matrix itself and the landscape configuration (Baguette et al. 2012). Consequently, it is expected that when the amount of habitat declines below a certain level, a group of species with a suite of characteristics (e.g. low dispersal ability) is expected to show changes in population size and density. This indicates that post-fragmentation species loss is not random, but rather affects organisms with similar ecological traits that make them more vulnerable to habitat disturbance (Estavillo et al. 2013).

Odonates provide a good model for assessing the effects of landscape changes on riparian animal populations because any assemblage will include species differing in their dispersal and thermoregulatory abilities, body size and behavior (Corbet 1999, De Marco et al. 2015). Additionally, they have an aquatic and terrestrial phase to their lifecycle (Simaika & Samways 2009). Thus, factors other than variation in local characteristics (e.g., integrity of the riparian forest and of the vegetation beyond the riverside) can influence Odonata communities by altering the environments available for dispersal and survival during the adult phase (Petersen et al. 2004). In addition, studies have shown that Odonata species may be affected by modifications in local environmental conditions, such as quality of riparian habitats, concentrations of pollutants in the water, air temperature, and the hydroperiod, physical-chemical characteristics, flow rates, and discharge rates of streams (Corbet 1999). The sensitivity to environmental conditions, plus the dependence of these insects on both terrestrial and aquatic systems, makes them a good model to study the biological consequences of human impacts on riparian ecosystems. Consequently, Odonata have been used as bioindicators to assess environmental integrity (Simaika & Samways 2009, Simaika &

Samways 2011), and adults and larvae show congruent responses to environmental changes (Valente-Neto et al. 2015).

We sampled damselflies around streams in a continuous gradient of native vegetation loss in a savanna landscape in the Central-West region of Brazil in order to assess whether a damselfly community (Odonata) demonstrates nonlinear responses in relation to changes of native vegetation amount around streams. We expected that a set of damselfly species would show a threshold response in relation to native vegetation loss, considering that: i) some damselfly species have low dispersive capacity, ii) some species generally require streams with dense riparian vegetation due to ecophysiological constraints (e.g. high body heat exchange rates with the environment temperature), iii) other species have narrow ecological requirements, and, iv) a high dependence on habitat structure as above-water vegetation is used by adults for perching, while belowwater roots and stems of riparian vegetation are important for larval motility and concealment (Corbet 1999, Simaika & Samways 2009, Juen & De Marco 2011, Keller & Holderegger 2013, Dutra & De Marco 2015, De Marco et al. 2015).

Methodology

Study area

Our study area is located in Central-West region of Brazil, and characterized by a mosaic of landscapes dominated by savanna (Cerrado) and semi-deciduous Atlantic Forest. The climate is classified as tropical humid, with two dry months (July and August), and a rainy season that runs from December to February during which 42% of the annual rainfall occurs – an average of 1500mm per rainy season. The annual mean temperature is 22°C, being the average of the coldest month (June or July) 18°C, and the average of the warmest month (September), 32°C (ZEE 2009). We conducted this study in watercourses surrounded by remnants of native vegetation embedded in a matrix

dominated by grazing pastures and monocultures of soya, maize and sugar cane plantations (Figure 1-A).

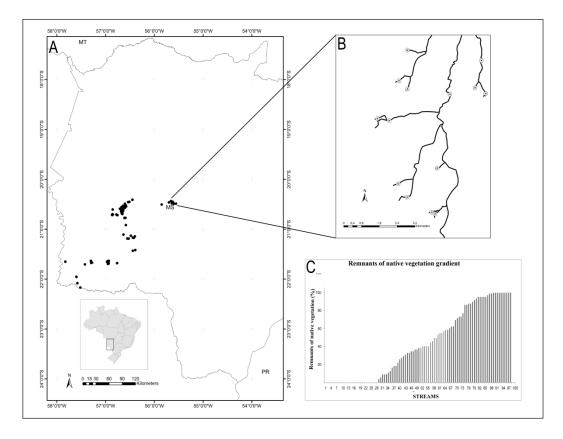


Figure 1-A) Map showing the 98 sampling sites on the Pantanal Plateau, state of Mato Grosso do Sul, Brazil. 1-B) Diagram showing how data collections were made in independent drainages along several watersheds in the same region. As an example, the map shows part of a sampled sub-basin in the region. 1-C) Gradient of remnants of native vegetation along streams.

2.1.2 Sampling

We collected adult damselflies between April 2011 and October 2013 (Odonata) in 98 streams. We used a hand net to sample a 100m transect parallel to the both stream banks. The collection points were distributed in independent drainage streams along watersheds in the same region (Figure 1-B). Sampling sites were dispersed along each stream so as to capture a complete gradient of native vegetation loss (from 0 to 100%)

(Figure 1-C). Most samples were conducted during the warmest and wettest periods (October to April), because most damselflies are more active during hot (above 19° C) and humid days (Corbet 1999). In addition, as there is a well-established thermal restriction in this insect order (Corbet 1999, De Marco et al. 2015), sampling was conducted once at each site, for one hour along each stream during sunny days between 10:00 and 15:00h. This method has been effectively used in other studies (e.g. Juen & De Marco 2011).

The identification of the collected specimens to species or morphotype was carried out by following taxonomic keys and original descriptions, and confirmed by taxonomists on this group (see acknowledgements). In addition, we used the DNA Barcoding approach for confirming the taxonomic identity of some species. Voucher specimens were deposited in the Zoological Collection (ZUFMS) of the Federal University of Mato Grosso do Sul (UFMS).

2.1.3 Analysis of the native vegetation loss around the streams

To describe the native vegetation loss in the study area we calculated the total proportion of riparian forest and seasonal forest within each buffer. Each buffer was delineated as circular buffer area (250 m radius) around a point located in the centre of each sampled stream (Figure 2). We used this buffer area considering that damselflies have low dispersive capacity, require streams with dense riparian vegetation due to ecophysiological constraints and the males are resident and show a territorial behavior (Corbet 1999, Keller & Holderegger 2013, De Marco et al. 2015). We chose the proportion of native vegetation loss as a landscape metric, because it is one of the main variables for explaining odonate species distribution, occurrence and persistence, extinction probability, and community structure (Fahrig 2003, Quesnelle et al. 2013).

The base map used to calculate the proportion of native vegetation loss was retrieved from a mapping conducted by the Environmental Institute of Mato Grosso do Sul State from images of the CCD (Couple Charged Device) receiver of the CBERS2 satellite (Sino-Brazilian Earth Resources Satellite), taken in 2007 at 30 meters resolution. The mapping process was performed by supervised classification at the 1: 100,000 scale. We did not include other configuration metrics in our analysis as the proportion of remnants native vegetation was highly correlated with aspects such as largest patch index given that a 250 meters buffer generally contents one forest fragment. In addition, to asses whether chosen scale may influence the detected pattern, we also calculated the amount of vegetation within a 500 meters buffer resulting in highly correlated values with the 250 meters buffer (r²=0.92). Then, considering that the amount of vegetation is considered the main driver of community changes (see Petersen et al. 2004, Quesnelle et al. 2013), and some Odonata species have low dispersal ability, we focused our attention on the amount of vegetation at 250m radius.

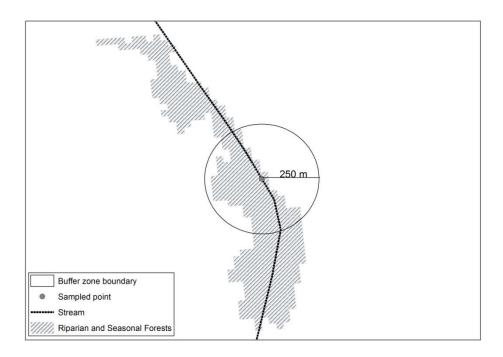


Figure 2: Diagram showing method used to calculate the percentage of native vegetation loss along streams within forest fragments, using circular buffers surrounding the sampling point with a radius of 250 meters.

2.1.4 Data analyses

To show the independence of data collection points in relation to the remnants of native vegetation, we first performed an autocorrelation analysis using information from the total remnants of native vegetation at each sampling point site and their geographic location (XY coordinates) using Moran's Index (Dray et al. 2006).

To identify species response to habitat loss, we used the Threshold Indicator Taxa Analysis - TITAN, a function that allows the identification of threshold(s) based on change point(s) along environmental gradients for each taxon. TITAN detects changes in species distributions along an environmental gradient over space or time, and assesses synchrony among species change points as evidence for community thresholds. To carry out the TITAN analysis we used only taxa with five or more records. We $log_{10}(x+1)$ transformed taxa abundance data to reduce the influence of highly variable taxa on indicator score calculations in each data set, which was particularly important for taxa with low occurrence frequencies (Baker & King 2010).

TITAN distinguishes between negative (Z-) and positive (Z+) taxa responses. Standardized taxa responses increasing frequencies and abundance at the changing point (Z+), and taxa responses decreasing frequencies and abundance at the changing point (Z-). Two important diagnostic indices measuring the quality of the indicator response for any taxon obtained from bootstrap resampling in the TITAN: *purity* and *reliability*. *Purity* is the proportion of change-point response directions (Z+ or Z-) among bootstrap replicates that agree with the observed response. *Reliability* is the proportion of

bootstrap change points whose IndVal scores consistently result in *p*-values below one or more user-determined probability levels (See Baker & King 2010). We performed TITAN analysis in *R* (R Development Core Team 2009, version 2.9.2) using a custom package "TITAN" (Baker & King 2010).

We also used segmented regression analysis in R ("Segmented") in order to identify the possible thresholds in levels of taxa richness (Muggeo 2004). Segmented regression analysis splits explanatory variables into two or more linear regressions in order to locate points where the linear relationship changes. The identification of thresholds or break points is estimated using different starting points and identified using the highest R^2 value (Muggeo 2004).

Results

We collected 1245 individual damselflies from 98 sampling sites, representing four families (Calopterygidae, Coenagrionidae, Dicteriadidae and Protoneuridae), 12 genera and 31 species. Among the 31 damselfly species, 25 had five or more occurrences and these were included in the TITAN analysis. The following species showed lower number of records (<5 occurrences) *Mnesarete guttifera*, *Metaleptobasis lillianae*, *Neoneura bilinearis*, *Heliocharis amazona*, *Oxyagrion terminale* appearing only in areas with less than 50% of native vegetation loss.

Moran's Index showed no spatial autocorrelation between total remnants of native vegetation at each sampling point and their geographic location (Figure 3). This implies that there is independence between geographic location of sampling points and the environmental variables used as predictor's variables.

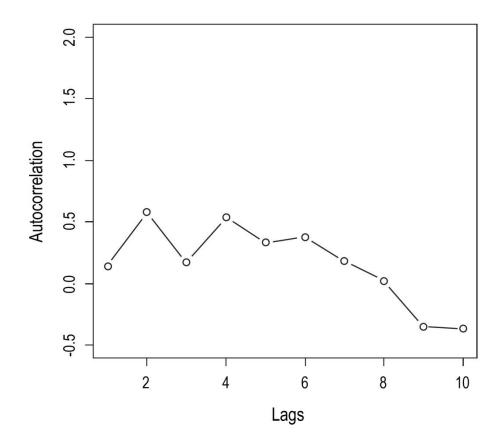


Figure 3: Autocorrelation spatial analysis using the Moran index showing the independence of the samples with the covariates. Open circles means non-significant values.

The TITAN framework identified 16 species (64%) with significant IndVal score (pval<0.05) of which 11 species were negative indicators (Z-), and five were positive indicators (Z+) in relation to native vegetation loss (Figure 4 and Supporting Information- Appendix S3). Of the 11 species, nine showed a significant association with native vegetation loss (Z-) and had significant purity (>0.95) and reliability (rel05>0.90): *Argia smithiana*, *Argia mollis*, *Argia croceipennis*, *Argia subapicalis* and *Enallagma novaehispaniae* (Coenagrionidae), *Epipleoneura venezuelensis*, *Neoneura sylvatica*, *Neoneura rubriventris* and *Peristicta aeneoviridis* (Protoneuridae). Two other

species (*Argia modesta* and *Hetaerina mortua*) also had high purity (purity>0.90) and moderate reliability (rel05= 0.73 and 0.79 respectively) (Appendix S1).

Through TITAN analysis, we identified six taxa with evidence of a nonlinear response: *Argia smithiana*, *Argia modesta*, *Argia subapicalis*, *Enallagma novaehispaniae*, *Hetaerina mortua*, *Epipleoneura venezuelensis*. These species exhibited a break point located between 40% and 60% native vegetation loss (Figure.4), however some species have broad intervals lower change-point quantiles (e.g. 5%) and narrow intervals upper change-point quantiles (e.g. 95%). Importantly, the upper limit (95%) showed similar bands of uncertainty located near 60% of native vegetation loss and with some congruence among the 6 species (Z-).

In the group of positive indicators (Z+), five species were associated with high native vegetation loss (above 40% loss of native vegetation), *Acanthagrion aepiolum*, *Argia chapadae*, *Argia hasemani*, *Argia tamoyo*, *Oxyagrion sulmatogrossense* (Coenagrionidae). These species have broad quantile intervals spanning most of the range of gradient of native vegetation loss (Figure 4).

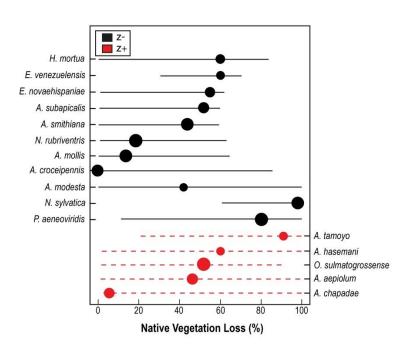


Figure 4: Threshold indicator taxa analysis (TITAN) of damselflies community response to native vegetation loss. With evidence synchronous declines in response to native vegetation loss, *Argia smithiana*, *A. modesta*, *A. subapicalis*, *Enallagma novaehispaniae*, *Hetaerina mortua* and *Epipleoneura venezuelensis*, exhibited a break point between 40% and 60% of native vegetation loss. The sized of circle is in proportion to the magnitude of the response (z scores; see Supporting Information S1).

The community-level threshold assessment, the TITAN sum (z) analysis, showed a large values of sum (z) score from -5 to 25, with some marked peaks corresponding to the maximum aggregate change in the frequency and abundance of their respective taxa. The cumulative probability curves indicate that loss of vegetation below 40-60% generates initial signs of community changes, with increases of generalist taxa followed by declines of sensitive taxa. Below 40% of native vegetation loss, generalist taxa increased markedly (Z+), and below 60% sensitive taxa showed tend to decline (Z-). Cumulative frequencies of sum(z) maximum seem to change exponentially (Figure 5).

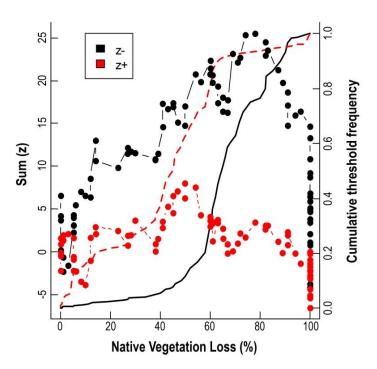


Figure 5: TITAN sum(z-) and sum(z+) values corresponding to all candidate change points (xi) along the analyzed environmental gradient. Black and red vertical lines represent the cumulative frequency distribution of change points for 500 bootstrap replicates for sum(z-) and sum(z+), respectively.

The segmented regression analysis showed a break point located at 54% (SE±15.56%) of native vegetation loss, however the standard deviation was quite large. Thus, although the break point coincides with the value obtained from the TITAN analysis (Figure 6), the extended confidence interval indicates certain degree of uncertainty to define where in term of the proportion of native vegetation loss the threshold point is located.

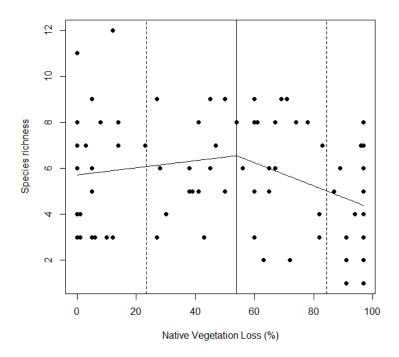


Figure 6: Segmented regression analysis, showed an evidence of a break point in the relationship between species richness and amount of native vegetation loss, with a break point located at 54% (SE±15.56%) of native vegetation loss, however the standard deviation was quite large.

Discussion

Our results provided some evidence for break point responses within damselfly community to the loss of native vegetation in riparian environments. However the uncertainty around aggregate measures (species richness) and synchronous responses among species indicate that considerable caution is needed in applying a nominal threshold value to this community. Most studies on landscape threshold were conducted on terrestrial systems and the general message is "reducing habitat loss should be a top priority for conservation planners" (Villard & Metzger 2014). Our study expands this message to riparian zones in savanna landscapes, but call for special attention to the variability of these systems.

Our results add some support to previous studies showing that biodiversity declines abruptly when native vegetation loss exceeds 60% (total remnant of native vegetation is below 40%) of the original level in Neotropical environments (Pardini et al. 2010, Hanski 2011, Estavillo et al. 2013, Rigueira et al. 2013, Lima & Mariano-Neto 2014, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015). This indicates that, in human dominated landscapes, there is a roughly common threshold for both freshwater (riparian zones) and terrestrial environments. When the percentage of habitat loss exceeds the threshold, aquatic and terrestrial organisms are affected simultaneously, due to disruptions involving linkages between terrestrial and stream habitats. However, in the riparian zones assessed in our work, the variability in the response of damselfly is quite high compared with those exhibited by forest specialist groups in other forested environments (e.g. Amazonia and Atlantic Forest) (Pardini et al. 2010, Estavillo et al. 2013, Lima & Mariano-Neto 2014, Ochoa-Quintero et al. 2015), and those found in riparian zones located in urban and mining areas (Baker & King 2010, King et al. 2011). The variation around a common value or even the lack of a clear signal can be

attributed to: (1) specific characteristics of the assemblage or individual species; (2) the predictor in which a threshold relationship is expected to occur; (3) the temporal dynamics of landscape change; (4) the type, intensity, and extent of landscape change (5) historical factors (e.g. climate and vegetational changes) that may shape resilient communities (Lindenmayer & Luck 2005).

Species that showed negative responses to native vegetation loss (z-), as well as rare species (those with <5 occurrences), were found only in highly forested areas (i.e., with less than 50% of native vegetation loss). The dependence of some damselflies on heavily-forested habitats is not a surprise, indeed it has long been reported in tropical streams (Dutra & De Marco 2015, Monteiro Junior et al. 2015). The species we found with negative Z values were previously reported inhabiting/occurring in protected streams (Juen & De Marco 2011, Dutra & De Marco 2015, Monteiro Junior et al. 2015). So taking these responses individually, the dependence of these species to conserved riparian zones may be related to specific conditions and requirements (such as humidity, temperature, sites for oviposition or territorial behavior).

According to Lindenmayer & Luck (2005), detecting thresholds in assemblages (aggregate measures, such as species richness and composition) is challenging because they require commonality of a trait or set of traits among a group/set of species to occur. In our case, although we detected that 6 species show change points near 60 %, the uncertainty is quite high. So we argue that more importantly that see the medium value as a critical number, we should see the upper and lower limits of variation as a precautious range. Under this reasoning, our results indicate that the upper limit of uncertainty, which is narrower than the lower limit, is congruent among the six species and may be considered the point where some species begin to disappear. This means that although the occurrence/frequency of these sensitive damselflies varies widely in

more forested sites (which can be attributed to many ecological factors, including ecological interactions), above some level of vegetation loss they show a common threshold. Consequently and in agreement with Lindenmayer & Cunningham (2005), we are not claiming a single value of threshold to explain the response of our entire community, instead we are saying that there is a common level where the risk of species loss is higher (see also Steffen et al. 2015).

The common response of some damselflies to vegetation loss around the streams may be related to their traits. Although our knowledge about the behavior, population level processes and landscape constraints related to aquatic insects (those that have at least an aquatic phase) is limited (Heino & Peckarsky 2014), there are some information about species' habitat requirements that support our point of view. These include i) a large body of natural history observations indicating that small-sized damselfly species, such as those that respond to habitat loss in our study, fly predominantly along the stream margins, and avoid flying across open areas (Corbet 1999, De Marco et al. 2015); ii) riparian insects living in streams, with limited dispersal ability, appear to have a high risk of mortality when venturing out of the habitat in which it reproduces (Petersen et al. 2004), and iii) a combination of landscape attributes determines the fate of dispersing individuals (Galic et al. 2013). Nonetheless, more information is still required to support the idea that landscapes with more than 50% native vegetation loss and a matrix composed by pastures and crops are impermeable to damselfly species. Moreover most species that show a synchronous response both their abundance and frequency were low. These results supports the idea that habitat cover thresholds would be related to the dynamics of small populations that are lost together because each one persisted with a relatively small population and shared similar susceptibility to extinction (Lindenmayer & Luck 2005).

The distance between habitat patches and matrix permeability influence individual dispersal abilities, and the condition around the streams affects individual persistence; furthermore forest specialist species have evolved in more stable systems (Juen & De Marco 2011, Keller & Holderegger 2013, Monteiro Junior et al. 2015, De Marco et al. 2015). Consequently, the loss of native vegetation directly affect adults by decreasing the number of perches and increasing the variability of temperature and exposure to light, which limits the dispersion of some species (Corbet 1999, Juen & De Marco 2011, Dutra & De Marco 2015, De Marco et al. 2015). Based on this information, we can hypothesize that non-exclusive mechanisms may affect the persistence and percolation of these species across the landscape resulting in a nonlinear response.

In tropical landscapes dominated by agriculture and pastures, the persistence threshold has been found to lie between 25 and 45 % for plants species (Rigueira et al. 2013, Lima & Mariano-Neto 2014), 30 % for forest-restricted small mammals (Pardini et al. 2010, Hanski 2011, Estavillo et al. 2013), and for arthropods (epigean soil fauna) from 12 to 25 % (Cardoso et al. 2013). Comparing these results, there is a similarity of responses among different groups, which can vary between 25 and 50% in environments under pressure from pasture/agriculture. Although these numbers show some variability, they suggest a common level where the risk of impact is high. According to Estavillo et al. (2013), common trends for landscape thresholds across different taxonomic groups corroborate the idea that species-specific extinction thresholds are similar among habitat specialist species. They are also associated with the exponential increase of distance between forest patches (With & King 1999, Petersen et al. 2004), which prevents dispersal among subpopulations (Püttker et al. 2011).

When we consider species which did not responded to native vegetation loss, and those species that have low purity indicators and reliability values, their responses to the environmental gradient did not differ from randomly expected value (Baker & King 2010). These species are more tolerant, being able to use different habitat types, and to disperse between forested patches. For such species, the effects of habitat loss and fragmentation are consequently less important (Ferreira-Peruquetti & De Marco 2002, Remsburg et al. 2008, Monteiro Junior et al. 2015). Others species require open areas, such as gaps within of native vegetation fragments in which to bask (Corbet 1999). Hetaerina rosea and Tigriagrion aurantinigrum are typical example of damselfly that show opportunistic behavior and are able to use open areas (De Marco & Peixoto 2004; De Marco & Vital 2008). Moreover, the increase in the sedimentation may change lotic habitats to lentic ones which promote the colonization of some odonata species (Ferreira-Peruquetti & De Marco 2002, Remsburg et al. 2008, Monteiro Junior et al. 2015). This opportunistic behavior may also explain the lack of clear response of total richness to the amount native vegetation loss around the streams. So, although the beta diversity of Odonata may change along environmental gradients of forest loss, the total richness is not affected due to compensatory mechanism, such as substitution and invasions (Ferreira-Peruquetti & De Marco 2002, Goertzen & Suhling 2013, Monteiro Junior et al. 2014, Monteiro Junior et al. 2015).

Habitat fragmentation and land conversion for agricultural purposes are the greatest threats to biodiversity conservation in savanna landscapes, such as the Brazilian Cerrado (Carvalho et al. 2009, Overbeck et al. 2015). This important biome is undergoing a rapid process of land conversion to soya, maize, sugar cane plantations and large-scale cattle raising (Klink & Machado 2005). Currently, about 39% of its area has already been converted to cattle ranching and agriculture production (Sano et al.

2008). In areas as the Pantanal Plateau, only 40% of its native vegetation remains (Conservation International et al. 2014). This highlights the relevance of our work, given that almost all our sampling sites are located within this region. Streams on the Cerrado plateau control the hydrological dynamics of the Pantanal (Junk et al. 2011), the biggest wetland in South America. It is, therefore, critical for biodiversity conservation that the native vegetation is maintained, at least between 30 and 40% at landscape scale. This is essential not only for the persistence of a wide range of taxonomic groups, but also to maintain the integrity of the riparian ecosystems.

Our results may also have important implications for environmental regulatory policy. According to the current Brazilian Forest Act (Law Number 12.651/2012), riparian forest of at least 30 m-wide must be preserved on both sides of waterways with up to ten meters wide as a permanent protected area (APP in Portuguese). In our study area, most of remnants of native vegetation are concentrated into river banks. The size of forest strip required by the Forest Act regulations represents only 10% of our buffer area. Consequently, if Brazilian Forest Act is applied in this region in the strict sense, it may cause impacts on the biodiversity of riparian zones, since the amount of remaining habitat will be lower than the "high impact risk level" determined for the damselfly community (40 a 60% of native vegetation loss), and, as we have seen above, a wide variety of other taxa. The potentially strongly negative impacts of the current Brazilian Forest Act regulations on biodiversity have already been highlighted by conservationists and scientists (Casatti 2010, Freitas 2010, Galetti et al. 2010, Toledo et al. 2010). Such circumstances call for the construction of a large-scale societal initiative to conserve, protect and restore the Pantanal Plateau, and the need of a critical review of some of the laws currently responsible for the protection of Brazilian freshwater-terrestrial ecosystems.

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Supplementary data

Appendix S1. Taxa-specific results from Threshold Indicator Taxa Analysis (TITAN) of Damselfly community composition in response fragmentation of forest habitat in the Mato Grosso Sul State. The observed (Obs) change point is shown for each taxon. "Freq" the mean frequency of taxa occurrence across 98 sites. IndVal is the unstandardized indicator score (scaled from 0-100%, with 100=perfect indicator). P is the probability of getting an equal or larger IndVal based on 250 random permutations of the data, and Z represents the standardized TITAN indicator score. Lower (5%) and (10%), middle (50%), and upper (90%) and (95%) values correspond to change point quantiles of 500 bootstrap replicates. Purity is the proportion of correct assignments as a negative (z-) or positive (z+) threshold indicator among 500 bootstrap replicates, and reliability "rel05" is the proportion of 500 bootstrap replicates in which p \leq 0.05. Only taxa that met significance criteria for P (\leq 0.05), are included in this table. The ID are taxa, the first letters are genera (e.g. A = Argia, Ac = Acanthagrion, En = Enallagma, Ep = Epipleoneura, H = Hetaerina, N = Neoneura O = Oxyagrion and P = Peristicta), the unabbreviated word is the name of species.

ID	Obs	freq	Maxgr	IndVa	P	Z	5%	10%	50%	90%	95%	purity	rel05
			p	l									
A. croceipennis	0.0	8	1	66	0.001	3.62	0.0	0.0	16.2	80.0	85.0	0.98	0.91
A. modesta	42.0	6	1	54	0.03	2.29	0.0	0.0	38.5	98.0	100	0.90	0.73
A. mollis	14.0	9	1	57	0.004	4.11	0.0	0.5	14.0	62.0	64.0	1.00	0.99

A. smithiana	44.0	5	1	55	0.008	3.97	0.0	4.0	38.5	52.0	58.0	1.00	0.98
A. subapicalis	52.0	7	1	56	0.004	3.40	0.5	27.0	44.0	60.0	60.00	1.00	0.96
En. novahispaniae	55.0	5	1	54	0.016	2.93	1.0	11.0	50.0	60.5	62.0	1.00	0.88
Ep. venezuelensis	60.0	5	1	54	0.004	2.5	29.0	42.0	60.0	65.00	68.0	0.99	0.77
H. mortua	60.0	8	1	54	0.004	2.70	0.0	0.0	58.0	67.0	83.0	0.91	0.79
N. sylvatica	98.0	36	1	68	0.004	4.05	63.0	71.0	92.0	100.0	100.0	0.98	0.97
<i>N</i> . rubriventris	18.0	6	1	54	0.004	4.41	1.0	5.0	14.0	60.0	63.0	1.00	0.93
P. aeneoviridis	80.0	33	1	68	0.004	4.40	13.0	34.0	80.0	100	100	1.00	0.99
Ac. aepiolum	46.0	37	2	62	0.02	2.8	0.5	3.8	46	66.0	100	0.94	0.87
A. chapadae	5.0	51	2	65	0.02	3.36	2.0	5.0	25.0	65.0	100	0.95	0.92
A. hasemani	60.0	42	2	58	0.04	2.36	0.0	2.0	60.0	91.0	100	0.80	0.77
A. tamoyo	91.0	10	2	54	0.02	3.94	18.0	38.0	100	100	100	0.88	0.74
O. sulmatogrossense	52.0	57	2	62	0.008	3.60	0.0	1.0	45.0	67.0	90.0	0.96	0.91

Chapter 2

Egg-laying behavioural traits in dragonflies determine which species survive $stream\ bank\ transformation **$



Argia sp. Photo: Francisco Valente-Neto

Abstract

Behavioral traits can be a key factor for understanding population dynamics and for assessing the effects of landscape changes on local assemblages and communities. Among these traits, oviposition behavior holds great potential for illustrating changes in aquatic and terrestrial environments. Dragonflies (Odonata) are known to have different oviposition strategies, which can be assigned to three types: exophytic, endophytic and epiphytic. Here, we address whether native vegetation loss around streams influence the maximum number of species with certain type of oviposition behavior in a dragonfly assemblage. We hypothesized that different behavioral traits relating to oviposition respond vary according to to spatial area of native vegetation. This study was conducted in 116 streams in the Neotropical Savanna and the Atlantic Forest. We collected adult dragonflies with a hand net along a 100-m transect parallel to the stream banks. We then calculated the total proportion of native vegetation around the streams inside a circular buffer area with a radius of 250 m. The relationship between species richness for each behavioral category and the proportion of native vegetation was tested using quantile regression analysis. The total richness and endophytic species richness were nonsignificant. The exophytic and epiphytic species richness relative to proportion of native vegetation was significant. In other words, the maximum richness of species with exophytic and epiphytic behaviors are affected by the loss of native vegetation, with epiphytic species most affected. The behavioral traits revealed important patterns that were masked when pooling all species altogether. Associating the oviposition behavior with the amount of native vegetation around of the streams is a useful tool for evaluating the biotic value of riparian zones and their transformation. Using these traits also has predictive value in that certain types of riparian zone change will have predictable effects on the surviving dragonfly assemblage.

Key words: Riparian zone; Native vegetation loss, Behavior traits, Dragonfly, Damselfly.
*I wrote this article in collaboration with Fabio de Oliveira Roque, Rhainer Guillermo-
Ferreira and Michael Samways.

Introduction

More than half of the metazoans are insects, which in turn show great wide variation in ecological interactions and behavior among species and even among the life stages of the same species (Fisher 1998). Their oviposition behavior is highly diverse, ranging from relatively unselective to highly specialized. Oviposition behavior is a key trait for understanding population dynamics and assessing the effects of landscape changes on local assemblages and communities (Malmqvist 2002, Peckarsky et al. 2010, Heino & Peckarsky 2014). Furthermore, the study of oviposition behavioral syndromes may reveal, at least in part, why typically measured environmental and spatial predictors explain only a small proportion of the variation in assemblage or community structure. This then helps to explain, for example, a species' absence or low density at apparently suitable sites (Peckarsky et al. 1997, MacCreadie & Adler 2012, Gröonroos et al. 2013, Heino & Peckarsky 2014).

Given that taxonomic or functional groups may make up only a particular dimension of biodiversity, recent research is investigating other ways of assessing animal assemblages and communities and their relationship with the environment. For instance, to date, behavioral diversity has been a neglected portion of biodiversity, even though it carries the most information of the organism's biology as an outcome of the interaction between genes and environment. Hence, such behavioral traits can be used as surrogates and indicators of anthropic impacts (e.g. Negrín et al. 2016) and is valuable in biodiversity conservation (Berger-Tal et al. 2015). Oviposition behavior, for example, can be regarded as one of the main sources of ecological information and a potential assessment tool owing to its inherent dependence on environmental conditions (e.g. Pickens & Root 2009, Alp et al. 2013).

Several aquatic organisms have complex life cycles and experience developmental niche shifts (e.g. larvae are aquatic and adults terrestrial i.e. amphibiotic). In such cases, the oviposition behavior is associated with the adult, mainly to females (Hinton 1981, Encalada & Peckarsky 2007, Remsburg & Turner 2009). Oviposition site selection is usually influenced by both aquatic and terrestrial cues, such as water reflexive properties, physical dimensions of the water body, presence of emergent aquatic vegetation, availability of food resources and predation risk (Corbet 1999, Johansson 2000, Bernath et al. 2002, Rouquette & Thompson 2005, Remsburg & Turner 2009). Therefore, changes in landscape features, mainly on the amount of vegetation coverage and configuration of the native vegetation remnants can affect the level of the reproductive success in aquatic insects, changing local species composition (Remsburg & Turner 2009, MacCreadie & Adler 2012).

Dragonflies are good models for integrating behavioral-level and landscape ecology approaches for understanding how land use influences population distribution and dynamics. Adult dragonfly diversity and abundance often are positively correlated with amount of local vegetation (Remsburg 2007, Rodrigues et al. 2016). Vegetation provides adults with perching structures for thermoregulation, foraging, territory defense, mate attraction, copulation, nocturnal roosting, protection from adverse weather, and oviposition sites (Rouquette & Thompson 2007, Remsburg & Turner 2009, Guillermo-Ferreira & Del-Claro 2011). Different oviposition behavior allows the selection of the best microhabitat to enhance egg survival and larval development (Michiels & Dhondt 1990, Wildermuth & Spinner 1991, Corbet 1999, Lancaster et al. 2010).

Human-induced loss of native vegetation loss around streams (e.g. going over to pastures, crops and urban landscapes) (Foley 2005, Vörösmarty et al. 2010) can act as a

"filter" of species with specific traits, such as oviposition behavior (Poff et al. 2006, Heino et al 2014). This means that species from the regional species pool must overcome this filter to potentially inhabit a given locale (Remsburg 2007, Remsburg & Turner 2009, Heino et al. 2014). Changes in natural landscapes usually reduce the number of appropriate oviposition sites, as well as the amount of food resources and breeding sites. Furthermore, change may increase interspecific competition and larval mortality rates, and decrease the dispersion capacity (Corbet 1999, Remsburg 2007, Remsburg & Turner 2009, Lancaster et al. 2010, Kutcher & Bried 2014, De Marco et al 2015, Dutra & De Marco 2015, Monteiro-Junior et al. 2015). Therefore, the association of behavioral traits that are sensitive to local environmental conditions might be considered a robust tool for indicative or even predictive studies in community ecology (Poff et al. 2006, Heino & Peckarsky 2014).

Here we address whether native vegetation loss around streams influences the maximum number of species with certain types of oviposition behavior in a dragonfly assemblage. We predict that different traits of oviposition behavior respond differently to the amount of native vegetation—along the streams i.e. in the riparian zone. In particular, we hypothesize: i) an increase in exophytic species richness in relation to the degrees of native vegetation loss of the natural riparian zone, because these species use the light polarization on water surface and backwater regions in streams as a criterion for oviposition site selection. Thus, the intensification of the sediment deposition process along stream channels, caused by the absence of riparian vegetation, modify parts of lotic channels, form pools or reduce stream flow, favoring species with this type of behavior (Corbet 1999, Stevani et al. 2000, Van de Koken et al. 2007, Paulson 2009, De Marco et al. 2015); ii) an increase in the richness of endophytic and epiphytic species that oviposit in macrophytes in relation to riparian zone reduction, because

aquatic plants are favored in open environments and intermediate stages of forest cover, facilitating the development and reproduction of these groups (Loo et al. 2009, Paulson 2009, Guillermo-Ferreira & Del-Claro 2011, Wood et al. 2012, Bando et al. 2015), and iii) a decrease in the richness of epiphytic species, in relation to extent of the natural riparian zone, because the absence of natural riparian vegetation along streams leads to a decrease and loss of available oviposition sites, such as rocks, roots, stems and leaves, decreasing the places for adult perchers to be able to thermoregulate to forage, to defend territories, attract mates, copulate, roost at night, and to have protection from adverse weather and predators. The natural riparian zone also helps in the maintenance of the physical structure of the river channels, avoiding the modification caused by excessive sediment deposition, essential for maintaining epiphytic species larval habitats (May 1979 and 1991, Corbet 1999, Paulson 2009, Remsburg & Turner 2009, De Marco et al. 2015) (Figure 1).

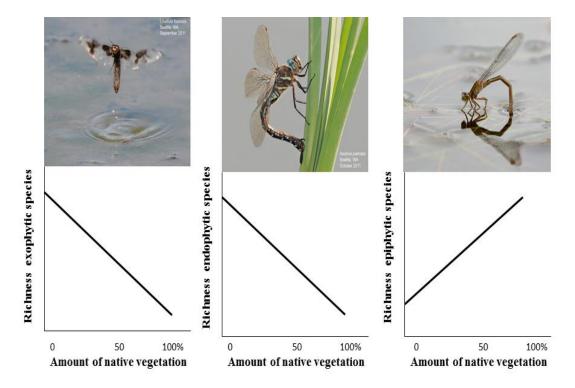


Figure 1: General description of comparisons performed between oviposition behaviors responses along gradient of loss riparian zone. On the left, we hypothesize a decline in

richness exophytic species in relation to increase in native vegetation. In the middle, we expect a decline in richness endophytic species in relation to increase of native vegetation, and on the right, we expect an increase in richness of epiphytic species in relation to an increase in native vegetation (photos: Google image).

Methodology

Study area

Our study area was located in central Brazil, more specifically in the southwest of Mato Grosso do Sul state, characterized by a landscape mosaic dominated by savanna (Cerrado) and semi-deciduous Atlantic Forest, two biomes considered globally important biodiversity hotspots (Myers et al. 2000). The climate is classified as tropical humid, with two dry months (July and August) and the months of December, January and February are among the rainiest. The annual mean temperature is 22°C, being the average of the coldest month (June or July) 18°C and the average of the warmest month (September) 32°C (ZEE 2009).

We conducted this study at 116 streams at which native fragments are embedded in a matrix dominated by pastures, monocultures and urban areas (figure 2). We sampled a gradient of forest cover ranging from dense, native riparian vegetation through different

degrees of native vegetation loss.

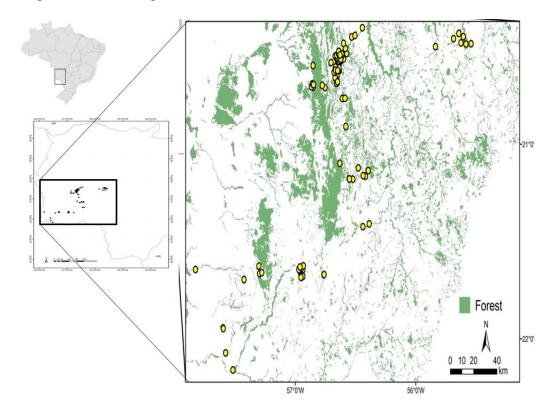


Figure 2: Map of the 116 sampling sites in Mato Grosso do Sul state, Brazil.

Sampling

We collected adult dragonflies (both true dragonflies, Anisoptera, and damselflies, Zygoptera) with a hand net along a 100-m transect at each stream and parallel to both the stream banks from 2011 to 2013. Most samples were collected during the wet period (December to April), because most damselflies in particular are more active during hot (above 19° C) and humid days (Corbet 1999). Sampling was conducted once at each site, for one hour in each stream, on sunny days between 10h00 and 15h00, an approach and timing that is known to be effective in this area (e.g. Monteiro-Junior et al. 2015).

Identification of specimens to species or morphotype followed taxonomic keys and original descriptions, and confirmation by experts (see acknowledgements).

Voucher specimens are deposited in UFMS's Zoological Collection (ZUFMS).

Oviposition types

Oviposition behavior in Odonata can be classified as: 1) Exophytic, species that lay eggs directly on the water and can be considered as: a) Dippers or tippers, which dip their abdomens multiple times and release a few eggs at a time, and b) Bombers, which drop all their eggs from the air while flying; 2) Endophytic, species that usually lay eggs inside plants, typically inside living tissue, where plant selection may be generalist or more selective, and these sites may be either aerial or under the water; and 3) Epiphytic, which lay eggs on the exposed surface of rocks, leaves, trunks or other substrates protruding from the stream surface, oviposition on the submerged undersides of these substrates, and species that lay eggs on leaves in the riparian vegetation (Fincke 1986, Corbet 1999, Paulson 2009). Most of the epiphytic and endophytic species are dependent on vegetation, because the availability of different sites for oviposition (leaves, roots, stems) and some species of plants or macrophytes are essential for reproduction and development of the larvae (Remsburg & Turner 2009, Guillermo-Ferreira & Del-Claro 2012, Hamada et al. 2014).

We characterized all species according to oviposition behavior traits. We selected the three traits that were readily available in the literature or that could be evaluated confidently by expert opinion (Fraser 1952, Longfield 1953, Paulson 1969, Fincke 1986, Corbet 1999, Paulson 2009, Garisson et al. 2006 and 2010, Vilela et al 2016), and we also made field observations. Behavioral observations were made in sessions of *ad libitum* data collection (Altmann 1974) focused on oviposition behavior

characterization. We assigned each species to only one behavioral trait state (Appendix 1). When a species behavioral categorization was not possible, we used the known behavior of congeneric species (Garisson et al. 2006 and 2010).

Analysis of riparian native vegetation loss

We first delineated a circular buffer area (250 m radius) around a point located in the center of each sampled stream channel, and calculated the total proportion of riparian forest and seasonal forest within each buffer (Figure 3). We used this buffer area because some species require streams with dense riparian vegetation due to ecophysiological constraints, and territorial males defend patches in the reproductive habitat (Corbet 1999, Remsburg & Turner 2009, Keller et al. 2012, Guillermo-Ferreira & Del-Claro 2012, Keller & Holderegger 2013, De Marco et al. 2015).

We chose the proportion of remnants of native vegetation as a landscape metric, because the amount of vegetation is considered the main driver of community changes (see Fahrig 2013, Quesnelle et al. 2013). It is also one of the main variables for explaining Odonate species distribution (Remsburg & Turner 2009, Monteiro-Junior et al. 2014, Dutra & De Marco 2015, Rodrigues et al. 2016). We did not include other configuration metrics in our analysis because the proportion of riparian zone was highly correlated with other aspects such as largest patch index, given that a 250 meters buffer generally contains a forest fragment. In addition, to assess whether the chosen scale influences the detected pattern, we also calculated the amount of vegetation within a 500 meters buffer, resulting in highly correlated values with the 250 meters buffer $(r^2=0.92)$.

The base map used to calculate the proportion of remnants of native vegetation was retrieved from a database of the Environmental Institute of Mato Grosso do Sul

state. We used images of the CCD (Couple Charged Device) receiver of the CBERS2 satellite (Sino-Brazilian Earth Resources Satellite), taken in 2010 at 30 m resolution. The mapping process was performed by supervised classification at the 1: 100,000 scale.

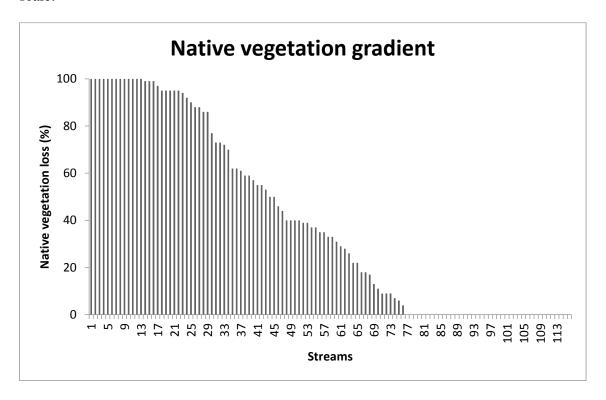


Figure 3: Riparian zone gradient around the 116 streams sampled, using circular buffers surrounding the sampling point with a radius of 250 m.

Data analyses

The relationship between species richness by behavioral group and the riparian zone gradient was tested using linear regression and a quantile regression analyses.

Quantile regression allows the analysis of the upper or lower limits of a variable rather than focusing on the mean. Assessing changes in a specified quantile of the response variable produced by one unit change in the predictor variable. This analysis assessed the number maximum or minimum number of species which could potentially coexist in an area given its environmental condition (Skov & Svenning 2004, Svenning et al.

2009). We performed linear regression and quantile regression analysis in R 3.2.2, and for quantile regression we used the quantreg library (R Development Core Team, version 3.2.2).

Results

We collected 2,413 specimens of Odonata, belonging to 8 families, 30 genera and 63 species. Furthermore, 25 species were classified as exophytic, 28 as epiphytic and 10 as endophytic (Supplementary material). The total species richness of Odonata did not show significant results for the linear regression and the quantile regression analyses (p>0.05) (Table 1, Figure 3). The richness of the endophytic species also did not show significant results for linear regression and for quantile regression in the 5th and 95th quartile (p>0.05). The intercept value had a small change between the linear and the quantile regression (Table 1, Figure 3).

Table 1: Linear regression and quantile regression analyses (5 th and 95 th), P-value and intercept. This analysis considers total species richness of Odonata and richness of each oviposition behavioral type.

	Linear		Quantile	Regression	Quantile	Regression	
	Regression	1	5 th		95 th		
	P-value	Intercept	P-value	Intercept	P-Value	Intercept	
Richness Odonata	0.17	1.381	1.00	0.000	1.00	0.000	
Richness Endophytic	0.98	-0.0019	1.00	0.000	1.00	0.000	
Richness Exophytic	0.016	-2.443	1.00	0.000	0.024	-2.276	
Richness Epiphytic	0.0001	3.927	0.01	2.614	0.00	5.285	

The exophytic and epiphytic species showed a significant value for the linear regression and the quantile regression 95th (p<0.05) (Table 1, Figure 4). The intercept of the regression coefficient showed a variation on the inclination considering the linear regression and the quantile regression (95th) from -244 to -227 for exophytic species, and from 3.92 to 5.28 for epiphytic species (Table 1, Figure 4). The significant variation in the 95th quartile for exophytic and epiphytic species indicates that the maximum richness of species that coexist is affected by the loss of native vegetation around streams. Increasing the maximum richnness of exophytic species and decreasing the maximum richness of epiphytic species along this gradient of native vagetation loss. The minimum richness of epiphytic species (5th), in areas with more than 60% vegetation, also increased richness from one to at least two species (figure 4).

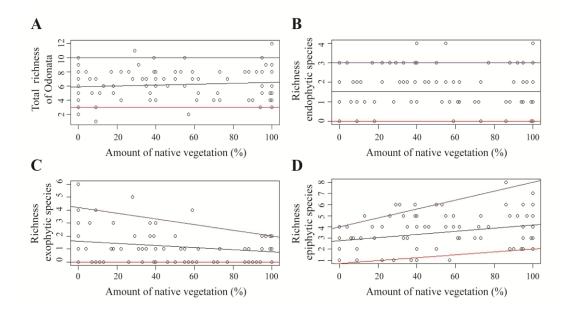


Figure 4: Linear regression (black line) and quantile regression 5th and 95th (red and blue line respectively) for: a) total richness of Odonata, b) Endophytic, c) Exophytic and d) Epyphitic species.

Discussion

There is considerable debate in community ecology concerning the importance of land use changes, including vegetation loss and fragmentation, and its affect on community structure (e.g. Laurence et al. 2014, Magrach et al. 2014). Dragonflies have been used as a focal group in such debate (Corbet 1956, Watson et al. 1982, Samways 1989, Ormerod et al. 1990). Most articles have documented that terrestrial landscape conversions affect odonate biodiversity in terms of composition and taxonomic richness, especially reltive to native vegetation loss and the physical and chemical changes in aquatic environments (Remsburg & Turner 2009, Simaika & Samways 2009, Stoks & Córdoba-Aguilar 2012, Kutcher & Bried 2014, Bried & Samways 2015, De Marco et al. 2015, Dutra & De Marco 2015, Monteiro-Junior et al. 2015, Rodrigues et al. 2016). General frameworks have also been proposed, based on dispersal traits such as size and termoregulation, which are fundamental for understanding how such changes can affect dragonfly diversity (Juen & De Marco 2011, Nobrega & De Marco 2011, De Marco et al. 2015). Hovewer, few studies have included traits linked to behavior (Poff 2006, Heino et al. 2014). Therefore, at least to our knowledge, here we show the first approach that links behavioral traits to riparian vegetation loss.

Indeed, behavioral traits and the natural history of organisms has been a neglected dimension of biodiversity (Ricklefs 2012, Tschinkel & Wilson 2014, Tewksbury et al. 2014), resulting in a huge gap in knowledge and a lack of its use as a tool for environmental monitoring (Berger-Tal et al. 2015). For instance, oviposition behavior is an important assessment tool that links adult behavior to changes in land use. The local habitat features are necessary for successful oviposition of the adults, and consequently for population establishment and dynamics (Malmqvist 2002, MacCreadie & Adler 2012, Heino et al. 2014). Here, by deconstructing an Odonada assemblage according to the various oviposition behavioral traits among its component species, we

demonstrate that habitat characteristics may filter the assemblage by selectively allowing species with differents oviposition behaviors to differentially occupy native or modified environments as breeding sites, which of course is strongly constrained by phylogeny. We suggest that this approach can improve our predictive ability to address issues related to effects of land use change in Odonata.

Here, the results show that species with the epiphytic oviposition behavior were negatively influenced by the native vegetation loss. The reduction in oviposition substrates as wood debris, leaves and roots, which are used by epiphytic species, have a strong relationship with the amount of vegetation (Remsburg & Turner 2009). This means that as nativevegetation decreases or disappears, the breeding and oviposition sites also become limited, increasing predation risk for larvae and adults, and ultimately resulting in a decline in species with this kind of behavior (Corbet 1999, Worthen & Patrick 2004, Lancaster et al. 2010, Stoks & Córdoba-Aguilar 2012, Kutcher & Bried 2014). Furthermore, in contrast, exophityc species showed a positive relationship with the native vegetation loss. The alteration in native vegetation density, caused by modifications on streams channels, increases the amount of backwaters along the channels and increases the incidence of sunlight in these areas. These two factors are used by a large number of exophytic species to choose the location for oviposition, allowing exophytic species richness to increase in places with little or no native vegetation around streams (Corbet 1999, Worthen & Patrick 2004, Stoks & Córdoba-Aguilar 2012, Dutra & De Marco 2015).

The presence of epiphytic species in forested habitats is related to the supply of suitable sites for egg laying and the integrity of stream channel physical structure (Remsburg & Turner 2009). For instance, *Heliocharis amazona* lays its eggs in soft vegetable matter, likely decomposing wood, in clean running waters (Garisson et al.

2006). Larvae of *Epipleoneura venezuelensis* develop in rapid flow streams within primary forest (De Marmels 2007). Thus, environments with high amounts of native vegetation increase the number of breeding and oviposition sites and maintain suitable refugia for larval development and protection against predators (Corbet 1999, Remsburg & Turner 2009, Garisson et al. 2010, Guillermo-Ferreira & Del-Claro 2011, Guillermo-Ferreira & Del-Claro 2012, Hamada et al. 2014).

Most epiphytic species recorded here are damselflies, and are known to prefer their natal place for breeding, where males defend their territories (Corbet 1999). Some of these epiphytic species showed a clear threshold in relation to a decline in native vegetation area, decreasing their abundance or occurrence in sites with less than 40% of native vegetation (Rodrigues et al. 2016). In our study, areas with more than 60% of vegetation had an increase in the minimum richness (5th) of epiphytic species from at least one to at least two species at these sites. These species may have difficulties in colonizing other sites because some species are likely to move only a short distance, or because of changes in land use there are new barriers in the landscape that decrease dispersal capacity (Moritz et al. 2013, Canedo-Arguelles et al. 2015). Therefore, species with low dispersal abilities are easily extinguished from the local population if the environmental changes make them improper for reproduction (Conrad et al. 2002, Rouquette & Thompson 2005).

The exophytic species showed a positive relationship with the decline of native vegetation. In general, these species choose the oviposition sites by visual cues in backwaters sites in streams (Corbert 1999, Garisson et al. 2006). *Miathyria marcella*, *Orthemis discolor* and *Pantala flavencens* are species that oviposit in ponds, lakes or slow moving waters (Corbet 1999, Van de Koken et al. 2007, Garisson et al. 2006). In our study, these species increased in abundance in sites with little or no vegetation cover

around of streams. The increase in sediment deposition processes along streams channels may alter parts of lotic channels and form pools or reduce stream flow, favoring species with this behavioral type.

Endophytic and epiphytic species that lay eggs in macrophytes did not respond to a decline in native vegetation. In streams with low amount of native vegetation, we expected a larger amount of macrophytes due to higher availability of light, which favors the growth of some plant species (Wood et al. 2012, Bando et al. 2015). We had a low number of species that were classified with this oviposition behavior. Thus, this response may be related to the small amounts of macrophytes in our study sites.

Oviposition traits do not co-vary completely with ecophysiological traits in Odonata. For example, in our study, considering only traits related to thermoregulatory capacity (the ecophysiological hypothesis of De Marco et al. (2015)), one could expect that themal conformers (heliotherms) would be favored by open areas around the streams. However, they were found in the open and forested areas. When we consider the behavior of oviposition, we found that some heliothermic species with epiphytic behavior were associated with sites with high prporations of natural vegetation. Heliocharis amazon Selys, 1853, Mnesarete guttífera (Selys, 1873), M. pudica pudica (Hagen, 1853) and *H. mortua* Hagen, 1853 are examples of such species that use roots, leaves and trunks for oviposition and are associated with high levels of native vegetation. On the other hand, heliothermic species with exophytic behavior, such as Perithemis mooma Kirby, 1889, and Erythrodiplax fusca (Rambur, 1842), were favored by open areas, mainly because oviposition behavior of these species are strictly associated with the light polarization on water surface and backwater regions in streams (Corbet 1999, De Marco et al. 2005, Corbet & May 2008, Garisson et al. 2010). These differences relate to the traits related to thermoregulatory capacity, and make

oviposition behavior a tool to be used when evaluating the effect of vegetation loss of vegetation on dragonfly assemblages. These observations emphasize the importance of considering multiple traits along environmental gradientes and their linkages in developing a traits-based predictive ecology (Poff et al. 2006, Webb et al. 2010, Heino & Peckarsky 2014).

Species that have had a long interaction time with their natural environment approach their fundamental adaptive capacity. However, when they experience the sudden changes in environmental conditions, as is the case with anthropogenic landscape modification, their adaptive capacity is challenged, leading to a realized adaptive capacity (Beever at al. 2015). Here, the dragonfly species making up the assemblage are variously given opportunities on the one hand and have opportunities taken away from them on the other through the vehicle of their oviposition behavioral traits. It is a sobering thought that this is just one set of traits when in reality any species has a whole host of traits subject to the new pressures from anthropogenic impacts (Eskildsen et al. 2015). This means that many species are currently facing severe obstacles in the immediate human environment, and which will have long term effects on reshuffling of assemblages as long as human pressures remain. Finding key traits, like the oviposition behavior here, will go a long way to enabling predictions about which species are likely to be the survivors into the future and which not.

The association between oviposition behavior and the riparian native vegetation conservation status can become a powerful assessment tool. Indeed, behavior can turn into an instrument for assessing the role of riparian zones in the maintenance of ethological diversity in aquatic insect communities, and also the conservation status of freshwater environments. This means that behavioral traits that differ among species may also differ between sites with different conservation levels of native vegetation

remnants. In other words, there are critical initial filters imposed by native vegetation loss that determine the occurrence of specific behaviors in aquatic communities.

Therefore, the conservation of the native vegetation around streams is essential to conserve the traits diversity in communities associated to aquatic-and-terrestrial environments.

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Supplementary data

Supplementary material: Species of Odonata, type of oviposition and observation in field and or reference. Personal observation of the authors of the manuscript (Guillermo-Ferreira, R. and Rodrigues, M.E.). *Epiphytic species that oviposite in macrophytes. ** References mentioning the species behavior within the same genera.

	Type	of
Species	oviposition	Observation in field and or Reference
Lestes forficula Rambur, 1842	Endophytic	Hamada et al. 2014
Progomphus sp.	Endophytic	Hamada et al. 2014
Remartinia sp.	Endophytic	
Staurophlebia reticulata (Burmeister, 1839)	Endophytic	
Castoraeschna sp.	Endophytic	Guillermo-Ferreira, R. (Personal observation)
Homeoura nepos (Selys, 1876)	Endophytic	Guillermo-Ferreira, R. (Personal observation)
Oxyagrion sulmatogrossense Costa, Souza &		
Santos, 2000	Epiphytic	Guillermo-Ferreira, R. (Personal observation)

Oxyagrion terminale Selys, 1876	Epiphytic	Guillermo-Ferreira & Del-Claro 2011; Tom Kompier, 2015**
Peristicta aeneoviridis Calvert, 1909	Epiphytic	Guillermo-Ferreira, R. (Personal observation)
		Guillermo-Ferreira, R. (Personal observation), Garisson et al.
Tigriagrion aurantinigrum Calvert, 1909	Epiphytic	2010
Hetaerina mortua Hagen, 1853	Epiphytic	
Hetaerina rosea Selys, 1853	Epiphytic	Guillermo-Ferreira & Del-Claro, 2011.
Mnesarete guttifera (Selys,1873)	Epiphytic	Guillermo-Ferreira, R. (Personal observation)
Acanthagrion aepiolum Tenessen, 2004	Epiphytic*	Guillermo-Ferreira, R. (Personal observation)
Acanthagrion ascendens Calvert, 1909	Epiphytic*	Garrison et al. 2010
Acanthagrion cuyabae Calvert, 1909	Epiphytic*	Tom Kompier 2015 (REGUA)
Acanthagrion gracile Rambur, 1842	Epiphytic*	Tom Kompier 2015 (REGUA)
Aeolagrion dorsale (Burmeister, 1839)	Epiphytic	
Argia chapadae Calvert, 1909	Epiphytic	Rodrigues, M.E. (Personal observation)
Argia croceipennis Selys, 1865	Epiphytic	
Argia hasemani Calvert, 1909	Epiphytic	Guillermo-Ferreira, R. (Personal observation)

Argia indocilis Navás, 1934	Epiphytic	Guillermo-Ferreira, R. (Personal observation)
Argia lilacina Selys, 1865	Epiphytic	Rodrigues, M.E. (Personal observation)
Argia modesta Selys, 1865	Epiphytic	
Argia mollis Hagen, 1865	Epiphytic	Rodrigues, M.E. (Personal observation)
Argia reclusa Selys, 1865	Epiphytic	Vilela et al. 2016, Guillermo-Ferreira & Del-Claro 2012
Argia smithiana Calvert, 1909	Epiphytic	
Argia subapicalis Calvert, 1909	Epiphytic	
Argia tamoyo Calvert, 1909	Epiphytic	
Heliocharis amazona Selys, 1853	Epiphytic	Guillermo-Ferreira, R. (Personal observation)
Mnesarete pudica pudica (Hagen, 1853)	Epiphytic	Vilela et al. 2016.
Neoneura bilinearis Selys, 1860	Epiphytic	Rodrigues, M.E. (Personal observation)
Neoneura ethela Williamson, 1917	Epiphytic	
Neoneura rubriventris Selys, 1860	Epiphytic	Guillermo-Ferreira, R. (Personal observation)
Neoneura sylvatica Hagen, 1886	Epiphytic	Vilela et al. 2016
Enallagma novaehispaniae Calvert, 1907	Epiphytic	Guillermo-Ferreira, R. (Personal observation) and Paulson D.

2009, Garisson et al. 2010

Guillermo-Ferreira, R. (Personal observation), Garisson et al.

Epipleoneura metallica Rácenis, 1955	Epiphytic	2010
Epipleoneura venezuelensis Rácenis, 1955	Epiphytic	Rodrigues, M.E. (Personal observation)
Erythemis peruviana (Rambur, 1842)	Exophytic	Rodrigues, M.E. (Personal observation)
Erythemis vesiculosa Fabricius, 1775	Endophytic	Vilela et al. 2016,
Erythrodiplax fusca (Rambur, 1842)	Exophytic	Tom Kompier 2015 (REGUA)
Erythrodiplax kiminsi Borror, 1942	Exophytic	
Erythrodiplax lativittata Borror, 1942	Exophytic	
Erythrodiplax paraguayensis (Förster, 1905)	Exophytic	Rodrigues, M.E. (Personal observation)
Erytrodiplax umbrata (Linnaeus, 1758)	Exophytic	Rodrigues, M.E. (Personal observation)
Miathyria marcella (Selys, 1857)	Exophytic	Rodrigues, M.E. (Personal observation)
Micrathyria iheringi Santos, 1946	Exophytic	Rodrigues, M.E. (Personal observation)
Micrathyria laevigata Calvert, 1909	Exophytic	
Micrathyria stawiarskii Santos, 1953	Exophytic	

Micrathyria ungulate Förster, 1907	Exophytic	Rodrigues, M.E. (Personal observation)
Mycrathyria hesperis Riss, 1911	Exophytic	Tom Kompier, 2015 (REGUA)
Orthemis cultriformis Calvert, 1899	Exophytic	Rodrigues, M.E. (Personal observation)
Orthemis discolor (Burmeister, 1839)	Exophytic	Vilela et al. 2016, Tom Kompier 2015 (REGUA)
Pantala flavencens (Fabricius, 1798)	Exophytic	Paulson D. 2009 and Tom Kompier 2015 (REGUA)
Pantala hymenaea (Say, 1840)	Exophytic	Tom Kompier 2015 (REGUA)
Perithemis lais (Perty, 1834)	Exophytic	Rodrigues, M.E. (Personal observation)
Perithemis mooma Kirby, 1889	Exophytic	Tom Kompier 2015 (REGUA)
Perithemis thais Kirby, 1889	Exophytic	Tom Kompier 2015 (REGUA)
Dasythemis venosa (Burmeister, 1839)	Exophytic	
Dythemis multipunctata Kirby, 1894	Exophytic	Rodrigues, M.E. (Personal observation)
Elasmothemis cannacrioides (Calvert, 1906)	Exophytic	Rodrigues, M.E. (Personal observation)
Erythrodiplax basalis (Kirby, 1897)	Exophytic	Rodrigues, M.E. (Personal observation)
Macrothemis flavencens (Kirby, 1897)	Exophytic	Rodrigues, M.E. (Personal observation)

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Chapter 3



Peristicta aeneoviridis Photo: Francisco Valente-Neto

Abstract

The dispersal ability of organisms is key to understand the organization of communities. However, different approaches to estimate spatial distance can help us in understanding these processes that structure these communities, especially when dispersal efficiency is related to quality and configuration of the elements that involved the different types of landscape changes. In this sense, our aim was investigate whether environment, geographic distances and landscape resistance determines dissimilarities of Odonata communities in riparian zone immersed in a matrix of pasture in a Savanna region. We used a deconstructed approach of the community based in the thermoregulatory abilities and body size as traits related to dispersal abilities in this taxonomic group. We collected 72 Odonata species in 98 streams. Considering the body size and thermoregulation ability we classified 42 species as low dispersal capacity and 30 species as high dispersal capacity. We found that geographic distances and landscape resistance were correlated with community dissimilarity for total, high and low dispersal capacity. Environment distance had a low correlation with total community dissimilarity and is strongly correlated with high dispersal community. Geographical distance and landscape resistance were moderately correlated. However, when controlled the correlation between resistance landscape and geographic distance, the landscape resistance was not correlated with community dissimilarity. We conclude that geographic and environmental distances are correlated with Odonata community dissimilarity between sites, being the geographic distance more correlated in all the communities. The deconstruction of community in traits related dispersion capacity helped us to understand the role of each distance in the dissimilarity of the community, mainly the environmental distance with the high dispersal community. The use of resistance measurements and dispersion capacity must be more refined to get a better

understanding of the role of geographical distance with landscape resistance in							
metacommunities studies.							
Key-words: Dragonfly, Damselfly, Dispersion Traits, Landscape changes.							
***I wrote this article in collaboration with Larissa Sayuri Moreira Sugai, Francisco							
Valente-Neto, Jose Manuel Ochoa Quintero, Fabio de Oliveira Roque							

Introduction

Dispersal is a fundamental event for the dynamics and the structure of communities, being one of the most challenging processes to measure at large scales, especially at community level (Bilton et al. 2001, Jacobson & Peres-Neto 2010, Vellend et al. 2014). The dispersal ability of organisms may determine the dispersal related process, increasing our understanding on communities' organization (Heino et al. 2014). This an issue identified among the 100 fundamental questions in Ecology, "how species traits and landscape attributes interact to determine animal dispersal" (Sutherland et al. 2013).

Despite the recognized role of environmental factors on community structure at local scales (Nekola & White 1999, Soininen et al. 2007, Heino et al. 2014), geographical distance has widely been attributed as one of the regional drivers of communities' similarities (Nekola & White 1999, Soininen et al. 2007, Heino et al. 2014, Kärnä et al. 2015, Saito et al. 2015). However, different types of spatial distance measurements can be use in order to understand the processes that structure the communities, especially when dispersal efficiency is related to the quality and configuration of the elements involved in the different types of landscapes. This is of particular relevance when we include aspects related to landscape change as native vegetation loss and fragmentation (Heino et al. 2014, Canedo-Arguelles et al. 2015).

In this sense, the landscape resistance quantifies 'distances' between communities in which the notion of distance does not need to be defined only in terms of spatial distance. Landscape resistance can be composed by a variety of factors affecting the movement and dispersal of organisms, such as landforms, artificial structures, altitudinal variation and landscape change (Douglas 1994, Smith et al. 2007, Canedo-Arguelles et al. 2015, Kärnä et al. 2015). For example, the modification in

natural landscapes can create and determined resistance level between the landscapes filtering the species dispersed in modified environments, especially if considering specialist species associated to habitats with certain characteristics (Pardini et al. 2010, Juen & De Marco 2011).

The strength of the forces shaping individual species responses are expected to be directly related to species habitat dependence (MacArthur & Levins 1964, Crist et al. 1992). Groups of species with similar biological and ecological traits are expected to respond consistently along specific environmental gradients (Poff et al. 2006, Webb et al. 2010). These set of traits as for example thermoregulation behavior and body size observed in each species, is the result of a complex interplay of evolutionary history and responses from selecting forces determined by particular habitat features (May 1976, Corbet 1999, Brown et al. 2011, Heino et al. 2015). Then, the dispersal ability of species can represents how they interact with environment, considering their dispersal capacity and tolerance to environmental changes and landscape resistance (Heino & Peckarsky 2014, Heino et al. 2015).

Changes on vegetation coverage and habitat configuration can alter species composition by facilitating or reducing the dispersal capacity of species, leading to changes in species diversity patterns and species interactions (Fahrig 2003, Chapin et al. 2000, Fahrig 2013). The landscape structure also influences species occupation patterns by providing different dispersal routes according to species dispersal-related abilities (Canedo-Arguelles et al. 2015, Kärnä et al. 2015). Therefore, landscape change has a crucial role in community structure, and understanding this driver has direct implications on the definitions of strategies of landscape management for biodiversity conservation and habitat restoration (Lindenmayer et al. 2008, Gama et al. 2013, Tambosi et al. 2013).

Dispersal is a fundamental process in odonate as it is in most insects groups.

Different physiological and morphological characteristics in damselflies and dragonflies species are important surrogates for measuring the flying capacity of odonate species.

These abilities allow us to classify the species in different dispersal capacities. For example, large and endothermic species, as *Pantala favencens* (Fabricius, 1798) have a high dispersal capacity. On the other hand, small and conformers species, as *Peristicta aeneoviridis* Calvert, 1909 shows low dispersal capacity (De Marco et al. 2005, Rundle et al. 2007, Samejima & Tsubaki, 2010). Then thermoregulatory abilities and body size are important surrogates for measured the flying capacities in odonate species and the understanding of these traits allow a better understanding of dispersal ability and how this capacity influence community structure (May 1976, Corbet 1999, Corbet & May 2008, De Marco et al. 2015, Dutra & De Marco 2015).

In this study, we use thermoregulatory abilities and body size as proxies of dispersal ability to investigate whether environment, geographic distances, and landscape resistance determines dissimilarities of Odonata communities in riparian zones in a Neotropical savanna region. We expected: (H1) an increase of total community dissimilarity with the increase of environment, geographic distance and landscape resistance between sites, a typical pattern detected in studies of metacommunities (Nekola & White 1999, Soininen et al. 2007, Canedo-Arguelles et al. 2015, Kärnä et al. 2015, Saito et al. 2015). (H2) Considering the deconstructed community, we expected that the dissimilarity of total community can be weaker than when we consider the community deconstructed in dispersion capacity traits. The wide variation between dispersion capacities and environmental requirements in odonates can disguise the effects of landscape resistance on total community dissimilarity (Corbet 1999, De Marco et al. 2015, Dutra & De Marco, 2015). (H3) Species with low

dispersion capacity will be more affected by landscape resistance, presenting more dissimilarity among communities. Odonates with low dispersion capacity present physiological and behavioral feature (eg. thermoregulation ability), that difficult the dispersal in areas where natural environments have been modified (Juen & De Marco 2011, De Marco et al 2015). We also expected that (H4) initial dissimilarity, should be lower in low dispersal than in high dispersal communities. Actively dispersing insect species would be prone to direct their own flight and should thus be able to track landscape resistance (Cañedo-Argüelles et al. 2015, De Marco et al. 2015, Dutra & De Marco 2015, Kärnä et al. 2015, Saito et al. 2015).

Methodology

Study area

We carried out this study in 98 streams along forested areas interspersed in a matrix composed mainly by pasture within the Cerrado biome in the Central West of Brazil (figure 2). The hidrographic region is characterized by limestone rivers, with high pH. The altitude varies between 450 and 800 meters (Boggiani et al. 2000). This region is located in a complex vegetation zone, with predominance of savanna formations typical from the Cerrado biome, and deciduous and semidecidual forest typical from Atlantic forest biome. The main activities in the region are large cattle farm and the tourism (Veloso et al. 1991, ZEE 2009).

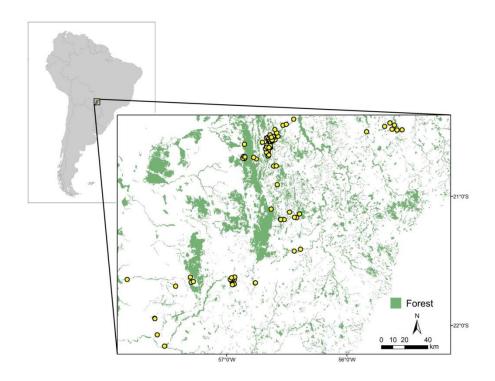


Figure 2: Location of the study area in South America and distribution of the 98 sampling sites along the forested area included in the Cerrado biome, west of Brazil.

Community sampling

The adults were collect between 2011 and 2013 (between September and April from each year). The samplings were standardized following the scanning method, with one hour of sampling effort made by an observer/collector, in an area of 100 meters of riparian forest along both sides of each stream (Silva et al., 2010). The specimens were sampled with an entomological net, between 9:00 and 15:00 hours. The identification followed taxonomic keys (Garisson et al. 2006 and 2010, Lencioni 2005 and 2006), and consulting experts (see acknowledgments). Voucher specimens are deposited in UFMS's Zoological Collection (ZUFMS).

Deconstruction of the communities in dispersal ability

We use morphological and physiological attributes to categorize species with low and high capacities of species dispersal (table 1). We choose body size as the trait related to morphology, because it is direct related with dispersal capacity for active dispersers (Corbet 1999, De Marco et al 2015). For body size, we used the methodology proposed by Dutra & De Marco (2015), at least 5 individuals of each species were arbitrarily selected for measuring total length with a digital caliper. The species were classified as small, medium and large using the average of measures between species and the classification proposed by Garrison et al. (2006 and 2010). Species measuring up to 30 mm total length body were classified as small, those between 31 and 45mm total length body were included in the category of medium size and those above 46mm total length body size as large.

We used thermoregulation ability to represent physiological attributes because those are important surrogates for dispersion of odonate species (May 1976, Corbet & May, 2008, De Marco et al. 2015). These classifications in thermoregulation ability are associated with wing length (Rundle et al. 2007, Samejima & Tsubaki 2010), body size is associated with strong and complex musculature (Schilder & Marden, 2004; Rundle et al. 2007), and fliers and perchers behaviors (Corbet 1999, Corbet & May 2008). In this way, endothermic species are large and fliers, heliothermic species are medium and perchers species, with capacity to heat by irradiation in sunny sites, and conformers species are small perchers with a higher surface/volume ratio are more strongly dependent on air temperature (figure 3). All thermoregulation classification was based on May 1976, Corbet 1999, De Marco et al. 2005, Corbet & May 2008, De Marco et al. 2015). The behavior of some species was also observed in the field, taking into consideration in this thermoregulatory classification, especially considering the behavior of flyers and perchers (Corbet & May 2008).

Table 1: Representation of morphological and physiological attributes used to classify low and high capacities of species dispersal. *None of the species in our data present this trait.

Traits						
Physiologic	Morphological					
Thermoregulation						
Ability	Body size					
	Small	Medium	Large			
Conformers	Low	Low	Low			
Heliothermic	Low	High	High			
Endothermic	High*	High	High			

Local stream environmental variables

We measured several environmental variables previously known to be important for stream invertebrate communities (Heino et al. 2014). Those variables include current velocity (m/s), depth (cm) and width of the sampling site. We also measured physicochemical variables as pH, conductivity, dissolved oxygen (mg/l), salinity and water temperature at each site in the field using a Hanna HI 9828 multiparamenter sensor. All environmental variables were measured at least twice, and we used the mean as environmental predictors. These variables were included because both physical habitat and water chemistry variables are related to adequate environments development and survival of larval, and reproduction and thermoregulation sites for adults (Corbet 1999, De Marco et al. 2015).

Distance measurement

We represented the community with a Bray-Curtis dissimilarity index based on the log-transformed (log x+1) abundance matrix, because this coefficient is highly suitable for quantitative abundance data (Faith et al.1987).

We calculated geographical distances measured by pairwise euclidean distances between sites (the shortest distance between sites in two-dimensional space) using package "vegan" (Oksanen et al. 2013). To calculate environmental distances, we first normalized environmental variables to mean zero and unit variance, and then calculated Euclidean pairwise distances between sites using package "vegan".

We calculated landscape resistance with Circuitscape 4.0, which calculates pairwise resistance based on electrical circuit and random walk theory, allowing multiple routes between sites (McRae 2006). We represented the landscape as conductive surface, with individual pixels of habitat (forest) areas assigned to value 1 and non-habitat values assigned to value 10,000. In general, species of Odonata of lotic environments use forested environments as habitat and for dispersion (Remsburg & Turner 2009). High resistance values indicate high resistance to movement, whereas low resistance values indicate suitable areas for movement. We did not opt to attribute arbitrary values to landscape features to perform a more conservative approach than expert opinion (Cañedo-Argüelles et al. 2015). Each pairwise resistance is represented as the sum of each pixel resistance value among pairs of sites in the input map.

Data analysis

We first analyzed the correlation among environmental, resistance, and geographic distances with mantel test. When strong correlations between matrices were detected (Mantel R>0.5 and P<0.01), we used partial Mantel tests to compare the relationships between community dissimilarity and the matrix of interest, while

controlling for the second matrix (Legendre & Legendre, 2012). We performed mantel tests and partial mantel tests correlating with the distance decay relationship using the total and deconstructed communities with environmental, resistance, and geographic distances. Despite the problems related to the use of Mantel test (e.g. Legendre et al. 2015), it was the only test that could be used in the context of landscape resistance, because the values are originally given in distances between sites and not are equivalent to spatial distances (Kärnä et al. 2015).

We also fitted general linear models to assess the intercept of the relationships to represent the initial similarity (IS) (Soininen et al 2007, Saito et al. 2015). To test whether IS was different or not from chance alone, we randomized the community using the independent swap algorithm, which maintains species occurrence frequency and the sampled species richness, being more conservative to reject null hypothesis (Gotelli 2000). We simulated 1000 communities for each community approach. The observed values of IS were considered different from the null generated IS when they were lower or higher than the 2.5 and 97.5 percentiles, corresponding to two-tailed test with an alpha value of 0.05 (Saito et al. 2015). Simulations were performed in "picante" package (Kembel et al. 2010).

Results

We sampled 72 Odonata species in 98 streams. Considering the body size and thermoregulation ability (table 1), we classified 42 species as low dispersal capacity and 30 species as high dispersal capacity. Environmental distances were not correlated with the geographic and landscape resistance. Geographical and landscape resistance distances were moderately correlated (Mantel r=0.54, p<0.001) for these two distances, we performed partial mantel correlation controlling for the effect of resistance on Euclidean distances and vice-versa.

Table 2:Summary of results of mantel correlation and partial mantel for Odonata community. The subsets represent biological traits related to dispersal capacity. Values with (*) indicate significant distance decay relationships.

		N	Environment	Resistance	Resistance	Euclidian	Euclidean
		11	Ziiviioimiene	resistance	pure	Zuellaluli	pure
Total		4753	0.093*	0.242***	-0,062	0.523***	0.4812***
Dispersal capacity	Low	3240	-0,045	0.221***	-0,113	0.517***	0.489***
	High	4095	0.117*	0.208**	0,029	0.337**	0.272**
			*p<0.05	**p<0.01	***p<0.001		

Geographic distances and landscape resistance were correlated with community dissimilarity for total community and both high and low dispersal capacity (Table 2). Environment distance show low correlation with community dissimilarity for total community and for high dispersal. However, when controlled for geographic effects, resistance was not correlated with community dissimilarity (total, high and low), whereas geographic distances maintain a correlation with community dissimilarity, with a small decrease of correlation (Table 2). The relationship between dissimilarity matrices (total, low and high dispersal) and distance predictors (environment, Euclidian distance and landscape resistance) are showed figure 2 when statistically significant.

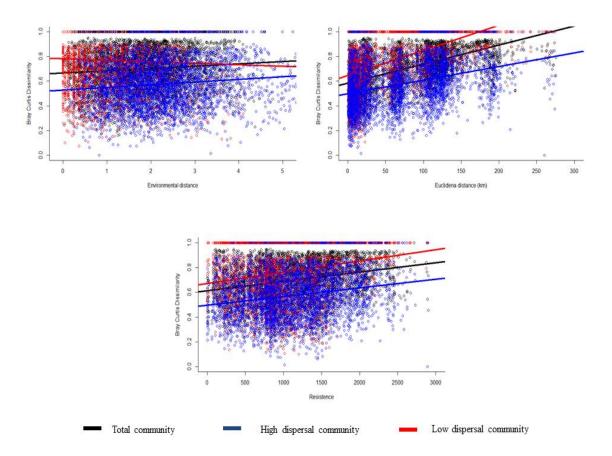


Figure 2: Distance decay which significant value between dissimilarity matrices (total, low and high dispersal) and distance predictors (environment, Euclidian distance and landscape resistance).

The initial dissimilarity (ID), was lower than expected by chance for geographic and resistance distances. For environmental distances, ID was only different from chance for total community and for high dispersal. Considering the landscape resistance and Euclidian distance the ID was significant for total community and for deconstructing communities (high and slow dispersal capacity) (Table 3).

Table 3: Initial dissimilarity (ID). Values intercepts of generalized linear model (GLM) between total and deconstructed community distances with environment, landscape resistance and geographic distance. Value refer to those observed communities and the

average of the communities generated by 1000 simulations communities, with algorithm "independentswap" (Gotelli. 2000). Significant relationship in communities obtained by the mantel test are represented in bold.

		Environment		Landscape resistance			Euclidian distance			
		DI Null DI p-value		DI Null DI p-value		DI Null DI p-va		p-value		
	Total	0,665	0,688	0,017	0,612	0,667	0,001	0,585	0,669	<0.001
Dispersion capacity	Low	0,781	0,784	0,431	0,672	0,763	<0.001	0,645	0,769	<0.001
	High	0,528	0,594	<0.001	0,496	0,567	0,001	0,498	0,573	<0.001

The landscape resistance was correlated with geographical distance. However, there is a wide range in the landscape resistance in short geographical distances (Euclidian distances), especially for species with low dispersion capacity, showing that landscape resistance has a weak correlation with the geographical distances in small distances (figure 3).

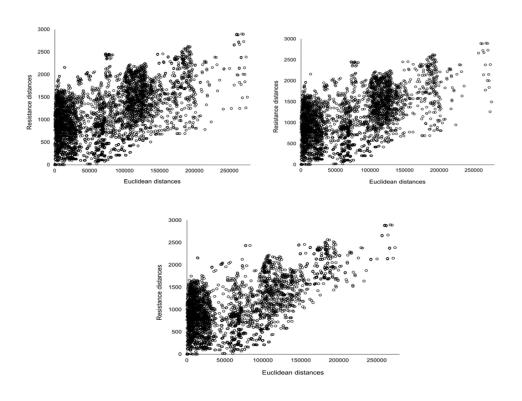


Figure 3: Correlation between geographic distance (Euclidian distances) and landscape resistance. A) total community B) high dispersers and C) low dispersers.

Discussion

Different types of distances (e.g. environmental, geographical, topographic, network and resistance landscape) have been used to explain the dissimilarity between communities (Brown & Swan 2010, Canedo-Arguelles et al. 2015, Heino et al 2014, Kärnä et al. 2015). Considering the total community, our results corroborate previous findings that assemblage similarity decays with increasing spatial and environmental distance between sites (e.g. Nekola & White 1999, Thompson & Townsend 2006, Brown & Swan 2010, Heino & Soininen 2010, Cãnedo-Arguelles et al. 2015, Kärnä et al. 2015, Saito et al. 2015). When deconstructing our community in dispersal capacity our results reveal important patterns that were masked when pooling all species together. First, the environmental distance was more correlated with community dissimilarity of high dispersal compared to total community. Second the initial dissimilarity is smaller compared to community deconstructed in high dispersal with the total community.

Geographic distance was correlated with dissimilarity in Odonata communities more strongly than environmental distance and landscape resistance. This finding partially supported our first hypothesis (H1). Studies have found noticeable differences in the magnitude of spatial structuring in the community composition among aquatic groups (Soininen et al. 2011, Astorga et al. 2012, De Bie et al. 2012, Wetzel et al. 2012, Heino et al. 2015). Odonata species have specific eco-morphological characteristics which can limit the dispersal capacity specially when landscape change is included (Remsburg & Turner 2009, Simaika & Samways 2009, De Marco et al. 2015). Both small species and conformers as many damselflies species, have low dispersal capacity.

In these cases the spatial distances are strong barriers for these species (Corbet 1999, Juen & De Marco 2011, De Marco et al 2015).

Considering that the dissimilarity of total community can be weaker than the community deconstructed, our second hypothesis (H2), we found that the environmental distance was more correlated with the community dissimilarity of high dispersal than with the total ones. Odonata species with high dispersal capacity can direct their flight and find suitable patches like which they emerged. It implies that the characteristics of the environment are essential for the maintenance of species with high dispersal capacity in the habitats (Corbet 1999, Bilton et al. 2001, Astorga et al. 2012). This can explain the relationship of environmental distances with the dissimilarity between high dispersal communities found in this study.

We did not find support for our third hypothesis (H3) expecting that low dispersion capacity will be more affect by landscape resistance. Low dispersers were more strongly associated with geographic distance. Small insect species may show more limited dispersal distances, increasing dispersal limitation effects on assemblage composition along optimal distance between sites (Heino et al. 2014, Kärnä et al. 2015). Odonates with low dispersion capacity present physiological and behavioral features (eg. thermoregulation ability) that difficult their dispersion in areas that differ from their natural environments (Juen & De Marco 2011, De Marco et al. 2015).

Considering the initial dissimilarity, our fourth hypothesis (H4), the results pointed out a low initial dissimilarity in high dispersal communities when compared to low dispersal communities. High dispersers can cross larger distances, colonizing distant places, then decreasing the effect of spatial distances (geographic distance and landscape resistance) and environmental distances between communities (Cañedo-Argüelles et al. 2015, De Marco et al. 2015, Dutra & De Marco 2015, Kärnä et al. 2015,

Saito et al. 2015). So, Odonata with high dispersal capacity have a small initial dissimilarity when comparing with species with low dispersal.

The landscape resistance had a considerable correlation in dissimilarity of communities (total, high and slow dispersion capacity). However, when we remove the parcel of explicability of Euclidian distances on Odonata beta diversity, we found no significant effect of landscape resistance on communities. Some studies have found low or none responses in the communities when considering the resistance measurements (Cañedo-Argüelles et al. 2015, Kärnä et al. 2015). We expected that areas with low resistance would have a smaller dissimilarity between communities (H1), especially for communities with high dispersal ability. However, the landscape resistance did not increase the explicability of the spatial processes compared the other spatial distance (Euclidian distance). In this sense, it is possible that in the region the landscape resistance is not strong enough to imprint a clear pattern of beta diversity in Odonata. In fact, the area is characterized by a mosaic of natural areas in a pasture matrix, so odanata species may use routes with smaller distances and not those with less resistance, even though unfavorable locations. Second, considering that the physical distance is one of the variables used for measuring the landscape resistance, we believe that this variable may be the most important measure accounting for landscape resistance to Odonata communities. We emphasize our landscape resistance measures on the configuration of habitat and non-habitat, which may be an oversimplification measure. In the other words, the Odonata community can respond to other factors that are not emphasized in our measure of resistance, as for example, proximity to aquatic environments and topographic distance.

Although our study did not show a better performance of the landscape resistance to detect spatial processes compared to geographic distance, we found a weak

correlation between landscape resistance and geographical distances in small distances and the wide range of landscape resistance in short distances (figure 3). This imply that landscape resistance can have an important role on the community structure in small geographical distances, mainly for low dispersers species. This shows that our landscape resistance proxies need to be more refined, as for example, minimum size of areas to be or not considered as habitat or dispersion routes, areas used as places for dispersion of the species and integrated more fully with information from the dispersal modes and distances actually travelled by organisms (Kärnä et al. 2015).

In this study, we conclude that the spatial and environmental distance control of Odonata community dissimilarity between sites, being the geographic distance more correlated with the Odonata community dissimilarity. The deconstruction of community in traits related dispersion capacity help us to understand the role of each distance for dissimilarity community, mainly the environmental distance with the high dispersal community. The use of resistance measurements and dispersion capacity must be more refined to get a better understanding of the role of geographical distance with landscape resistance in metacommunity studies.

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Final message

The use of different approaches for assessing the loss of Odonata species in aquatic environments as a consequence of native vegetation loss and land use changes in riparian zones, is essential to understand the effect of landscapes changes on Odonata community. Our results showed that community of Odonata species evidence nonlinear responses to land use change, and that deconstructed community of Odonata species according to traits related to dispersal ability and oviposition is essential to evaluate the effect of changes in natural landscapes on these communities. Different species traits can reveal important patterns that are masked when pooling all species together. It implies that there are critical initial filters, in our case, the native vegetation loss, that determine the occurrence of certain species with specific behaviors. In conclusion, the loss of native vegetation and changes on landscape configuration are drivers of Odonata communities change the Brazilian Cerrado, consequently the protection of remaining vegetation, specifically the riparian vegetation, is a key strategy to maintain the diversity of species and conserve the diversity of traits in communities associated to the interface between aquatic-and-terrestrial environments. Assessing the biodiversity status of native vegetation areas based on bioindicators is proving to be an important tool in ecology studies and information generated through this assessment is fundamental for assisting in the decision-making in conservation of species and especially of aquatic environments that are essential for maintaining a large part of the planet's biodiversity.

Appendix

List of articles published, manuscripts in revision and book resulted from different collaborative projects.

Articles

Published:

Rodrigues ME, Roque FO, Ochoa-Quintero JM, Pena JCC, Sousa DC & De Marco P. 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. Biological Conservation, 194, 113-120. http://dx.doi.org/10.1016/j.biocon.2015.12.001

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Koroiva R, Valente-Neto F, Rodrigues ME, Roque FO. 2016. As reveladoras libélulas da Bodoquena. Ciência Pantanal-Divulgação Científica, 26-27.

Saito VS, Valente-Neto F, Rodrigues ME, Roque FO, Siqueira T. Phylogenetic clustering among aggressive competitors: evidence from odonate assemblages along a riverine gradiente. Oecologia.

In review:

Valente-Neto F, Roque FO, Rodrigues ME, Siqueira T & Christopher Swan. Is metamorphosis a new beginning? Species sorting drives variation in both larval and adult odonates in a riverine network. Freshwater Biology.

Book

Fava WS; Zucca CF; Delatorre M; Valente-Neto F; Rodrigues ME; Paula G A; Araujo AC; Fischer E; Roque FO; Laps RR. (Eds). 2014. Ecologia do Pantanal curso de campo. Editora UFMS, Campo Grande. 387pp.