Hydrobiologia
https://doi.org/10.1007/s10750-021-04642-6

PRIMARY RESEARCH PAPER

A matter of suborder: are Zygoptera and Anisoptera larvae influenced by riparian vegetation in Neotropical Savanna streams?

Larissa F. R. Silva · Diego M. P. Castro · Leandro Juen · Marcos Callisto · Robert M. Hughes · Marcel G. Hermes

Received: 2 November 2020 / Revised: 9 June 2021 / Accepted: 12 June 2021

Abstract Initial Odonata larval distributions are primarily influenced by adult females at the moment of oviposition. However, after oviposition, the larvae are strongly associated with environmental conditions. In the case of both adults and larvae, anthropogenic disturbances that change these conditions may alter the composition and structure of Odonata assemblages. Therefore, based on the differing environmental requirements of Zygoptera and Anisoptera adults and larvae, together with their morphological and physiological differences, we suspected differing riparian preferences of larvae and adults for each suborder. We evaluated the richness and abundance of Odonata larvae. We hypothesized that Zygoptera larvae would have greater richness and abundance in streams with canopy shading, lower temperature ranges, and high physical habitat heterogeneity. On the other hand, Anisoptera larvae would be more abundant in streams without canopy cover. We sampled 186 headwater stream sites in the Neotropical Savanna along an anthropogenic disturbance gradient and used a model selection approach to test our hypotheses, correlating environmental metrics with Odonata larval richness and abundance. We found

Handling editor: Marcelo S. Moretti

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-021-04642-6.

L. F. R. Silva (✉) · M. G. Hermes
Laboratório de Sistemática e Biologia de Insetos, Setor de Zoologia Comparada, Departamento de Biologia, Universidade Federal de Lavras, CEP 37200-900 Lavras, Minas Gerais, Brazil
e-mail: larissamg05@hotmail.com

M. G. Hermes
e-mail: marcelhermes@ufla.br

D. M. P. Castro · M. Callisto
Laboratório de Ecologia de Bentos, Departamento de Genética, Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, CP 486, CEP 31270-901 Belo Horizonte Minas Gerais Brazil
e-mail: diegobioufla@gmail.com

M. Callisto
e-mail: callistom@ufmg.br

L. Juen
Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará, Av. Perimetral, 2-224, CEP 66077-830 Belém, Pará, Brazil
e-mail: leandrojuen@ufpa.br

R. M. Hughes
Amnis Opes Institute, 2895 SE Glenn Street, Corvallis, OR 97333, USA
e-mail: hughes.bob@amnisopes.com

R. M. Hughes
Department of Fisheries, Wildlife, & Environmental Sciences, Oregon State University, Nash 104, Corvallis, OR 97331, USA

Published online: 23 June 2021

higher richness of Zygoptera larvae in shaded sites with canopy cover > 5 m high, whereas bare ground without riparian vegetation was important for Anisoptera richness and abundance. Our results indicated that Odonata larvae follow the same distribution, richness and abundance patterns as adults. Anthropogenic disturbances related to the removal or reduction of riparian vegetation can favor Anisoptera over Zygoptera larval assemblages in streams. Preserving riparian canopy cover is needed to maintain the richness of Zygoptera larvae in Neotropical Savanna streams.

Keywords Cerrado streams · Damselflies · Dragonflies · GLM · Immatures · Odonata

Introduction

Insects show macroecological patterns related to thermal tolerance, body size, niche range, and dispersion capacity—all of which determine species distributions. For example, body size is related to dispersion capacity and regulated by temperature (Oliveira-Junior et al., 2017; Rocha-Ortega et al., 2020). Although insects can grow and mature over wide temperature ranges (from 10 to 20°C to maximum 40 to 50°C) (Neven, 2000; Dixon et al., 2009), in general, those with smaller body sizes live at higher temperatures, whereas those with larger body sizes can persist at lower temperatures (Chown & Gaston, 2010). When conditions like temperature are adverse, it is their dispersion capacity that allows insects to change habitat locations (Rocha-Ortega et al., 2020; Firmiano et al., 2021).

Adult Odonata respond differently to anthropogenic disturbances, according to Adult Anisoptera and Zygoptera respond differently to anthropogenic disturbances. Those differences result from a combination of physiological (e.g., thermoregulation), ecological (e.g., niche range and dispersion capacity), and morphological (e.g., body size) factors (Mendes et al., 2015; Oliveira-Junior & Juen, 2019). Restrictions imposed mainly by body size and thermoregulation determine the distribution and structure of adult Odonata assemblages in Neotropical streams (De Marco et al., 2015; Oliveira-Junior & Juen, 2019). Headwater streams with lower temperatures and dense canopy cover favor adult Odonata assemblages composed predominantly by Zygoptera (De Marco et al., 2015; Oliveira-Junior et al., 2017; Oliveira-Junior & Juen, 2019). On the other hand, Anisoptera species tend to dominate in larger streams that are less shaded (Vannote et al., 1980) and in streams where riparian vegetation has been removed (De Marco et al., 2015). In heavily degraded streams, even Anisoptera species cannot survive (Monteiro Júnior et al., 2015). This pattern of adult Odonata suborders is well established for the neotropics (De Marco et al., 2015; Oliveira-Junior & Juen, 2019).

Because larvae are strongly associated with environmental conditions, the anthropogenic disturbances that change these conditions may alter the composition and structure of Odonata larval assemblages (Souza et al., 2015; Luke et al., 2017; Mendes et al., 2019; Pires et al., 2020). Odonata larvae have some advantages over adults as bioindicators, including limited dispersion capacity, which makes them more susceptible to local changes (Valente-Neto et al., 2016) and easier field sampling (Oertli, 2008). Also, the larvae clearly differ in their morphologies. Zygoptera larvae have more delicate bodies and breathe through relatively delicate external lamellae (Corbet, 1980). Anisoptera larvae have more robust bodies, breathe through rectal tracheal gills (Corbet, 1980), and possess morphological structures that help defend them against predators (De Marco et al., 2015; Mendes et al., 2019).

Based on the different environmental requirements of Zygoptera and Anisoptera adults, we evaluated the distribution patterns of Odonata larvae along a gradient of riparian disturbance in Neotropical Savanna streams. We hypothesized that Odonata larvae would display the same patterns as Odonata adults. We expected that Zygoptera would have higher taxa richness and proportional abundances in sites with minimal riparian disturbance, considerable canopy shading, lower temperature range, and high physical habitat heterogeneity. Conversely, we expected that Anisoptera larvae would have higher taxa richness and proportional abundances in sites with less canopy cover or without riparian vegetation.

Methods

Study area and survey design

We studied 160 randomly selected 1st to 3rd order (Strahler, 1957) stream sites in the Nova Ponte, Volta Grande, São Simão and Três Marias hydrological units (Fig. 1; Table S1). The sampled sites exhibited a wide disturbance gradient, from minimally disturbed sites with high dissolved oxygen and low nutrient concentrations, sites with moderate levels of human-altered land (pasture, row crops) to highly degraded urban sites with poor water quality and physical habitat conditions (Macedo et al., 2014; Silva et al., 2017). We sampled each of the hydrological units in September (2010 in Três Marias, 2011 in Volta Grande, 2012 in São Simão, and 2013 in Nova Ponte), ensuring that samples were all taken in the low flow

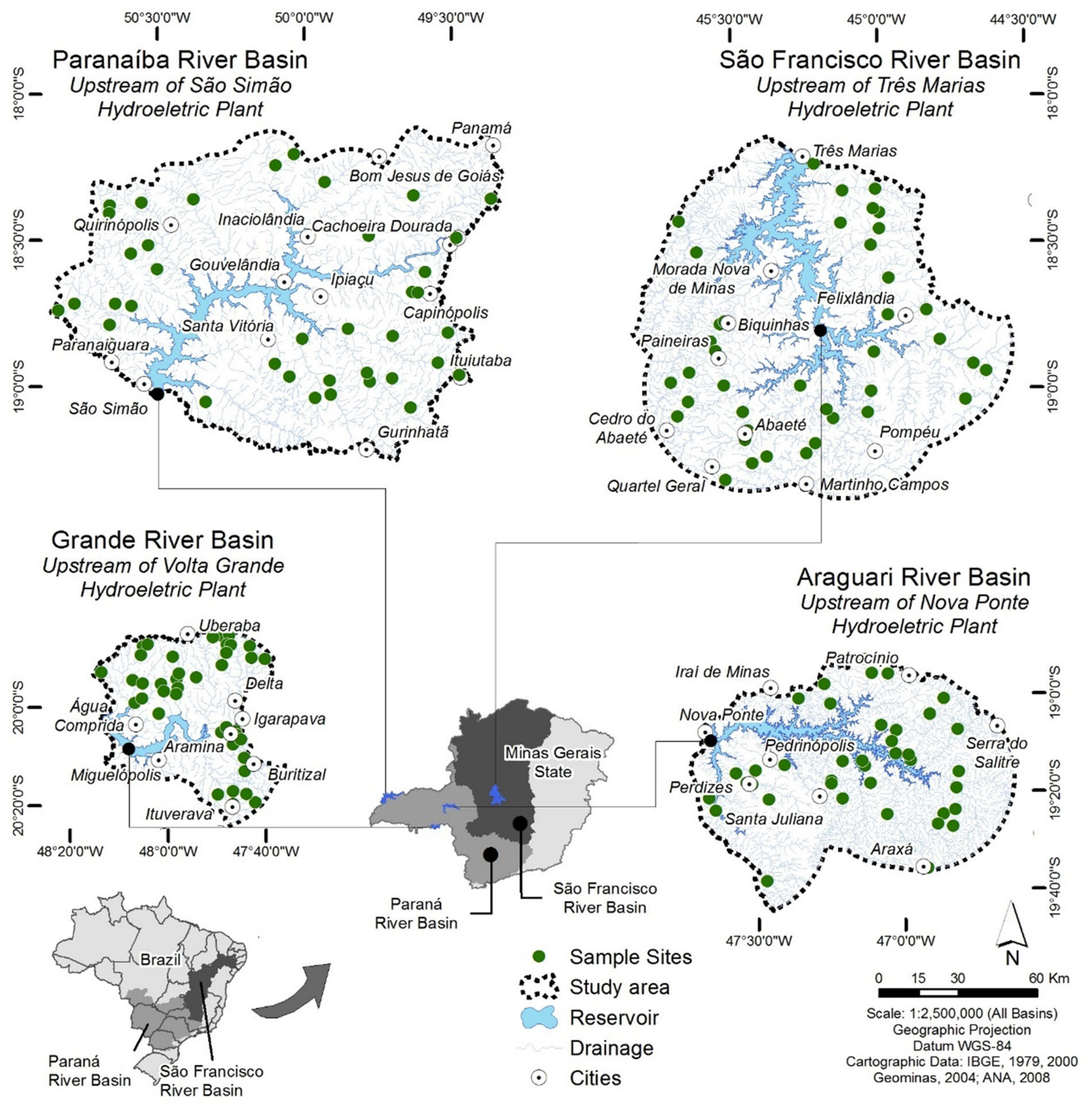

Fig. 1 Locations of the Cerrado stream sites and hydrological units

season. An additional set of 26 reference sites were sampled in April and May 2014, in Serra da Canastra National Park and Serra do Salitre. Those sites differed by exhibiting minimal human catchment disturbance, absence of direct anthropogenic disturbances at the sites, and the presence of native riparian vegetation (Martins et al., 2018).

Sampling of Odonata larvae

In each hydrological unit, we sampled 40 stream sites. Site selection followed a probabilistic sampling design, according to the methodology used by the U.S. Environmental Protection Agency (Peck et al., 2006; Callisto et al., 2014). This design allows the impartial selection of sampling sites representing the region as a whole, avoiding bias in site selection and spatial autocorrelation (Silva et al., 2018).

The length of each site was 40 times its mean wetted width, respecting a minimum of 150 m, and divided into 11 equidistant transects. Odonata larvae were sampled with a kick-net sampler (500 µm mesh, 0.09 m^2 area), following a zigzag trajectory across the transects (left, center, and right). The samples were fixed in 4% formalin. In the laboratory, samples were washed, stored in 70% alcohol, processed and then deposited in the reference collection of the Instituto de Ciências Biológicas of the Universidade Federal de Minas Gerais.

Odonata larvae were examined under a stereoscopic microscope and identified to genus using taxonomic keys (Costa et al., 2004; Neiss & Hamada, 2014; Pessacq et al., 2018) as well as descriptions and reviews available for each taxon. We identified larvae to genus because the larval stages of most species are not described (von Ellenrieder, 2009) and the genus level is sufficient to evaluate the responses of Odonata assemblages to anthropogenic disturbances (Mendes et al., 2019).

Environmental metrics

Environmental metrics at each site were described in terms of local riparian vegetation cover based on Stoddard et al. (2005) and Peck et al. (2006). This protocol assesses metrics related to physical habitat structure, near-stream anthropogenic stressors, and riparian vegetation structure and cover. We selected 11 metrics related to riparian vegetation (Kaufmann et al., 1999), and also calculated local, catchment, and integrated disturbance indices (Ligeiro et al., 2013), totaling 14 predictor variables as described below (Table S2). These metrics have been successfully used in previous studies of these sites (Firmiano et al., 2017; Castro et al., 2018; Silva et al., 2018).

Canopy cover was determined at each of the 11 transects in each site. Four canopy cover measurements were taken: upstream, downstream, right, and left at mid-channel. For this, we used a hemispherical convex densiometer, in which readings potentially varied from zero (without canopy cover) to 17 (maximum canopy cover). The measurements were made at 0.3 m above the water surface, observing the 17 intersection points of the grid on the densiometer. If the reflection of a tree or tall branch or leaf overlaps any intersection points, that specific intersection is counted as having coverage. The mid-channel measurements are used to estimate the canopy coverage over the channel (XCDENMID).

Riparian vegetation structure was determined through visual estimation, with a semi-quantitative assessment of the type and amount of riparian vegetation. Observations were made at both margins in each of the 11 cross-sections, 5-m upstream, 5-m downstream and 10-m landward, creating a 10 × 10 m plot on each side of the stream. Within this plot, we divided riparian vegetation into three layers: canopy (> 5 m high), understory (0.5–5 m high), and ground-cover (< 0.5 m high). In each layer, we determined the class of covered area in large trees (> 0.3 m diameter at breast height) and small trees (< 0.3 m). These data were used to calculate: mean woody canopy cover (XC), mean woody understory cover (XM), mean woody ground layer cover (XG) and bare ground cover (XGB) (Kaufmann et al., 1999).

To assess local and catchment anthropogenic disturbances in each site, we calculated three indices: Local Disturbance Index (LDI), Catchment Disturbance Index (CDI), and Integrated Disturbance Index (IDI) based on Ligeiro et al. (2013).

Data analyses

We calculated ten biological metrics for each site: total Odonata richness and abundance (combining the two suborders); Anisoptera richness and abundance; Zygoptera richness and abundance; proportional richness and abundance of Anisoptera; and proportional richness and abundance of Zygoptera (Table S3). The combined statistical analysis of the two suborders may lead to misinterpretations about what affects these assemblages, which can be avoided if each suborder is analyzed separately (Oliveira-Junior et al., 2015; Mendes et al., 2017).

To explore our hypothesis that riparian vegetation condition affects the distribution of Odonata larvae along a gradient of anthropogenic disturbance, we used a model selection approach (Burnham & Anderson, 2002). First, we tested for Spearman correlations among environmental metrics (Fig. S1), eliminating those that were highly correlated ($r > 0.7$) and retaining those that are the most ecologically relevant. In this step, we retained seven environmental metrics (Table 1). We used our selected variables as predictor variables with each biological metric in generalized linear models (GLMs). For count biological metrics (i.e., richness and abundance), we used a Poisson distribution. Using our most parameterized model, we evaluated a possible overdispersion in each analysis. Once overdispersion was detected, standard errors were corrected using a quasi-Poisson error structure. We next used a binomial or quasi-binomial distribution model for the proportional richness of Anisoptera versus the proportional richness of Zygoptera, and the proportional abundance of Anisoptera versus the proportional abundance of Zygoptera. We then constructed models based on all possible additive variable combinations followed by a model selection procedure using backward elimination to obtain the most parsimonious model. The selected model significance was tested by an Analysis of Deviance (Chi-squared for Poisson or quasi-Poisson distributions and F-test for binomial or quasi-binomial distributions). We checked model residuals using the DHARMa package (Hartig, 2018). All analyses were performed in R version 3.4.3 (R Core Team, 2017), using the Vegan (Oksanen et al., 2019) and lme4 (Bates et al., 2015) packages.

Results

We collected and identified a total of 3209 Odonata larvae, distributed along 30 genera and ten families. Fifteen hundred individuals, eight genera and six families belonged to Zygoptera; 1709 individuals, 22 genera and four families belonged to Anisoptera (Tables S4, S5). After initial model selection, the candidate metrics IDI, LDI, XCDENMID, XM and XG were excluded because none of them were significantly related to the biological metrics.

For total Odonata larval richness, no model was statistically significant. However, when testing Zygoptera and Anisoptera richness separately, models showed a positive relation between Zygoptera and mean canopy cover (XC) ($x^2 = 8.954$, $df = 174$,

Table 1 Environmental metrics used in the generalized linear models (GLM)

Acronyms	Environmental metrics' name	Meaning of environmental metrics	References
IDI	Integrated Disturbance Index	LDI & CDI	Ligeiro et al. (2013)
LDI	Local Disturbance Index	All types of riparian anthropogenic disturbance	Ligeiro et al. (2013)
XCDENMID	Canopy cover midstream	% vegetation covers the middle of the channel	Kaufmann et al. (1999) and Peck et al. (2006)
XGB	Bare ground cover	% exposed soil	Kaufmann et al. (1999) and Peck et al. (2006)
XC	Mean canopy cover	Woody vegetation > 5 m high	Kaufmann et al. (1999) and Peck et al. (2006)
XM	Mean understory cover	Woody vegetation 0.5 to 5 m high	Kaufmann et al. (1999) and Peck et al. (2006)
XG	Mean ground-layer cover	Woody ground cover < 0.5 m high	Kaufmann et al. (1999) and Peck et al. (2006)

$N = 175$, $P = 0.003$) and a positive relation for Anisoptera and bare ground cover (XGB) ($x^2 = 14.206$, $df = 174$, $N = 175$, $p < 0.001$) (Fig. 2).

For total Odonata larval abundance, a model showed a positive relation with bare ground cover ($x^2 = 122.53$, $df = 174$, $N = 175$, $P = 0.004$). However, when testing Zygoptera and Anisoptera abundance separately, no model was statistically significant for Zygoptera, but Anisoptera showed a positive relation with bare ground cover ($x^2 = 95.312$, $df = 174$, $N = 175$, $P = 0.001$) (Fig. 3).

For Zygoptera proportional taxa richness, a model showed a negative relation with bare ground cover ($x^2 = 14.966$, $df = 174$, $N = 175$, $p < 0.001$) and a positive relation with mean canopy cover ($x^2 = 6.255$, $df = 174$, $N = 175$, $P = 0.005$) (Fig. 4 A). Reverse relationships were observed for Anisoptera proportional taxa richness with bare ground cover ($x^2 = 14.966$, $df = 174$, $N = 175$, $p < 0.001$) and mean canopy cover ($x^2 = 6.255$, $df = 174$, $N = 175$, $P = 0.005$) (Fig. 4 B). No model was statistically significant for proportional individual abundances of Anisoptera or Zygoptera.

Discussion

We found congruences between the patterns of distribution, richness and abundance shown by larvae in this study with those documented for Zygoptera and Anisoptera adults in the literature. Our results corroborate the prediction that Zygoptera larvae have greater richness in streams with minimal human disturbances of riparian vegetation canopy cover. We also corroborate the prediction that Anisoptera larvae have greater richness and abundance in streams with less canopy cover or without riparian vegetation, indicated by bare ground cover.

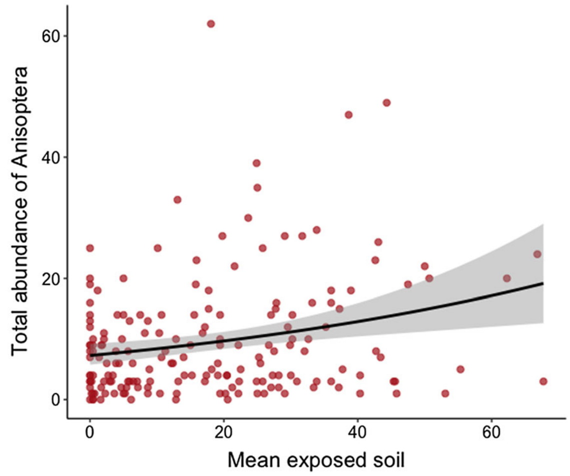

Fig. 3 Poisson GLM relation between mean exposed soil versus Anisoptera total abundance. The dark line indicates predicted values; dots indicate observed values, and the grey band indicates 95% confidence intervals

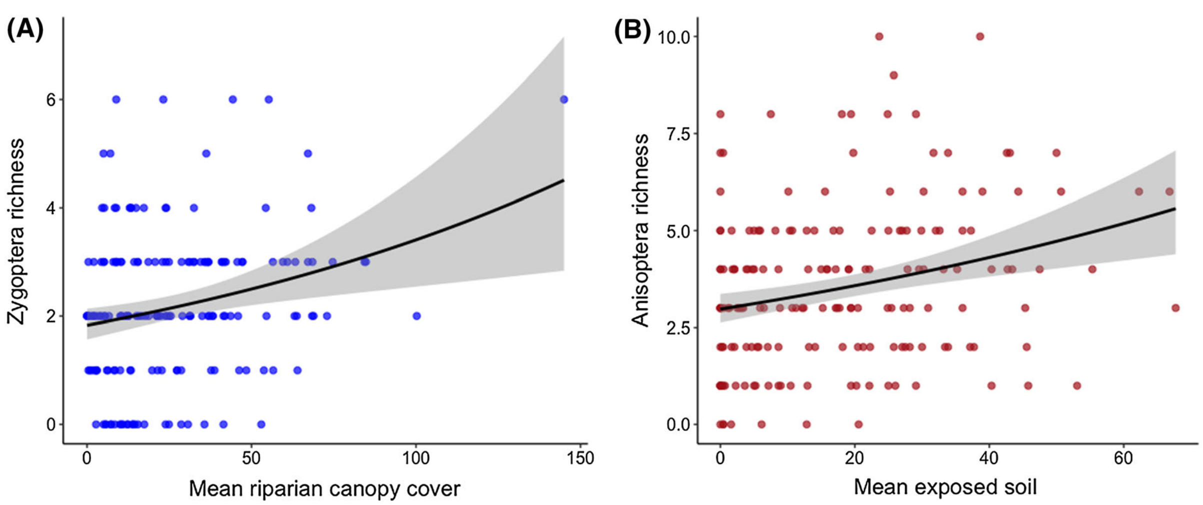

Fig. 2 Poisson GLM relationships between mean riparian canopy cover versus Zygoptera richness (**A**) and mean exposed soil versus Anisoptera richness (**B**). The dark line indicates predicted values; dots indicate observed values, and the grey band indicates 95% confidence intervals

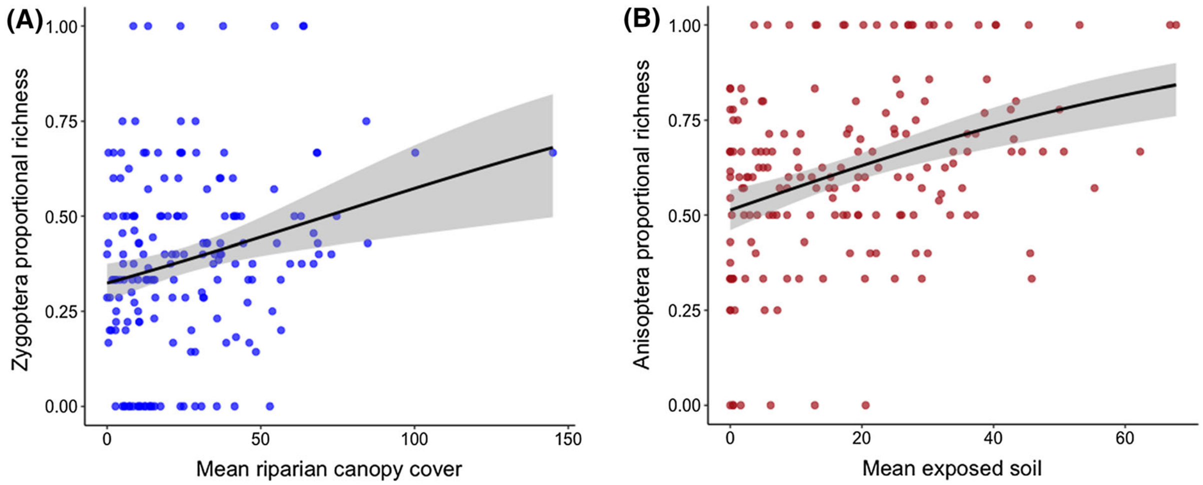

Fig. 4 Binomial GLM relationships between mean riparian canopy cover versus Zygoptera proportional richness (**A**) and mean exposed soil versus Anisoptera proportional richness (**B**). The figures for mean exposed soil versus proportional Zygoptera taxa richness and mean riparian canopy cover versus proportional Anisoptera taxa richness are not shown because they are inversely proportional. The dark line indicates predicted values; dots indicate observed values, and the grey band indicates 95% confidence intervals

Initial Odonata larval distribution is related to adult females' choices of ovipositing location (Corbet, 1980). There is strong selective pressure for oviposition in habitats where the larval survival rate is high, and for this, these habitats must match the ecological requirements, habitats, and behavior of the larvae (Buskirk & Sherman, 1985). After oviposition, larval establishment in the habitat depends on the morphological and behavioral traits of the species as well as on environmental features (Corbet, 1980). The species traits are related mainly to breathing, feeding, and refuge (Corbet, 1980) whereas key environmental features are water quality (Oertli, 2008; Mendes et al., 2015; Souza et al., 2015), substrate composition (Assis et al., 2004; Pires et al., 2020), and riparian vegetation (Remsburg & Turner, 2009; Mendes et al., 2019; Pires et al., 2020). Although oviposition is a female choice, the presence of larvae in the water guarantees that they are living there or nearby (Luke et al., 2017) and, therefore, are being influenced by site environmental conditions. In addition, larval stages are more restrictive because they tend to be much less mobile than adults (Oertli, 2008) and consequently more susceptible to environmental conditions.

In our study, anthropogenic disturbance in the riparian vegetation affected Odonata assemblages more than various anthropogenic disturbances in the local area and catchment, as evaluated by IDI and LDI. This is likely because water quality conditions and site vegetation structure affect Odonata larvae more than other types of environmental disturbances (Luke et al., 2017; Pires et al., 2020).

Zygoptera and Anisoptera larvae have physiological (Neiss & Hamada, 2014) and ecological (Mendes et al., 2017) differences that drive their different responses to riparian vegetation structure. For Zygoptera larvae, riparian vegetation is important because higher density and canopy cover provides greater stream shading and moderated water temperatures (Samways & Steytler, 1996; Peck et al., 2006). Waters with lower temperatures and higher dissolved oxygen provide better conditions for larval survival (Jooste et al., 2020). Zygoptera larvae breathe mostly using their caudal lamellae (Ramirez, 2010), which requires higher levels of dissolved oxygen in the water. Although we did not test for differences in water temperature and dissolved oxygen directly, these variables are affected by riparian vegetation canopy cover, and consequently, the assemblage of Zygoptera larvae may also be affected.

Besides breathing, larval Zygoptera use riparian vegetation for hunting, as predator refuges, and crawling out of the water to emerge as adults (Jooste et al., 2020). Some larvae hold onto overhanging pieces of vegetation, branches or leaves, that hang submerged in the stream, and remain motionless. The combination of vegetation and motionlessness provides refuge against visual aquatic and aerial predators. At the same time, it provides camouflage to facilitate capturing their prey (Sesterhenn et al., 2013). In short, removal of riparian vegetation and open canopies lead to low richness and abundance of Zygoptera adults and larvae (Mendes et al., 2015; Oliveira-Junior et al., 2019).

Unlike Zygoptera, Anisoptera larvae breathe with rectal gills in the internal abdominal cavity, filling and emptying the abdomen with water (Ramirez, 2010). The gill physiology increases capture of dissolved oxygen (Kohnert et al., 2004), facilitating survival in waters with low dissolved oxygen concentrations. Moreover, most Anisoptera larvae live buried or semi-buried in sandy and muddy substrates (Carvalho & Nessimian, 1998). This substrate type is correlated with erosion, frequently caused by removal of riparian vegetation (Wood & Armitage, 1997). Removal of riparian vegetation also may lead to an increase in stream macrophyte biomass (Fares et al., 2020), which is an important predictor of Anisoptera larvae occurrence (Juen et al., 2007). The presence of thermoreceptors in Libellulidae larvae (Rebora et al., 2007) suggests why Anisoptera larvae can remain in unshaded aquatic environments and why bare ground cover was a significant predictor for this suborder. French & McCauley (2018) evaluated the importance of canopy cover for Anisoptera larvae and adults and found no effect on larval survival. Thus, dense canopy cover could reduce adult oviposition, thereby affecting larval distribution.

The amount of riparian vegetation is important for Odonata adults because of their different thermoregulation mechanisms (De Marco et al., 2015; Oliveira-Junior & Juen, 2019). In general, Zygoptera species have smaller body sizes and are known as "thermal conformers", that is, their body temperature is directly influenced by air temperature (May, 1976; De Marco & Resende, 2002). Most of them cannot survive near streams where there is little or no riparian vegetation because the shading is less, the solar incidence is increased and temperatures oscillate more, causing overheating and desiccation (Oliveira-Junior et al., 2017; Oliveira-Junior & Juen, 2019). On the other hand, Anisoptera species are larger and endothermic, that is, they generate and store heat in the body and control the circulation of hemolymph to facilitate thermoregulation (May, 1976; De Marco & Resende, 2002). They do not depend on the presence of riparian vegetation to control their body temperature and can thrive such environments without dessication (Oliveira-Junior et al., 2017; Oliveira-Junior & Juen, 2019). Previous studies concluded that adult Zygoptera assemblages were bioindicators for the loss of riparian vegetation (Carvalho et al., 2013; Monteiro Júnior et al., 2015; Oliveira-Junior et al., 2017). In our study, the positive correlation between Zygoptera larvae and mean canopy cover indicated that they were also highly sensitive to removing riparian vegetation, following the pattern observed for adults. The opposite is true for Anisoptera larvae, which were tolerant to riparian vegetation removal, similarly to adults (Oliveira-Junior et al., 2017).

Also, it is important to recognize that the proportion of each suborder in larval Odonata assemblages could be used for assessing environmental impacts, without necessarily identifying individuals to genus or species levels. The same was true for the proportion of each suborder in adult Odonata assemblages (Oliveira-Junior et al., 2017; Oliveira-Junior & Juen, 2019). This makes the proportions of Odonata suborders useful for Neotropical biomonitoring programs, including those implemented by citizen scientists (França et al., 2019), because the two suborders are easily identified by eye.

For conservation purposes, it is important to determine the thresholds of riparian vegetation loss affecting the assemblages of Odonata larvae in Neotropical streams. Anisoptera can persist in streams with riparian vegetation width < 15 m, whereas Zygoptera genera require riparian vegetation widths > 15 m (Pires et al., 2020). Our study indicated that riparian vegetation height was also important because canopy cover > 5 m was the metric that best explained larval Zygoptera richness and abundance. However, for larval Anisoptera, riparian vegetation height had no significance because they benefited from bare ground cover. This suggest that vegetated riparian buffers at least 5 m high and 15 m wide might suffice for sustaining Zygoptera taxa, despite somewhat disturbed catchments.

Conclusions

Odonata larvae followed the pattern of distribution and abundance shown by adults and were driven by the degree of riparian vegetation, especially canopy cover.

Zygoptera larvae exhibited higher richness and proportional richness in streams with increased levels of canopy cover. On the other hand, Anisoptera larvae showed higher abundance, richness, and proportional richness in streams surrounded by bare ground and decreased levels of riparian vegetation canopy cover. We conclude that anthropogenic removal or reduction of riparian vegetation can affect Odonata larval assemblages in Cerrado streams. Therefore, such metrics can be used for assessing environmental impacts related to riparian vegetation. Although it is not known exactly how much Neotropical riparian vegetation cover should be preserved so that it does not affect aquatic macroinvertebrate assemblages (Dala-Corte et al., 2020), for Odonata we have this information. We know that areas with reduced riparian vegetation have higher larval Anisoptera richness. On the other hand, streams with canopy cover < 5 m high should have their riparian vegetation preserved to maintain Zygoptera larval richness.

Acknowledgements The authors are grateful for continued funding by Programa Peixe Vivo of Companhia Energética de Minas Gerais (P&D Aneel-Cemig GT-487, and GT-599) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Ph.D. scholarship to LS. LJ, MC and MGH were awarded National Council for Scientific & Technological Development (CNPq) research productivity grants 304710/2019-9, 304060/2020-8 and 304102/2018-0. RMH received a Fulbright Brasil grant. DMPC received a postdoctoral scholarship from P&D Aneel-Cemig GT-611. Carlos B. M. Alves provided logistical support and Ulisses Neiss provided specimen identification. Colleagues from the Universidade Federal de Minas Gerais (UFMG), Universidade Federal de Lavras (UFLA), Centro Federal de Educação Tecnológica de Minas Gerais (CEFET-MG) and Pontifícia Universidade Católica de Minas Gerais (PUC-MINAS) helped with field sampling. Several colleagues from the Laboratório de Ecologia de Bentos ICB/UFMG helped with sample processing.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

References

Assis, J. C. F., A. L. Carvalho & J. L. Nessimian, 2004. Composição e preferência por microhábitat de imaturos de Odonata (Insecta) em um trecho de baixada do Rio Ubatiba, Maricá-RJ, Brasil. Revista Brasileira de Entomologia 48: 273–282.

Bates, D., M. Mächler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference. Springer, New York.

Buskirk, R. E. & K. J. Sherman, 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. Insect Behavioral Ecology 68: 39–51.

Callisto, M., R. M. Hughes, J. M. Lopes, & D. M. A. Castro, 2014. Ecological conditions in hydropower basins (1st ed.). Belo Horizonte: Companhia Energética de Minas Gerais.

Carvalho, A. L. & J. L. Nessimian, 1998. Odonata do estado do Rio de Janeiro, Brasil: hábitats e hábitos das larvas. Oecologia Brasiliensis 05: 3–28.

Carvalho, F. G., N. S. Pinto, J. M. B. de Oliveira Júnior & L. Juen, 2013. Effects of marginal vegetation removal on Odonata communities. Acta Limnologica Brasiliensia 25: 10–18.

Castro, D. M. P., S. Dolédec & M. Callisto, 2018. Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. Ecological Indicators 84: 573–582.

Chown, S. L. & K. J. Gaston, 2010. Body size variation in insects: a macroecological perspective. Biological Reviews 85: 139–169.

Corbet, P. S., 1980. Biology of Odonata. Annual Review of Entomology 25: 189–217.

Costa, J. M., L. O. I. Souza & B. B. Oldrini, 2004. Chave para identificação das famílias e gêneros das larvas conhecidas de Odonata do Brasil: Comentários e registros bibliográficos (Insecta, Odonata). Publicações Avulsas do Museu Nacional 99: 1–44.

Dala-Corte, R. B., A. S. Melo, T. Siqueira, L. M. Bini, R. T. Martins, A. M. Cunico, A. M. Pes, A. L. B. Magalhães, B. S. Godoy, C. G. Leal, C. S. Monteiro-Júnior, C. Stenert, D. M. P. Castro, D. R. Macedo, D. P. Lima-Junior, É. A. Gubiani, F. C. Massariol, F. B. Teresa, F. G. Becker, F. N. Souza, F. Valente-Neto, F. L. Souza, F. F. Salles, G. L. Brejão, J. G. Brito, J. R. S. Vitule, J. Simião-Ferreira, K. Dias-Silva, L. Albuquerque, L. Juen, L. Maltchik, L. Casatti, L. Montag, M. E. Rodrigues, M. Callisto, M. A. M. Nogueira, M. R. Santos, N. Hamada, P. A. Z. Pamplin, P. S. Pompeu, R. P. Leitão, R. Ruaro, R. Mariano, S. R. M. Couceiro, V. Abilhoa, V. C. Oliveira, Y. Shimano, Y. Moretto, Y. R. Súarez & F. O. Roque, 2020. Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. Journal of Applied Ecology 57: 1391–1402.

De Marco, P. & D. C. Resende, 2002. Activity patterns and thermoregulation in a tropical dragonfly assemblage. Odonatologica 31: 129–138.

De Marco, P., J. D. Batista & H. S. R. Cabette, 2015. Community assembly of adult odonates in tropical streams: an ecophysiological hypothesis. PLoS ONE 10: 1–17.

Dixon, A. F. G., A. Honěk, P. Keil, M. A. A. Kotela, A. L. Šizling & V. Jarošík, 2009. Relationship between the minimum and maximum temperature thresholds for development in insects. Functional Ecology 23: 257–264.

Fares, A. L. B., L. B. Calvão, N. R. Torres, E. S. C. Gurgel & T. S. Michelan, 2020. Environmental factors affect macrophyte diversity on amazonian aquatic ecosystems inserted in an anthropogenic landscape. Ecological Indicators 113:

Firmiano, K. R., M. Cañedo-Argüelles, C. Gutiérrez-Cánovas, D. R. Macedo, M. S. Linares, N. Bonada & M. Callisto, 2021. Land use and local environment affect macroinvertebrate metacommunity organization in neotropical stream networks. Journal of Biogeography 48: 479–491.

Firmiano, K. R., R. Ligeiro, D. R. Macedo, L. Juen, R. M. Hughes & M. Callisto, 2017. Mayfly bioindicator thresholds for several anthropogenic disturbances in neotropical savanna streams. Ecological Indicators 74: 276–284.

França, J. S., R. Solar, R. M. Hughes & M. Callisto, 2019. Student monitoring of the ecological quality of neotropical urban streams. Ambio 48: 867–878.

French, S. K. & S. J. McCauley, 2018. Canopy cover affects habitat selection by adult dragonflies. Hydrobiologia 818: 129–143.

Jooste, M. L., M. J. Samways & C. Deacon, 2020. Fluctuating pond water levels and aquatic insect persistence in a drought-prone Mediterranean-type climate. Hydrobiologia 847: 1315–1326.

Juen, L., H. S. R. Cabette & P. De Marco, 2007. Odonate assemblage structure in relation to basin and aquatic habitat structure in Pantanal wetlands. Hydrobiologia 579: 125–134.

Kaufmann, P. R., P. Levine, E. G. Robison, C. Seeliger, & D. V Peck, 1999. Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. U.S. Environmental Protection Agency, Washington, D.C.

Hartig, F., 2018. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.0. https://CRAN.Rproject.org/package=DHARMa.

Kohnert, S., S. F. Perry & A. Schmitz, 2004. Morphometric analysis of the larval branchial chamber in the dragonfly *Aeshna cyanea* Müller (Insecta, Odonata, Anisoptera). Journal of Morphology 261: 81–91.

Ligeiro, R., R. M. Hughes, P. R. Kaufmann, D. R. Macedo, K. R. Firmiano, W. R. Ferreira, D. Oliveira, A. S. Melo & M. Callisto, 2013. Defining quantitative stream disturbance gradients and the additive role of habitat variation to explain macroinvertebrate taxa richness. Ecological Indicators 25: 45–57.

Luke, S. H., R. A. Dow, S. Butler, C. Vun Khen, D. C. Aldridge, W. A. Foster & E. C. Turner, 2017. The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo. Freshwater Biology 62: 491–506.

Macedo, D. R., R. M. Hughes, R. Ligeiro, W. R. Ferreira, M. A. Castro, N. T. Junqueira, D. R. Oliveira, K. R. Firmiano, P. R. Kaufmann, P. S. Pompeu & M. Callisto, 2014. The relative influence of catchment and site variables on fish and macroinvertebrate richness in Cerrado biome streams. Landscape Ecology 29: 1001–1016.

Martins, I., R. Ligeiro, R. M. Hughes, D. R. Macedo & M. Callisto, 2018. Regionalisation is key to establishing reference conditions for neotropical savanna streams. Marine and Freshwater Research 69: 82–94.

May, M. L., 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecological Monographs 46: 1–32.

Mendes, T. P., H. S. R. Cabette & L. Juen, 2015. Setting boundaries: environmental and spatial effects on Odonata larvae distribution (Insecta). Anais da Academia Brasileira de Ciências 87: 239–248.

Mendes, T. P., J. M. B. Oliveira-Junior, H. S. R. Cabette, J. D. Batista & L. Juen, 2017. Congruence and the biomonitoring of aquatic ecosystems: are odonate larvae or adults the most effective for the evaluation of impacts. Neotropical Entomology 46: 631–641.

Mendes, T. P., N. L. Benone & L. Juen, 2019. To what extent can oil palm plantations in the Amazon support assemblages of Odonata larvae? Insect Conservation and Diversity 12: 448–458.

Monteiro Júnior, C. D. S., L. Juen & N. Hamada, 2015. Analysis of urban impacts on aquatic habitats in the central Amazon basin: adult odonates as bioindicators of environmental quality. Ecological Indicators 48: 303–311.

Neiss, U. G. & N. Hamada, 2014. Ordem Odonata. In: Hamada, N., J. L. Nessimian, & R. B. Querino (eds), Insetos Aquáticos na Amazônia brasileira: Taxonomia, biologia e ecologia. Instituto Nacional de Pesquisas da Amazônia, Manaus: 217–282.

Neven, L. G., 2000. Physiological responses of insects to heat. Postharvest Biology and Technology 21: 103–111.

Oertli, B., 2008. The use of dragonflies in the assessment and monitoring of aquatic habitats In: Córdoba-Aguilar, A. (ed), Dragonflies and damselflies: Model organisms for ecological and evolutionary research. Oxford: 79–95.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, & H. Wagner. 2019. Vegan: community ecology package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Oliveira-Junior, J. M. B. & L. Juen, 2019. The Zygoptera/Anisoptera ratio (Insecta: Odonata): a new tool for habitat alterations assessment in amazonian streams. Neotropical Entomology 48: 552–560.

Oliveira-Junior, J. M. B., Y. Shimano, T. A. Gardner, R. M. Hughes, P. de Marco Júnior & L. Juen, 2015. Neotropical dragonflies (Insecta: Odonata) as indicators of ecological condition of small streams in the eastern Amazon. Austral Ecology 40: 733–744.

Oliveira-Junior, J. M. B., P. De Marco, K. Dias-Silva, R. P. Leitão, C. G. Leal, P. S. Pompeu, T. A. Gardner, R. M. Hughes & L. Juen, 2017. Effects of human disturbance and riparian conditions on Odonata (Insecta) assemblages in eastern Amazon basin streams. Limnologica 66: 31–39.

Oliveira-Junior, J. M. B., K. Dias-Silva, M. A. Teodósio & L. Juen, 2019. The response of neotropical dragonflies (Insecta: Odonata) to local and regional abiotic factors in small streams of the Amazon. Insects 10: 446.

Peck, D. V., J. M. Lazorchak, & D. J. Klemm, 2006. Environmental Monitoring and Assessment Program-Surface Waters Western Pilot Study: Field Operations Manual for Wadeable Streams. Washington, D.C.

Pessacq, P., J. Múzon, & U. G. Neiss, 2018. Order Odonata. In: Hamada, N., J. H. Thorp, & D. C. Rogers (eds), Ecology and General Biology: Thorp and Covich's freshwater invertebrates. London: 355–494.

Pires, M. M., N. F. D. Müller, C. Stenert & L. Maltchik, 2020. Influence of different riparian vegetation widths and substrate types on the communities of larval Odonata (Insecta) in southern brazilian streams. Acta Limnologica Brasiliensia 32: 1–16.

R Core Team, 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. https://www.R-project.org/.

Ramirez, A., 2010. Capítulo 5: Odonata. Revista de Biologia Tropical 58: 97–136.

Rebora, M., S. Piersanti, T. J. Almaas & E. Gaino, 2007. Hygroreceptors in the larva of *Libellula depressa* (Odonata: Libellulidae). Journal of Insect Physiology 53: 550–558.

Remsburg, A. J. & M. G. Turner, 2009. Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. Journal of the North American Benthological Society 28: 44–56.

Rocha-Ortega, M., P. Rodríguez, J. Bried, J. Abbott & A. Córdoba-Aguilar, 2020. Why do bugs perish? Range size and local vulnerability traits as surrogates of Odonata extinction risk. Proceedings of the Royal Society B: Biological Sciences 287: 1–9.

Samways, M. J., & N. S. Steytler, 1996. Dragonfly (Odonata) distribution patterns in urban and forest landscape, and recommendations for riparian management. Biological Conservation 78(3): 279–288.

Sesterhenn, T. M., E. E. Reardon & L. J. Chapman, 2013. Hypoxia and lost gills: respiratory ecology of a temperate larval damselfly. Journal of Insect Physiology 59: 19–25.

Silva, D. R. O., A. T. Herlihy, R. M. Hughes & M. Callisto, 2017. An improved macroinvertebrate multimetric index for the assessment of wadeable streams in the neotropical savanna. Ecological Indicators 81: 514–525.

Silva, D. R. O., A. T. Herlihy, R. M. Hughes, D. R. Macedo & M. Callisto, 2018. Assessing the extent and relative risk of aquatic stressors on stream macroinvertebrate assemblages in the neotropical savanna. Science of the Total Environment 633: 179–188.

Souza, A., F. Fogaça, A. Cunico & J. Higuti, 2015. Does the habitat structure control the distribution and diversity of the Odonatofauna? Brazilian Journal of Biology 75: 598–606.

Strahler, A., 1957. Quantitative analysis of watershed geomorphology. Transactions, American Geophysical Union 38: 913–920.

Stoddard, J. L., D. V. Peck, A. R. Olsen, S. G. Paulsen, J. Van Sickle, A. T. Herlihy, P. R. Kaufmann, R. M. Hughes, T. R. Whittier, G. Lomnick, D. P. Larsen, S. A. Peterson, & P. L. Ringold, 2005. An ecological assessment of western streams and rivers. U.S. Environmental Protection Agency, Washington, DC. EPA. 620/R-05/005.

Valente-Neto, F., F. De Oliveira Roque, M. E. Rodrigues, L. Juen & C. M. Swan, 2016. Toward a practical use of neotropical odonates as bioindicators: testing congruence across taxonomic resolution and life stages. Ecological Indicators 61: 952–959.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

von Ellenrieder, N., 2009. Databasing dragonflies: state of knowledge in the neotropical region. Agrion 13: 58–72.

Wood, P. J. & P. D. Armitage, 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21: 2013–2017.