Neotropical dragonflies (Insecta: Odonata) as indicators of ecological condition of small streams in the eastern Amazon

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Abstract Sensitive and cost-effective indicators of aquatic ecosystem condition in Amazon streams are necessary to assess the effects of anthropogenic disturbances on those systems in a viable and ecologically meaningful manner. We conducted the present study in the municipality of Paragominas, state of Pará, northern Brazil, where we sampled adult dragonflies in 50 100-m-long wadeable stream sites in 2011. We collected 1769 specimens represented by 11 families, 41 genera and 97 species. The suborder Zygoptera contributed 961 individuals and Anisoptera 808. Among the 97 recorded species, nine were classified as useful indicators of ecological condition, with four species being associated with more degraded streams (three Anisoptera, one Zygoptera) and five with more preserved streams (all were Zygoptera). Anisoptera (dragonflies) tend to provide more useful indicators of more degraded environments because they have more efficient homeostatic mechanisms and are more mobile, enabling them to tolerate a wider range of environmental conditions. By contrast, Zygoptera (damselflies) tend to provide a more useful role as indicators of more preserved environments and high levels of environmental heterogeneity because of their smaller body sizes and home ranges and greater ecophysiological restrictions. We conclude from our assessment of this low-order Amazonian stream system that (i) the occurrence of specific odonate species is strongly associated with the configuration of riparian vegetation, (ii) agricultural activities appear to be the main factor determining changes in the composition of odonate assemblages and (iii) these insects can act as useful indicators of the ecological consequences of riparian habitat loss and disturbance. Because generalist species invade moderately degraded areas, those areas may have high species richness but host few species of Zygoptera. Therefore, preserving dense riparian vegetation is necessary to maintain aquatic ecological condition, and that condition can be rehabilitated by planting new trees. Both require enforcing existing environmental regulations, various types of incentives and educating local communities.

Key words: Anisoptera, bioindicator, disturbance, environmental alteration, land use, riparian conservation, Zygoptera.

INTRODUCTION

Human-modified landscapes vary from largely undisturbed areas with little evidence of human modification to severely degraded landscapes that comprise a complex mosaic of agricultural areas and fragmented and logged forest. Modified landscapes are also characterized by the clearance of, and disturbances to, riparian forests (Stoddard et al. 2006) that are crucial for protecting a variety of different ecosystem services including the maintenance of landscape-scale hydrological cycles and the conservation of aquatic biodiversity (Allan & Castillo 2007). Conversion of forests to agriculture also often leads to an increase in the sedimentation of aquatic ecosystems (Nakamura &
Yamada 2005), a degradation of physical habitat structure of the in-stream and near-stream environment (Monteiro-Júnior et al. 2013), and increased nutrient concentrations. The combination of all these changes can lead to a loss of biodiversity and the homogenization of aquatic ecosystems towards a subset of more resilient generalist taxa (Couceiro et al. 2011).

Widespread concerns regarding environmental disturbance and biodiversity loss have led to a demand for reliable and cost-effective approaches to assessing changes in ecological condition. However, many studies focus exclusively on a small number of direct abiotic environmental measurements (Silva et al. 2010), and it is necessary to include measures of biological indicators to assess the impacts of multiple disturbances, including pollution, habitat fragmentation and deforestation on the ecological condition of disturbed ecosystems (Gardner 2010). Because groups of indicator species aggregate the effects of multiple stressors during their lifetimes, they can serve as a partial surrogate for the community as a whole (Meffe & Carroll 1994) and can provide valuable guidance on the way in which natural resource management approaches can be improved (Smith et al. 2007).

Variations in the abundance and incidence of aquatic fauna have been shown to provide a useful approach for assessing changes in the biotic integrity of stream and other aquatic systems (Carvalho et al. 2013). Aquatic insects in particular have been used to demonstrate the effect of disturbance on aquatic environments (Blocksom & Johnson 2009; Leunda et al. 2009). However, in most studies, only the insects restricted to aquatic environments are considered and mainly at larval stages (Silva et al. 2010).

Among the many aquatic insect groups used as bioindicators, odonate distribution, richness and composition are known to be closely associated with changes in environmental features (Gerlach et al. 2013). Odonates have relatively long lives (up to 1 year in the tropics) (Stoks & Córdoba-Aguilar 2012), are broadly distributed in aquatic systems (Corbet 1999; Dolný et al. 2012), and have biphasic lifestyles with aquatic larvae and terrestrial/aerial adults (Oertli 2008). The fact that larval and adult odonates occupy two distinct environments means that they can provide valuable information of alterations to both aquatic and terrestrial conditions (Butler & de Maynadier 2008).

Studies relating odonate diversity with environmental changes have gained attention throughout the world (Clausnitzer et al. 2009). In South Africa, Simaika and Samways (2012) used a Dragonfly Biotic Index to assess stream biotic condition. In Indonesia, Dolný et al. (2011) evaluated the effect of habitat modification on the diversity of dragonflies in East Kalimantan, and in Central Europe (Czech Republic), Harabis and Dolný (2010) demonstrated the major ecological factors determining the density and distribution of odonate in all types of freshwater environments.

In recent years, an increasing number of studies of aquatic insects as bioindicators have been conducted in the Neotropics, but information about odonates is still scarce (Foote & Hornung 2005; Bried et al. 2007; Monteiro-Júnior et al. 2013). However, a number of studies have been aimed at evaluating patterns of assemblage structure in Neotropical odonates in response to environmental changes (Foote & Hornung 2005; Osborn 2005; Bried et al. 2007; Silva et al. 2010; Monteiro-Júnior et al. 2013).

Adult odonates can be divided into two groups with distinct ecophysiological requirements: perchers and fliers (Corbet 1999; Corbet & May 2008). Perchers are in general ectothermic: they use sunlight or the ambient temperature for heating. They can be thermal conformers or heliothermic. The conformers, small-sized Zygoptera (damsel flies) have high thermal conductance, and their body temperatures vary with ambient temperature, mainly by convective heat transfer (Heinrich & Casey 1978). Heliothermic odonates have larger body sizes (some Zygoptera and most Anisoptera; dragonflies) and, hence, lower conductance; their activity is determined mainly by sunlight incidence (Corbet & May 2008). Endothermic odonates that are classified as fliers (the largest Anisoptera species) produce heat by controlling haemolymph circulation (Corbet 1999; Sformo & Doak 2006).

De Marco and Resende (2002) demonstrated how physiological differences related to body size in the gradient from conformers to heliotherms may determine broad behavioural patterns among species, thus helping to understand species responses to environmental change. Because of the differing ecophysiological demands of odonate species, they are useful for assessing the biological effects of riparian disturbances and for setting conservation priorities for stream ecosystems (Osborn 2005; Simaika & Samways 2009).

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Here we used odonates to assess environmental impacts on the ecological condition of streams in the eastern Brazilian Amazon. Our hypothesis was that altered and degraded streams, which are characterized by brighter and warmer environments, would have a different composition of odonates than preserved streams. In particular, we expected that the Anisoptera (large-bodied) would be less specialized because of their thermoregulatory abilities (May 1991), greater dispersal capacity and low environmental specificity (McCauley 2007). On the other hand, we expected that the Zygoptera being thermal conformers (small bodied) would be more dependent on local environmental conditions and thus include a number of
habitat specialists (McCauley 2006), with lower levels of species richness in altered and degraded sites (Juen et al. 2007; Dolný et al. 2012) and more species in preserved environments (cooler environments with more shade) (Clausnitzer 2003).

METHODS

Study area

We studied 50 100-m-long stream sites in the municipality of Paragominas, state of Pará, northern Brazil (2°25′–4°09′S and 46°25′–48°54′W) (Gardner et al. 2013) (Fig. 1). Sampled streams were selected to encompass a broad gradient of landscape level forest cover (historical deforestation and restoration) and dominant land-uses, including agriculture, grazing, horticulture and forestry (Gardner et al. 2013).

According to the Köppen classification, the predominant climate in the region is ‘Af’, characterized by tropical rains, with a short dry season and rainfall below 60 mm in the driest month, annual average temperature of 27.2°C, relative humidity of 81% and average rainfall of 2000 mm year⁻¹. The period of lowest water availability occurs from June to December (Gardner et al. 2013). The local vegetation is classified as dense rainforest, also known as equatorial humid terra firme forest, open rainforest with lianas and palm trees, and alluvial dense rainforest, also known as equatorial humid várzea forest (Gardner et al. 2013).

Some large forest remnants remain in the region, with the largest area of primary forest belonging to a certified logging company in the southwestern region of the municipality (Gardner et al. 2013). Large tracts of pristine forest habitat represent the region’s original climax vegetation (preserved sites) (Gardner et al. 2013; Moura et al. 2013). The most deforested region is located in the central part of the municipality, around federal highway BR-010 (Gardner et al. 2013). Land uses range from new secondary forest, plantations of eucalypts (Eucalyptus sp.), teak (Tectona grandis) and Brazilian fire tree (Schizolobium parahyba var. amazonicum), pasture, small truck crop farms and large mechanized farms that typically produce rice and soybeans.

Data collection

Biological sampling

We sampled in the dry season, from June to August 2011. We chose this period because the intensity of precipitation during the rainy season hinders site access and the activity...
patterns of odonate adults (see May 1976; 1991; Corbet 1999). Studies in the Neotropics have shown that more individuals and species of adult and larval odonate can be found during the dry season than the wet season (Baptista et al. 2001; Fulan & Henry 2007). We always sampled the sites between 1000 and 1400 h, and only when sunlight reached the stream, because these conditions are necessary to ensure that all odonate groups (thermal conformers, heliothermic and endothermic) are active at the sample time (May 1991; De Marco & Resende 2002).

Each 100-m-long stream site was divided into 20 5-m-long segments for sampling. Odonate adults were sampled through use of an entomological net (diameter: 40 cm, depth: 65 cm) attached to a 90-cm-long aluminium handle. Each site was sampled for 1 h (De Marco 1998), 3 min in each segment. The distance between the sample points increases the probability of independence and minimizes the impact of collecting in one point on sampling effectiveness in another point. This method was used successfully in other studies (Juen & De Marco 2012; Calvão et al. 2013; Oliveira-Junior et al. 2013) and has been shown to be efficient for rapid assessments. We followed the protocol described by Lencioni (2006) to preserve specimens; data from all 20 segments were pooled to estimate local species richness but kept separate to inspect species accumulation curves.

For taxonomic identification, we used specialized keys (Borror 1945; Belle 1988, 1996; Garrison 1990; Lencioni 2005, 2006; Garrison et al. 2006, 2010) and compared museum specimens with collection vouchers. When necessary, we sent specimens to specialists. After identification, insect specimens were deposited in the Zoological Museum of the Universidade Federal do Pará, Belém, Brazil.

Assessment of site physical condition

We measured the temperature and relative humidity in a shady location, and we assessed stream physical habitat structure following the procedure described for calculating a Habitat Integrity Index (HII) (Nessimian et al. 2008). The application of this protocol was performed by a single collector in all study sites, to avoid bias and reduce sampling noise in the data. This protocol employs 12 metrics that assess: land use near the stream; width of the riparian forest and its conservation status; riparian forest condition within 10 m; substrate size; presence of large wood; structure and erosion of stream banks; bed complexity in terms of substrate, aquatic vegetation and debris; and mesohabitats (rapids, deep pools, meanders) present. Each metric of the habitat protocol has four to six ordered alternatives, which represent more degraded to more preserved systems. The HII scores can vary from 0 to 1, from degraded to preserved streams. The continuous scale was broken into high, intermediate and low scores. This index is directly related to the degree of environmental conservation and has been successfully used in other studies to evaluate aquatic system integrity (Pereira et al. 2012; Monteiro-Júnior et al. 2013; Monteiro-Júnior et al. 2014; Giehl et al. 2014). Our HII values varied from 0.28 to 0.96; hence, we classified the 50 streams into three arbitrary environmental condition categories (splitting the range equally into three): degraded (0.28–0.49; 19 sites), altered (0.50–0.75; 19 sites) and preserved (0.76–0.96; 12 sites). The sites ranged from first to third order (Strahler 1957), and they differed physically and chemically in terms of conservation status (Table 1).

<table>
<thead>
<tr>
<th>Environmental characteristics</th>
<th>Preserved</th>
<th>Altered</th>
<th>Degraded</th>
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<tbody>
<tr>
<td>PFR (%)</td>
<td>97.8</td>
<td>52.4</td>
<td>44.42</td>
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<tr>
<td>WT (°C)</td>
<td>24.4</td>
<td>25.11</td>
<td>26.35</td>
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<tr>
<td>DO (mg/L)</td>
<td>4.78</td>
<td>4.45</td>
<td>4.22</td>
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<tr>
<td>pH</td>
<td>5.14</td>
<td>5.49</td>
<td>5.39</td>
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<tr>
<td>CO μS/cm</td>
<td>27.32</td>
<td>33.16</td>
<td>33.76</td>
</tr>
<tr>
<td>Q (m3/s)</td>
<td>0.14</td>
<td>0.28</td>
<td>0.26</td>
</tr>
<tr>
<td>WV (m/s)</td>
<td>6.32</td>
<td>3.78</td>
<td>3.85</td>
</tr>
<tr>
<td>CW (m)</td>
<td>2.74</td>
<td>3.2</td>
<td>3.91</td>
</tr>
</tbody>
</table>

CO, conductivity; CW, channel width; DO, dissolved oxygen; PFR, % Primary Forest at Riparian Network 100 m buffer scale; Q, discharge; WT, water temperature; WV, water velocity.

Data analysis

To estimate species richness in individual sites, we used the non-parametric first-order Jackknife estimator (Colwell & Coddington 1994) and controlled for sampling effort. The sampling efficiency for odonates was tested with sample-based species accumulation curves and with species-area rarefaction by the Mao Tau method, using the same estimator with 1000 randomizations based on an increasing number of segments (1–20 segments per stream) (Colwell et al. 2004).

To minimize multicolinearity among environmental variables, a Pearson correlation matrix was constructed for all variables. When a correlation of 0.7 or more was found between two variables, only one was chosen for subsequent analysis. The relative importance of the 12 HII variables was
assessed through the use of principal component analysis (PCA). To determine which principal components would be retained for subsequent analysis, we used the degree of randomness calculated with the broken-stick model (Jackson 1993). The variable that contributed the most to the formation of the first axis of the PCA was used as the response variable to compare stream sites under different levels of conservation. To test for significant differences in environmental variables and species composition between the three arbitrary stream categories (preserved, altered and degraded), we applied permutational multivariate analysis of variance (PERMANOVA; Anderson & Walsh 2013), with 9999 replications.

To test differences in species richness based on conservation categories, we used inference based on the confidence interval of 95%. We also used the richness estimated by the first-order Jackknife (Gotelli & Colwell 2001), in which the groups were considered different when the confidence intervals did not overlap between groups.

We used the indicator value (IndVal) method to test whether some odonate species could be considered indicators of ecological condition (Dufrêne & Legendre 1997). This analysis was carried out separately for each species and estimates the fidelity (relative frequency) and specificity (relative abundance) of each species in relation to an environmental filter (Dufrêne & Legendre 1997), in this case our categorical variable of site conservation status: preserved, altered and degraded. A perfect indicator species should occur only in sites from a given category (specificity) and also in all sites of that given category (fidelity). We estimated significance of the IndVal with a Monte Carlo test with 10 000 randomizations ($P < 0.05$).

We estimated species richness through use of EstimateS 7.5.0 (Colwell 2005). The PERMANOVA was performed using the software Primer v.6 (Clarke & Gorley 2006) and we conducted the other analyses in R (R Development Core Team 2011), using the package Indicspecies for calculating the IndVal (De Cáceres et al. 2010).

RESULTS

Description of the odonate assemblage in the study region

We collected 1769 odonate individuals representing 11 families, 41 genera and 97 species. The suborder Zygoptera contributed 961 individuals in eight families (Calopterygidae, Coenagrionidae, Dictenidae, Megapodagrionidae, Perilestidae, Polythoridae, Protoneuridae and Pseudostigmatidae), 19 genera and 56 species. The Coenagrionidae was the most abundant Zygoptera family, with 343 individuals; the Argia was the most abundant genus ($n = 230$), followed by Acanthagrion ($n = 72$) and Tigriagrion ($n = 26$). The Anisoptera contributed 808 individuals in three families (Aeshnidae, Gomphidae and Libellulidae), 22 genera and 41 species. The Libellulidae was the most abundant Anisoptera family, with 787 individuals; the Erythrodiplax ($n = 375$), Oligoclada ($n = 136$) and Diastatops ($n = 105$) were the most abundant genera.

Species accumulation curves

None of the species accumulation curves (Jackknife 1) or species-area rarefaction curves (Mao Tau) reached an asymptote (Fig. 2). However, sampling efficiency was 79% (observed richness/estimated richness) (Jackknife 1) and 78% (Mao Tau) for odonates, 77% and 76% for Anisoptera, and 80% and 79% for Zygoptera. Those levels of sampling efficiency indicate that the sampling effort is adequate for making meaningful comparisons among sampling sites.

The highest estimated species richness for odonates was observed in altered sites ($78.23 \pm 4.45$; mean ± confidence interval), which showed, on average, 12 more species than the degraded sites and 24 more species than the preserved sites (Fig. 3a). Considering the results for each suborder, Zygoptera had the highest richness in altered sites ($48.06 \pm 3.13$), which averaged 19 more species than the degraded sites and seven more species than the preserved sites (Fig. 3c). For Anisoptera, richness was higher in degraded sites ($38.31 \pm 3.51$), which averaged seven more species than altered sites and 25 more species than preserved sites (Fig. 3b).

Site environmental characteristics and their relationship to odonate species richness

The variable riparian forest width (RFW) had the highest pairwise correlation with conservation state of the riparian forest (CSRF) and CSRF within a 10-m range (CSRF10) (Table 2). Riparian forest width was most strongly correlated with PCA axis 1. The structure of riparian vegetation differed significantly between streams of differing conservation status ($F(2, 47) = 23.904, P < 0.001$). Preserved sites had an average of 46% more vegetation than altered sites (Tukey $P < 0.001$) and 54% more than degraded sites (Tukey $P < 0.001$). Altered streams did not differ from the other sites in the percentage of degraded riparian vegetation (Tukey $P < 0.504$) (Fig. 4).

The species composition of odonate assemblages differed significantly among sites of differing conservation status (PERMANOVA, pseudo $F = 9.652$, $P = 0.001$). Of the 97 species collected, 10 occurred only in preserved sites, 14 only in altered sites and 20 only in degraded sites. Preserved and altered sites shared 17 species, altered and degraded sites shared 26 species, and 10 species occurred in all three site categories. Preserved and degraded sites shared no odonate species (Fig. 5).
Dragonflies as indicators of ecological condition

Among the 97 odonate species collected, nine were classified as positive indicators of ecological condition (IndVal values >70%). Four species were indicators of degraded sites (three Anisoptera and one Zygoptera), and five species indicated preserved sites (all Zygoptera). There were no indicator species for altered sites. The species with the highest indicator scores were *Erythrodiplax basalis* (Anisoptera) (89.2%), an indicator of degraded streams, and *Heteragrion aurantiacum* (Zygoptera) (88.9%) and *Protoneura tenuis* (Zygoptera) (87.2%), both of which were considered indicators of preserved streams (Table 3).

DISCUSSION

We found that some odonates were strongly associated with differences in the condition of aquatic ecosystems in the eastern Amazon, similar to results from other regions (Oertli 2008), which corroborates our claim that they can be used as reliable indicators of the ecological condition of neotropical stream environments.

The greater richness of Zygoptera in altered habitats agrees with the intermediate disturbance hypothesis first proposed by Connell (1978) and matches findings of increased species richness at intermediate levels of habitat disturbance for other groups of organisms, including mammals (Racey & Euler 1982), reptiles (Germaine & Wakeling 2001), butterflies (Blair & Launer 1997) and aquatic biota (Terra et al. 2014). In stream environments, moderate environmental alterations can increase the numbers of non-native or disturbance-tolerant species, increase nutrient loads and temperature (thereby increasing productivity), and increase exposure of the soil to sunlight, thereby favouring the presence of Anisoptera, given their need to thermoregulate (May 1991). But degraded streams tend to decrease Zygoptera richness, resulting...
Fig. 3. Estimated species richness (first-order Jackknife; average ± confidence interval) by site conservation status: (a) Odonata, (b) Anisoptera and (c) Zygoptera.

Table 2. Correlation among 12 variables considered in the Habitat Integrity Index (HII) that describe the environmental conditions of sites.

<table>
<thead>
<tr>
<th></th>
<th>LURBRV</th>
<th>RFW</th>
<th>CSRF</th>
<th>CSRF10</th>
<th>RD</th>
<th>SFC</th>
<th>SBC</th>
<th>SBE</th>
<th>RB</th>
<th>ARPM</th>
<th>AV</th>
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<td>LURBRV</td>
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<td>CSRF10</td>
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<td>RD</td>
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<td>SFC</td>
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<td>SBC</td>
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<td>SBE</td>
<td>0.24</td>
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<td>AV</td>
<td>0.27</td>
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<td>0.48</td>
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<td>0.40</td>
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<td>0.27</td>
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</table>

Values underlining express highly correlated variables (>0.70). ARPM, areas of rapids, deep ponds and meanders; AV, aquatic vegetation; CSRF, conservation state of the riparian forest; CSRF10, CSRF within a 10-m range; D, debris; LURBRV, land use regime beyond the riparian vegetation; RB, riverbed; RD, retention dispositives; RFW, riparian forest width; SBE, streambank erosion; SBC, streambank cover; SFC, sand and fines in the channel.
in assemblage homogenization (Carvalho et al. 2013). Thus, we follow a large body of existing research in concluding that species richness is a poorer metric for assessing environmental changes than functional or trait-based metrics (Marzin et al. 2012; Terra et al. 2014) or species composition (Barlow et al. 2007).

In general, Zygoptera stood out as positive indicators of preserved habitats. Species of this suborder usually live in tropical regions, in small streams covered by dense vegetation. Because they are small, delicate and have slender bodies, their high surface/volume ratio probably makes them susceptible to overheating and dehydration. Hence, they are restricted to shaded environments, which tend to be better preserved (Juen & De Marco 2011). Individuals with small bodies, as is the case with most Zygoptera, should be more sensitive to environmental variation because of their ecophysiological restrictions (Corbet & May 2008) or high habitat specialization. In cases of environmental disturbance, species with a preference for forest habitats may disappear (Clausnitzer 2003), with only generalist and tolerant taxa having lower conservation values remaining (Kalkman et al. 2008). Because of their demands for thermoregulation, the Anisoptera respond positively to habitat destruction by large mammals, as observed by Samways and Grant (2008) in Africa. Usually, those areas with intense impact of trampling by elephants and other large mammals tend to have low diversity of Zygoptera (Samways & Grant 2008). Many Zygoptera species occur mainly in streams with large areas of riparian forest remaining (Hartung 2002) and often exhibit high degrees of habitat specialization. A good example of habitat specialization may be observed in Chalcopteryx: females need a specific habitat to oviposit and, hence, are only found in preserved environments (Resende 2010). Many Zygoptera species also have a broad local distribution and abundance meaning that they are likely to be collected, further underpinning the utility of these species as useful indicators of aquatic environmental quality (Carle 1979; Oertli 2008).

We observed the highest species richness of Anisoptera and some species stood out as bioindicators of more degraded environments. Anisoptera are heliothermic and perchers, and their abundance is highly dependent on incident sunlight (Remsburg et al. 2008), which they use for thermoregulation (Resende 2010; Calvão et al. 2013). Some studies have emphasized the importance of shade for odonate habitat selection in tropical streams, indicating that adults of many Anisoptera species avoid shaded areas and that their abundances decreased with increased shading from vegetation (Ward & Mill 2005; Remsburg et al. 2008). Some Zygoptera are dependent on macrophytes, as reported by Raebel et al. (2012) in English lakes. The only Zygoptera species associated with degraded environments was Acanthagrion adustum, which is frequently found in lentic environments, such as swamps and ponds, and its larvae are associated with macrophytes and debris (Fulan & Henry 2007). Because their oviposition is endophytic (the eggs remain protected within plant tissues), their relationship with degraded environments may result from an increase in macrophyte cover (Fulan & Henry 2007). Macrophyte proliferation is associated with the dams present in most degraded streams (forming lentic stretches) as a consequence of the construction of roads across streams, which is also commonly associated with high levels of vegetation loss (Ribera & Vogler 2000). Another possibility is that macrophytes increase the environmental complexity of aquatic
systems and provide specific habitats for climbing species, such as Acanthagrion species, which need this kind of microhabitat for their development (Nessimian et al. 2008). Monteiro-Júnior et al. (2015) also recorded species of this genus as bioindicators of altered areas associated with fragmented riparian vegetation.

Because of the environmental sensitivities of the order (Chovanec & Waringer 2001; Simaika & Samways 2011), several authors have proposed using odonate species as indicators of ecological condition or environmental quality of aquatic ecosystems (Chovanec & Waringer 2001; Dolný et al. 2011; Monteiro-Júnior et al. 2015). However, in the Neotropics, the only work we are aware of to support this proposal is that of Monteiro-Júnior et al. (2013) who suggested that odonate could provide an excellent ecological indicator group for the eastern Amazon region based mainly on restrictions imposed by the thermoregulation mechanism of these individuals (Sformo & Doak 2006). As observed by Monteiro-Júnior et al. (2013), odonate adults, combined with the HII, were useful for assessing anthropogenic impacts. Many of the characteristics measured by the HII, such as the removal of riparian vegetation, directly affect odonates, reinforcing the importance of vegetation for maintaining wildlife (Monteiro-Júnior et al. 2014, 2015).

Zygoptera species richness was greatest at altered sites, whereas Anisoptera richness was greatest in degraded sites (Fig. 3), but the IndVal method showed a different pattern (Table 3). We found that small-bodied species (Zygoptera) exhibited a high fidelity to more preserved environments, whereas large-bodied species (Anisoptera) had high fidelity to more degraded environments. That is, despite the greater Zygoptera richness in altered sites, specific species were indicators of preserved streams. Differences between the Anisoptera and Zygoptera can be explained mainly by differences in their thermoregulatory capacities, with Anisoptera probably benefiting from environmental changes as a result of their thermoregulatory abilities and capacities to tolerate more diverse environmental conditions (Tscharntke et al. 2002; Calvão et al. 2013). Our results are consistent with the conclusions of Samways and Sharratt (2010) for African rivers and also corroborate the hypothesis that odonates respond to modifications of riparian vegetation. Thus, microhabitat selection by odonate species can be confidently predicted from their thermoregulatory abilities, supporting the suggestion that such traits are important considerations for studies of biological indicators (Davies et al. 2008; Remsburg et al. 2008).

Vegetation loss is a key factor degrading the biological integrity of watercourses (Gregory et al. 1991; Roy et al. 2003) and is also known to affect odonate assemblage structure (Dijkstra & Lempert 2003; Monteiro-Júnior et al. 2013). Hence, vegetation loss threatens some species adapted to preserved environments (Resh et al. 1988) but improves conditions for disturbance-tolerant species. This association was very apparent in our study when comparing taxa with marked differences in ecophysiological requirements (Sformo & Doak 2006).

The higher species richness of odonates in more degraded sites mainly resulted from the high incidence of Anisoptera, which is probably related to vegetation loss followed by replacement of a few specialized species by many generalist species. Initially, intermediate short-term disturbances may maximize species richness in a given site (Connell 1978). However, if these alterations persist and become more extensive, species with restricted distributions will become extirpated because several microhabitats are lost (Clausnitzer 2003). Among the consequences is a decrease in abundance and local and regional species diversity (Clausnitzer 2003).

Table 3. Odonate species with ecological condition indicator values (IndVal) >70%.

<table>
<thead>
<tr>
<th>Suborders/indicator species</th>
<th>Indication</th>
<th>Average</th>
<th>SD</th>
<th>IndVal</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erythrodiplax basilis</td>
<td>Degraded</td>
<td>10.550</td>
<td>8.715</td>
<td>89.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Erythrodiplax fusca</td>
<td>Degraded</td>
<td>4.350</td>
<td>4.095</td>
<td>82.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Diastatops obscura</td>
<td>Degraded</td>
<td>4.650</td>
<td>5.878</td>
<td>81.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Zygoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heteragrion aurantiacum</td>
<td>Preserved</td>
<td>4.455</td>
<td>4.321</td>
<td>88.9</td>
<td>0.001</td>
</tr>
<tr>
<td>Protoneura tenus</td>
<td>Preserved</td>
<td>4.909</td>
<td>4.636</td>
<td>87.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Mnesarete aenea</td>
<td>Preserved</td>
<td>4.636</td>
<td>4.905</td>
<td>86.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Argia infumata</td>
<td>Preserved</td>
<td>4.091</td>
<td>4.134</td>
<td>75.5</td>
<td>0.001</td>
</tr>
<tr>
<td>Chakopteryx rutilans</td>
<td>Preserved</td>
<td>2.182</td>
<td>2.857</td>
<td>74.6</td>
<td>0.001</td>
</tr>
<tr>
<td>Acanthagrion adustum</td>
<td>Degraded</td>
<td>1.250</td>
<td>1.713</td>
<td>72.6</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Results are presented as average and standard deviation (SD) of abundance medians.
Understanding species ecological associations is important for determining conservation priorities. Although species with specific environmental requirements are replaced by generalist species in degraded areas, those areas have high species richness at early degradation stages, but a significant loss of Zygoptera. This indicates the need for further studies on the conservation of preserved areas and the rehabilitation of disturbed areas, particularly those altered by cattle pasturing, small farms and large mechanized farms. We emphasize that governmental agencies need to enforce environmental laws to ensure that riparian vegetation is preserved, maintain and rehabilitate the ecological condition of water bodies, and conserve aquatic biodiversity (mainly by planting new trees, providing various incentives and educating local citizens) (Noss 1999).

ACKNOWLEDGEMENTS

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES for scholarships and PPG Ecologia e Conservação (UNEMAT), Instituto Nacional de Ciência e Tecnologia-Biodiversidade e Uso da Terra na Amazônia (CNpq 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária-Embrapa (SEG: 02.08.06.005.00), the United Kingdom Darwin Initiative (17–023), The Nature Conservancy and the Natural Environment Research Council (NERC) (NE/F01614X/1 and NE/G000816/1) for institutional and academic support. LJ received productivity grant 303252/2013-8 from Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNpq. Fulbright Brasil funded participation by RM Hughes. We thank L Brasil for help in collecting biological material, NS Pinto for help in identifying Anisoptera, F Lencioni for help in identifying Anisoptera, F Lencioni for help in identifying Anisoptera, F Lencioni for help in identifying Anisoptera, F Lencioni for help in identifying Anisoptera, F Lencioni for help in identifying Anisoptera. We thank L Brasil for help in collecting biological material, NS Pinto for help in identifying Anisoptera, F Lencioni for confirming the identification of Zygoptera, L Montag, HSR Cabette and N Hamada for invaluable suggestions on early versions of this manuscript, and E Cunha for kindly drawing the map. This paper is #29 in the Sustainable Amazon Network publication series.

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doi:10.1111/aec.12242
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doi:10.1111/aec.12242