Evidence of species sorting driving aquatic beetles associated with woody debris in a transitional region between Cerrado and Atlantic Forest biomes

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Abstract We investigated (1) the variation of both species composition and species relative abundances of aquatic beetles associated with submerged woody debris in a transitional region between Cerrado (Brazilian savannah) and Atlantic Forest biomes; and (2) which assembling processes are more associated with the observed patterns, species sorting or mass effects. We hypothesized that the marked differences between Cerrado and Atlantic Forest streams regarding vegetation composition and structure would produce different environmental conditions for stream beetle faunas assembling. We used spatial explicit multivariate techniques to analyze whether metacommunity patterns were more associated with environmental variables, indicating a major role of species sorting, or with spatial variables, indicating intense dispersal. We found distinct communities within each biome in terms of both changes in taxonomic composition and species relative abundance driven by environmental factors. Biome type, a regional scale variable, and variation in dissolved oxygen levels, a local scale variable, were the best explanatory variables of variation in metacommunity structure. We did not find any evidence of the influence of processes related to the spatial configuration of streams. Altogether our results pointed to species sorting structuring saproxylic beetles assemblages patterns.

Keywords Ecotone · Metacommunity · Saproxylic · Tropical streams

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Introduction

Communities within a biome are more similar when compared to communities among biomes (Lomolino et al. 2010) and aquatic communities do not seem to be an exception of this pattern (Corkum 1992; Mykrä et al. 2004). Studies in aquatic systems show that community dissimilarity among biomes could be attributed to the process of environmental filtering and to the biogeographic history of biomes (Corkum 1992; Feminella 2000). Communities can also vary according to geographic distance—closer communities are more similar than distant ones because of differential dispersal forces among them (Nekola and White 1999). Transitional regions between biomes are defined by a change in the dominant life forms or generalist taxa due to climatic variation and other environmental variables (e.g., soil) across a region (Gosz and Sharpe 1989). Species diversity and community variation is predicted to be greater in transitional regions than in core biome areas, because these areas allow species dispersal between biomes and co-occurrence (McKnight et al. 2007; van Rensburg et al. 2009). Thus, transitional areas are key to understand the ecological processes driving community variation (van Rensburg et al. 2009).

Metacommunity ecology provides a general framework to understand the relative role of local control (biotic and abiotic factors) and dispersal-related process in structuring communities (Leibold et al. 2004; Logue et al. 2011). Metacommunity ecology were originally outlined in four perspectives (species sorting, patch dynamics, mass effects and neutral), varying in the relative role given to dispersal, species characteristics and local forces (both abiotic and biotic processes) (Leibold et al. 2004). In transition regions between biomes, different metacommunity processes may drive species composition in aquatic systems. For example, biomes have specific environmental conditions (e.g. climatic, soil) and, consequently, plant species, which provide different environmental conditions for animal species. In this sense, communities would vary between biomes due to these differences, following a species sorting model. However, due to proximity in transitional regions, intense dispersal from neighboring sites between biomes could mask the effects of species sorting and strengthen the effects of spatial configuration. For example, intense dispersal

from a source population of one biome could maintain sink populations in the neighboring biome, even if this biome requires different species fitness and traits (mass effects, Mouquet and Loreau 2003; Leibold et al. 2004).

Streams are part of dendritic networks surrounded by a terrestrial matrix that includes the biome vegetation. Aquatic beetles rely on terrestrial organic matter inputs for feeding and habitat, especially those associated with submerged woody debris (Valente-Neto and Fonseca-Gessner 2011; Valente-Neto et al. 2015). For example, wood gougers and borers, the most abundant beetles associated with submerged woody debris, play an important role converting coarse (woody debris) into fine organic matter (fecal pellets) (Steedman and Anderson 1985; Mckie and Cranston 1998). In the Neotropical region, *Lutrochus germari* and *Stegoelmis* sp produce a large amount of fecal pellets (Valente-Neto and Fonseca-Gessner 2011; Valente-Neto et al. 2015). Environmental factors appear to be the dominant drivers of composition of aquatic insects associated with wood debris, despite very few studies have examined the role of processes related to spatial dynamics. Some authors claim that insect species inhabiting woody debris are generalists showing a relationship with factors such as wood breakdown stage and stream characteristics (Spänhoff et al. 2000; Kaller and Kelso 2007). Others argue the importance of woody type and surrounding vegetation, providing evidences for insect communities composed of opportunistic or specialist species (McKie and Cranston 1998; Hoffmann and Hering 2000; McKie and Cranston 2001; Valente-Neto et al. 2015). Following these strict relationship of these beetles with the surrounding vegetation (Mckie and Cranston 1998; Hoffmann and Hering 2000; McKie and Cranston 2001), biome type would be important driver of aquatic beetles associated with submerged woody debris, since different biomes have a specific plant community, including the riparian zone. Thus, aquatic beetles associated with woody debris (saproxylic beetles) are interesting models for understanding processes responsible for their distribution in transition regions between biomes.

In Brazil, the contact region between Cerrado (Brazilian savannah) and Atlantic Forest in São Paulo state provides an opportunity to understand the influence of different drivers shaping biodiversity

distribution in transition regions. Cerrado and Atlantic Forest are characterized by distinct plant composition, including the riparian vegetation (Oliveira-Filho and Ratter 2002; Online resource 1). This difference in composition between the two biomes creates different niche opportunities for aquatic beetles that are dependent on woody debris, including woody traits—e.g., Cerrado wood species have higher density compared to those of Atlantic Forest (Marcati et al. 2001; Chave et al. 2006). Accordingly, the distinct riparian vegetation found in Cerrado and Atlantic Forest and their proximity in some regions lead to an intriguing question: what is the relative role of different factors structuring the composition of aquatic beetles associated with wood debris in transitional zones?

With this in mind, we aim to answer the following questions: (1) Do Cerrado and Atlantic Forest streams have distinct aquatic beetles associated with woody debris, in terms of species composition and species relative abundances, in a transitional region between these two biomes? (2) Which metacommunity processes are driving these patterns? For instance, riffle beetles, the most abundant organisms of beetle communities associated with submerged woody debris (Valente-Neto et al. 2015), do not seem to disperse intensively enough to maintain source-sink dynamics (see reviews Brown 1987; Ellicott 2008). We hypothesized that the marked differences between Cerrado and Atlantic Forest streams regarding vegetation composition and structure of (Chave et al. 2006; Oliveira-Filho and Ratter 2002) would create different environmental conditions for stream beetle faunas and would drive community assembling, in accordance with species sorting metacommunity perspective.

Methods

Study area

We conducted the study in the central and eastern region of São Paulo State (Brazil), during the dry season (June–September) of 2010. The central region of São Paulo is characterized by a transition between Cerrado (Brazilian savannah) and Atlantic Forest fragments (Durigan 2006), whereas the eastern region is characterized by two mountain chains, Serra da Mantiqueira and Serra do Mar, both covered only by Atlantic Forest vegetation. The transition region is

highly fragmented, mainly due to agriculture and cattle ranching. This area has both Cerrado and Atlantic Forest fragments (Fig. 1). We selected 18 low order perennial streams (first to third order), all located inside conservation units or legal forest reserves, with minimal anthropogenic impacts. Also, all streams had sand as the main bottom sediment. Among the 18 streams, 8 were located in Cerrado fragments and 10 in Atlantic Forest fragments (Fig. 1). In the central region we selected 8 Cerrado and 2 Atlantic Forest streams, while another 8 Atlantic Forest streams were selected from the eastern region. We had difficulties finding low impacts streams on the Cerrado, so we included 8 streams.

In general, the Cerrado biome is characterized by hot and seasonal weather with rainy summer and dry winter and an acidic sandy latosol soil type. Cerrado biome has a mosaic-like aspect, composed by savannas (the dominant vegetation), patches of dry forests and forests (Oliveira and Marquis 2002). Thus, this variation is recognized by five main structures types (*cerradão, cerrado strict* sensu, *campo cerrado, campo sujo* and *campo limpo*). The typical vegetation is a fairly dense woody savanna of shrubs and small trees. Tree species common in Cerrado included *Annona crassiflora, Astronium fraxinifolium, Byrsonima coccolobifolia, B. verbascifolia, Hancornia speciosa, Kielmeyera coriacea, Qualea grandifolia,* and *Q. parviflora,* among others (Ratter and Dargie 1992). The vegetation is adapted to drought and fire stress. Riparian vegetation has, in general, open and narrow riparian vegetation structure, interspersed between savanna vegetation. Cerrado has an area around 1,082,640 ha in São Paulo State (Kronka et al. 2005). The Atlantic Forest biome is characterized by high temperatures and rainfall, fertile soil, large variations in altitude and dense forests, where riparian vegetation is immersed (Morellato and Haddad 2000). The most common species included *Euterpe edulis, Psychotria nuda, Eugenia cuprea, Guapira opposite* and *Rudgea jasminoides* (Scudeller et al. 2001). Dense vegetation is the typical structure of Atlantic Forest biome and, differently from Cerrado biome, no borders could be recognized between Atlantic Forest typical structure and riparian forests, constituting a continuum vegetation structure. In São Paulo State Atlantic Forest occupies an area of 2,375,211 ha (Fundação SOS Mata Atlântica 2013). Both biomes are fragmented in
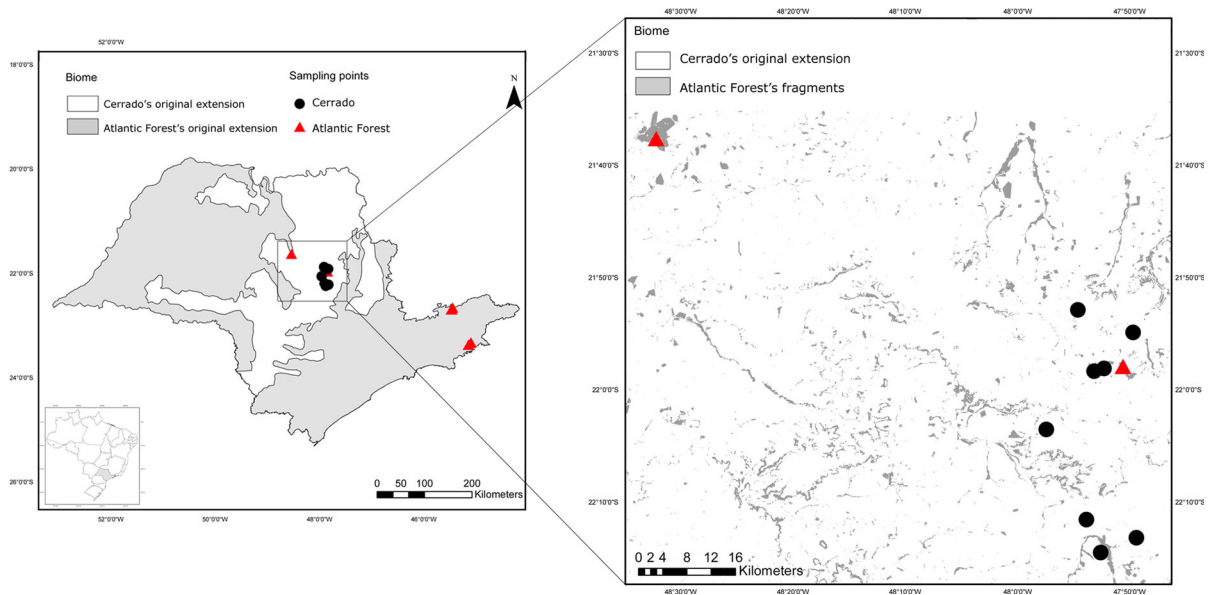
Fig. 1 *Left* map of São Paulo State, Brazil, showing the stream sampling sites (some are superimposed) and the original extension of both Cerrado and Atlantic Forest biomes. *Right* central area of São Paulo State showing part of the transitional region between Cerrado and Atlantic Forest. Note that the map shows Atlantic Forest fragments and the original extension of Cerrado biome, not including land use by human activities

São Paulo State, particularly due to disorganized urban growth and agribusiness activities (Morellato and Haddad 2000).

We used literature knowledge to provide evidence that common plant species are different in Atlantic Forest and Cerrado riparian vegetation (respectively, Sanchez et al. 1999; Soares et al. 2003) (Online resource 1). We only included woody species with at least 30 cm of diameter at breast height (following Lorenzi 2002), i.e., capable to input woody debris in streams.

Biological and environmental data

We carried out fieldwork in the dry season of 2010 (June–September) using a 100 m reach in each stream to sampling and measure aquatic variables. All aquatic variables (temperature, conductivity, dissolved oxygen and pH) were measured in this segment with a Yellow Spring 556 (YSI Incorporated, Yellow Springs, USA) multiparameter probe in backwater areas to avoid variation in different habitat types. Current velocity was measured in five locations (each 20 m) at 10 cm form the stream bottom using a Global Water FP101 Flow Probe. We also recorded the geographic coordinates and altitude of each stream using GPS (Online resource 2).

We visited the streams once and considered each stream as a sample and the woody debris volume per stream as a sampling unit. We selected submerged woody pieces based on the following criteria (Cranston and McKie 2006; Valente-Neto et al. 2015; Roque et al. 2015): (1) presence of hollows that indicate the activity of boring organisms (both terrestrial and aquatic), (2) indications of biofilm demonstrating permanent submersion (visual detection of algae and fungi), (3) approximate size of 5–8 cm in diameter and maximum length of 30 cm, to facilitate sample processing (4) absence of bark cover. Considering these criteria, we standardized the sample to a volume of 10,800 cm^3 in backwater areas, with a high accumulation of woody debris. This volume was measured with a standardized box. The volume we used per stream was sufficient to include about 30–45 pieces, depending on their dimensions, ensuring, at the same time, variability of the woody debris collected (see Valente-Neto et al. 2015).

For insect surveys, wood pieces were lifted carefully from the stream bottom and placed inside a plastic bag to avoid losing insects. We transported wood pieces to the laboratory in plastic bags filled with

water. In the laboratory, following Valente-Neto et al. (2015), we placed wood in a 0.2-mm-mesh sieve and washed it several times with a forced water jet to remove organisms. Then, we placed them in plastic containers filled with water under a lighting system. Beetles found on the wood surface were collected first. We broken up wood pieces to obtain and sort boring and internal organisms. We preserved each specimen in 70 % ethanol for further identification. The specimens were identified to the lowest practical taxonomic level, with the help of taxonomic keys (Domínguez and Fernández 2009; Segura et al. 2011).

Data analysis

We ran Permutation Multivariate Analysis of Variance (PERMANOVA; Anderson 2001) to compare the beetle community composition (response matrix) in Cerrado versus Atlantic Forest regions (explanatory variable), and to test whether communities were structured based on changes in species identity or changes in abundances. To provide a continuum in community structure measures, from those emphasizing changes in species composition to those emphasizing changes in relative abundance, we ran PERMANOVA using three dissimilarity measures as suggested by Anderson et al. (2006): a Jaccard index, a Bray–Curtis index, and a Manhattan index. The Manhattan distance gives more emphasis to changes in the relative abundance of species than Bray–Curtis, as it was developed for quantitative descriptors. In this case, we transformed the compositional matrices using Hellinger transformation (Legendre and Gallagher 2001) prior to analyses. We calculated a p value from 1000 permutations of least-squares residuals (Anderson et al. 2006). Complementary to that approach, we used a principal coordinate analysis to ordinate community composition using the different indexes.

To identify species that were specific to each biome, we used species indicator analysis (Dufrêne and Legendre 1997). In this analysis, indicator species are those with high abundance in one biome and low abundance in the other (specificity), and those present in most streams of this biome (fidelity) (Dufrêne and Legendre 1997). A random reallocation of sites among biomes was used to test the significance of indicator values.

To test our main hypothesis about the role of environmental and spatial-related processes

structuring aquatic beetles metacommunity, we construct two explanatory matrices (environmental and spatial). The environmental predictor matrix included the biome (Cerrado and Atlantic Forest) as a categorical (dummy) variable (Legendre and Legendre 2012), mean current velocity, altitude, water temperature, dissolved oxygen, pH, and conductivity (Online resource 2). We standardized (centered and divided by their standard deviation) environmental predictors. A Pearson correlation analysis was carried out to test the degree of association between independent environmental variables (the cutoff level for statistical significance was set at $p < 0.05$ and $r_s > 0.8$). No variables were correlated, and all explanatory variables were included in the analysis.

The spatial variables were generated through distance-based Moran's eigenvector maps (db-MEM; Borcard and Legendre 2002). To run db-MEM, we first calculated a distance matrix—based on Euclidean distances between streams and then submitted this matrix to a principal coordinate analysis (PCoA). From this analysis, we included PCoA axes (eigenvectors) with significant patterns of spatial autocorrelation, i.e., with positive and significant ($p < 0.05$) Moran's I (see Sokal and Oden 1978). These eigenvectors represent distinct spatial patterns that are both mutually orthogonal and linearly uncorrelated (Griffith and Peres-Neto 2006). The selected spatial eigenvectors were used as (spatial) explanatory variables in our analyses (see Borcard and Legendre 2002). Spatial eigenvectors associated with high eigenvalues (e.g., the first eigenvectors) represent broad-scale patterns of relationships among sampling sites, whereas those associated with low eigenvalues represent fine-scale patterns (Griffith and Peres-Neto 2006). Spatial eigenvectors can be interpreted to represent spatial structures generated by environmental autocorrelation and biotic processes, for instance, colonization and dispersal (Dray et al. 2006).

We tested the relative importance of environmental (E) and spatial (S) variables in explaining the variation in the composition of aquatic beetles associated with woody debris by using a variation partitioning procedure (Borcard et al. 1992) applied to redundancy analysis (RDA) models (Fig. 2). Our spatial matrix is composed by eigenvectors with positive and significant ($p < 0.05$) Moran's I (see above). Environmental variables were selected by fitting environmental RDA models with forward selection procedure (Blanchet
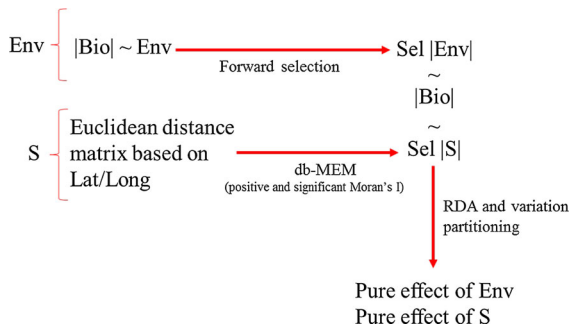
Fig. 2 Flow chart of statistical analyses employed to assess the role of environmental and spatial components in explaining community variation. First, we selected environmental (Env) and spatial (S) variables (*upper*). Environmental variables were standardized and then selected by forward selection applied to redundancy analysis (RDA). Spatial variables (S) were generated by distance-based Moran's eigenvector maps and selected using positive and significant ($p < 0.05$) Moran's *I*. These selected variables (Sel) were included in variation partitioning applied to RDA analysis (*bottom*) as explanatory matrices (environmental and spatial) to explain community matrix (Bio). Variation partitioning was used to disentangle the effects of environment and spatial variables on community variation

et al. 2008). In this method, selection of variables is stopped if a candidate variable had a non-significant *p* value ($p < 0.05$) or if the adjusted R^2 of the reduced model was over the value of the adjusted R^2 of the global model (see details in Blanchet et al. 2008). Then, we used the selected variables into variation partitioning, which measure the percent variation in the species data that could be attributed exclusively to environmental or spatial variables. The different components of the explanation generated by variation partitioning were as follows: total explained variation, environmental variation, spatial variation, environmental variation without the spatial component (a), spatial variation without the environmental component (c), the common fraction of variation shared by E and S (b), and the residual fraction of variation not explained by E and S (d) (Peres-Neto et al. 2006).

All analyses were performed in R software using *vegan* (Oksanen et al. 2014) and *pack for* packages (Dray et al. 2011).

Results

We collected and identified 1617 specimens belonging to 29 genera (Online resource 3). Elmidae was the most abundant family (48 %) and had 15 genera, of which

Elmidae spB was the most abundant taxa of this family, followed by *Heterelmis*. Lutrochidae is a monogeneric family that was represented by *L. germari* with 42 % of the total abundance, i.e., the most abundant genus in this study. Other families were found in low numbers, for example Dryopidae constituted 3 % of total abundance and Ptilodactylidae, Hydraenidae, Staphylinidae, Scirtidae, Hydrophilidae, Gyrinidae and Dytiscidae with less than 1 % of the total abundance.

In general, community composition differed between Cerrado and Atlantic Forest streams using all dissimilarity measures (PERMANOVA, Table 1; PCoA, Fig. 3). Three taxa were considered indicators of specific biomes. *L. germari*, and Staphylinidae sp.1 were strictly related to Atlantic Forest and *Stegoelmis* was an indicator for Cerrado streams (see Table 2 for indicator values and significance values). The other taxa did not have strong fidelity (presence in most streams of a biome) and specificity (high abundance in one biome and low abundance in the other) to Cerrado or Atlantic Forest biomes.

Distance-based Moran's eigenvector maps generated six eigenvectors; however, just one was positive and significant (spatial eigenvector 1; Moran = 0.95; $p = 0.01$), which was used as our spatial component. Biome type, dissolved oxygen, altitude and temperature were the main environmental variables responsible for grouping Cerrado and Atlantic Forest community composition (Fig. 4). Biome type (Adj $R^2 = 0.20$, $p < 0.01$) and dissolved oxygen (Adj $R^2 = 0.24$, $p = 0.04$) were retained by forward selection in the environmental component (Table 3) and used in variation partitioning. Environmental component, rather than spatial, better explained the variation in community composition of beetles associated with woody debris. Variance partitioning showed that in total, we could explain 22 % ($p = 0.01$) of the variation in community structure by environmental and spatial variables. Pure

Table 1 Results of PERMANOVA analysis between Cerrado and Atlantic Forest streams using the following distance measures: Jaccard index, Bray–Curtis index, and Manhattan index

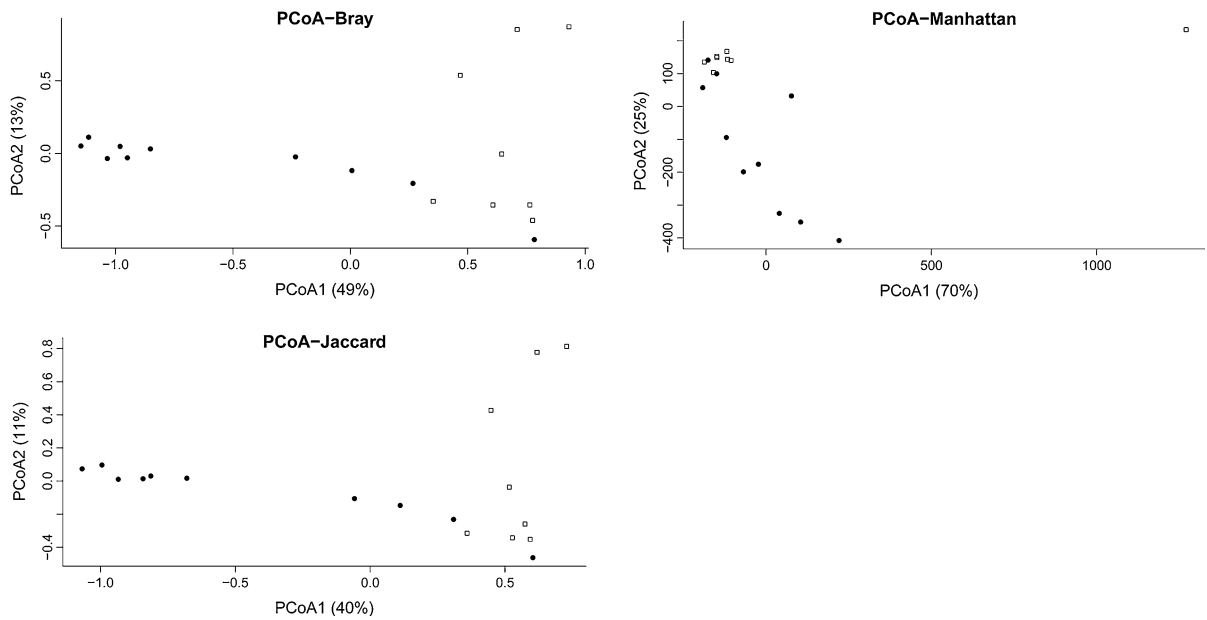| Measure	*F*-statistic	*p* value
Jaccard	3.02	0.002
Bray–Curtis	4.06	0.001
Manhattan	6.22	0.001

Fig. 3 Ordination produced by principal coordinate analysis of aquatic beetles community in Atlantic Forest (*filled circles*) and Cerrado (Brazilian savannah) (*open squares*) streams using different index (Bray Curtis, Manhattan and Jaccard)

environmental component explained 15 % ($p = 0.05$) of variation, while pure spatial variables did not contribute to explain metacommunity variation (Table 4).

Discussion

Environmental factors were the main driver structuring communities of saproxylic beetles in streams, even in a region of contact between biomes, where dispersal should not be limited. Biome type, a regional scale variable, and dissolved oxygen, a local scale variable were the main variables explaining the difference between Cerrado and Atlantic Forest communities. This supports the hypothesis that communities are structured by environmental filters operating at successive scales (Poff 1997). Our results are in accordance with the general role of species sorting structuring metacommunities (Logue et al. 2011; Soininen 2014). However, they disagree partially with a recent study showing the influence of dispersal limitation shaping elmid metacommunity structure (almost half of our beetles abundance) (McCreadie and Bedwell 2014), and with studies from the same region that showed influence of spatial variables in the

distributions of stoneflies (Roque et al. 2008) and chironomids (Roque et al. 2010). Two characteristics may have influenced the lack of a spatial signature in our study. First, some groups found in both biome types, such as the elmids *Heterelmis*, *Hexacylloepus* and *Neolmis*, are associated with multiple organic substrates (generalists) and did not show specificity for any biome as shown by the species indicator analysis. In this sense, these taxa could inhabit any stream in our study area extension and thus would not show any spatial signature. Second, the specialist beetle borers and gougers of submerged woody debris (Valente-Neto and Fonseca-Gessner 2011)—e.g., *Stegoelmis* sp and *L. germari*—were indicators of Cerrado and Atlantic Forest streams, showing a strict dependence of organic resources from surrounding vegetation to carry on their life history activities. Thus, they would hardly colonize streams outside their preferred biome and so all the explanation of their distribution would be due to environmental filtering, and not due to spatial distance.

The above-mentioned discussion is based on the premise that the studied organisms have the dispersal ability to arrive in streams of different biomes types. In this sense, aquatic beetles have a wide range of dispersal capacity, being, for example Hydrophilidae,

Table 2 Results of species indicator analysis for saproxylic beetle *taxa* in streams of Cerrado and Atlantic Forest

| Taxa	Abbreviation	Frequency (%)	Indicator value		*p* value
			Atlantic Forest	Cerrado	
Lutrochus germari	Lut	55	0.890	0.001	**0.003**
Heterelmis	Het	77	0.581	0.205	0.209
Xenelmis	Xen	50	0.187	0.312	0.696
Stegoelemis	Steg	22	0.000	0.500	**0.019**
Microcylloepus	Mic	5	0.100	0.000	1.000
Huleechius	Hul	22	0.133	0.083	0.922
Phanocerus	Pha	22	0.400	0.000	0.097
Macrelmis	Mac	11	0.200	0.000	0.469
Promoresia	Pro	5	0.100	0.000	1.000
Hexacylloepus	Hex	33	0.037	0.406	0.209
Neoelmis	Neo	33	0.084	0.197	0.792
Cylloepus	Cyl	5	0.100	0.000	1.000
Elmidae spA	ElmA	16	0.300	0.000	0.198
Elmidae spB	ElmB	5	0.000	0.125	0.458
Elmidae spC	ElmC	11	0.000	0.250	0.177
Austrolimnius	Aus	5	0.100	0.000	1.000
Dryops	Dry	50	0.472	0.081	0.217
Ptilodactilidae spA	Pti	44	0.368	0.098	0.359
Hydraenidae spA	Hyd	11	0.200	0.000	0.485
Staphylinidae spA	Sta	33	0.600	00.000	**0.011**
Scirtidae spA	Sci	33	0.282	0.073	0.435
Berosus	Ber	11	0.200	00.000	0.482
Enochrus	Eno	27	0.331	0.021	0.253
Derallus	Der	16	0.300	0.000	0.213
Epimetopus	Epi	5	0.100	0.000	1.000
Tropisternus	Tro	5	0.100	0.000	1.000
Hydrochus	Hyd	5	0.100	0.000	1.000
Gyretes	Gyr	16	0.152	0.029	0.722
Genus H	Gen	5	0.000	0.125	0.463

Bold signifies *p* < 0.05
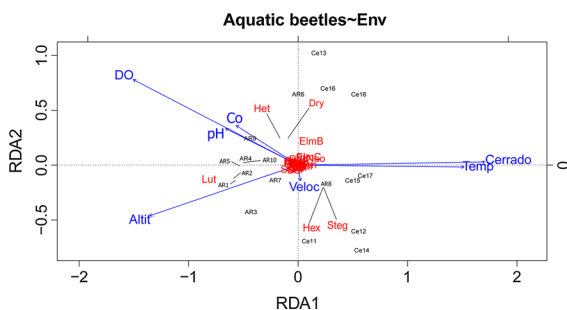
Fig. 4 Redundancy analysis using environmental variables as predictors for variation on community composition of aquatic beetles. *DO* dissolved oxygen, *Altit* altitude, *Co* conductivity, *Veloc* current velocity, *Temp* temperature. See Table 2 for taxa abbreviations

Dytiscidae and Gyrinidae known as good dispersers (Bilton et al. 2001). Although authors differ in opinions about riffle beetle dispersal, some genera were found in light traps in terrestrial systems, including *Stegoelmis* and *Lutrochus* (Brown 1987), and in general, the ability to fly varies among species and individuals of the same species (see reviews Brown 1987; Ellicott 2008). Indeed, after emergence (larvae pupate under debris or land alongside stream banks), adults could disperse away or entering in the water, but once the adults enter the water, they never leave it and cannot survive outside it (see review of Ellicott 2008). McCreadie and Bedwell (2014) also found that variation in elmid assemblages within a

Table 3 Forward selection coupled with redundancy analysis for environmental matrix showing the fraction of variation explained by vegetation type (Cerrado) and dissolved oxygen concentration (DO) in taxonomic composition of aquatic beetles community

		Variables order	R^2	R^2 Cum	Adj R^2	F	p value
1	Cerrado	7	0.251	0.251	0.204	5.363	0.001
2	DO	2	0.0817	0.332	0.243	1.839	0.047

Table 4 Relative importance of environmental and spatial variables selected in forward selection in explaining variation on taxonomic composition of aquatic beetles community

	Df	R^2	Adj R^2	Testable	p value
Env + Shared	2	0.332	0.243	True	0.025
Spa + Shared	1	0.125	0.070	True	0.037
Env + Shared + Spa	3	0.363	0.227	True	0.012
Individual fractions					Ns
Pure Env	2		0.157	True	0.05
Shared Env +Sp	0		0.086	False	Ns
Pure Sp	1		−0.016	True	0.1
Residual			0.772	False	Ns

Env environmental variables (Cerrado and dissolved oxygen), *Spa* spatial variables (spatial eigenvector 1). Shared refers to the spatial structuring in the species data that is shared by the environmental data. *Ns* not significant

stream basin scale was not explained by overland distance, indicating that they can probably disperse by overland routes. In this case, species could track environmental variation among streams in the extent of our study area, which is an integrated part of species sorting mechanism.

Cerrado and Atlantic Forest have distinct riparian composition (Oliveira-Filho and Ratter 2002) and also the plant species and individuals from these biomes have distinct woody structure (Marcati et al. 2001; Chave et al. 2006). As these small forested streams depend on allochthonous organic matter energy and aquatic beetles associated with woody debris use them, the composition and structure of riparian woody species should be important in providing specific habitats to this specialized fauna (McKie and Cranston 1998). This evidence is in line with the idea that woody species identity is an important factor affecting groups that use woody debris (McKie and Cranston 1998, 2001). In addition, the vegetation structure (forest canopy openness) together with geomorphological features of the channel could act in wood availability to aquatic beetles. In general, Cerrado streams are located in plain areas and have open and narrow riparian vegetation structure, which increase

retention and facilitate wood falling by mechanical actions of winds (Liquori 2006; Cadol et al. 2009). On the other hand, high levels of declivity generally characterize Atlantic Forest, resulting in streams with poor retention of detritus. The continuous and dense structure of riparian vegetation constitutes a barrier for mechanical actions of winds, fundamental force for wood falling and input into streams (Cadol et al. 2009). This could produce less amount of woody debris available for aquatic beetles in Atlantic Forest streams compared with Cerrado streams. Although we did not measure wood availability during the fieldwork and recognized this caveat, the difference between Cerrado and Atlantic Forest streams was visually apparent. This difference in wood availability between Cerrado and Atlantic Forest streams is able to influence the assemblages of aquatic beetles since the availability of resources is a strong driver of the structure and dynamics of ecological systems (Nowlin et al. 2008).

Together with biome type, dissolved oxygen was an important environmental variable explaining the community composition of aquatic beetles corroborating the importance of local variables, such as physical and chemical characteristics of streams, for explaining

aquatic insect community distribution (Siqueira et al. 2009; Roque et al. 2010). This variable was not correlated with other variables assessed here, including velocity, altitude and biome type, so it may affect community variation independently. Levels of dissolved oxygen such as those found in this study (ranging from 3 to 9 mg/l) do not appear to be lethal to aquatic insects, but could be sufficient to lead variation in community composition (Connolly et al. 2004). Low levels of dissolved oxygen may affect growth through long-term, sub-lethal effects, such as suppressed emergence (Connolly et al. 2004). In addition, woody debris may create a microhabitat with lower levels of oxygen than water column (Spänhoff et al. 2000), intensifying these sub-lethal effects on specialist species.

The distinction between Cerrado and Atlantic Forest beetle assemblages was due to changes in both species identity and changes in species abundances. Most genera (19) occurred exclusively in one biome type but in low abundance and frequency, which do not characterize them as indicator species. The majority were generalist predators (e.g., *Gyretes* and Hydrophilidae genera), and their occurrence is sporadic in woody debris (Hoffmann and Hering 2000; Valente-Neto et al. 2015; Roque et al. 2015). In such cases, community patterns are mainly driven by abundant taxa, such as specialists and few generalists elmids. Although generalist elmids (e.g., *Heterelmis*, *Hexacylloepus* and *Neolmis*) were found in both biome types, their abundance differs between biomes. This difference could be related to differences in declivity among Cerrado and Atlantic Forest streams, since Atlantic Forest streams has greater variation in declivity and would have more habitats for riffle beetles. Specialists also contributed for the assemblage variation between biomes, such as the specificity showed by *Stegoelmis* for Cerrado streams, as also found by Segura et al. (2011) and *Lutrochus* for Atlantic Forest stream. Some elmids are poorly known regarding their affinity and dependence of woody debris as habitat and feeding source (Segura et al. 2012), but our observations during sample processing suggested that Elmidae spB and spC (found exclusively in Cerrado streams) are borers and gougers of woody debris. Altogether, these results are in line with studies showing the importance of organic substrates (specific to each biome) and that colonizers of woody debris are a set of opportunistic to specialist species

(Steedman and Anderson 1985; McKie and Cranston 1998; Valente-Neto et al. 2015).

Streams are highly variable systems, both hydrographic and environmentally. These characteristics would be responsible for a high temporal variation of community composition and could affect explanation power of environmental variables. In this sense, although snapshot studies do not include this variation in community composition as well as in environmental variables, they are suitable to capture overall trends in community composition, mainly the most abundant organisms. We detected that dissolved oxygen and biome type explained about 25 % of community variation, an amount of explanation that is similar to other snapshot metacommunity studies (see review Soininen 2014). Moreover, our study did not include more samples on the transition region. Both Cerrado and Atlantic Forest biomes are highly fragmented in the transition region, turning streams under low human impact hard to find. Including more samples from the transition region could not change our result of environment filtering but would likely reinforce it, because the most abundant taxa appear to be biome specific, i.e., *Lutrochus* and *Stegoelmis* in Atlantic Forest and Cerrado streams, respectively.

In conclusion, we found evidence for a role of biome type and dissolved oxygen explaining the structure of saproxylic beetles in streams. The relationship of wood debris and the surrounding vegetation explained the distinct community of insects associated with this substrate among Cerrado and Atlantic Forest streams. Specialized taxa, such as *Stegoelmis* and *L. germari* were, respectively, restricted and abundant in only one biome, while generalist species were common in both biomes. The relationship among saproxylic beetles and their substrate, together with the lack of evidence of dispersal-related processes, corroborate an explanation of species sorting driving variation in community structure of saproxylic beetles, both via changes in species identity and in species relative abundance.

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