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STREAM ECOLOGY

Invertebrate metrics based on few abundant taxa outperform functional and taxonomic composition as indicators of agricultural impacts in Atlantic rainforest streams

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Abstract Metacommunity studies have demonstrated that local macroinvertebrate communities are structured not only by local environmental conditions but also by spatial processes. Effective bioassessment tools should account for spatial processes while doing so with the least amount of cost. In this study, we applied variance partition techniques based on redundancy analysis to assess the performance of three sets of benthic invertebrate metrics in detecting agricultural land-use effects in a SE Brazil rainforest watershed. Macroinvertebrate data were analyzed separately regarding their taxonomic, functional structure and bioindicator metrics developed for the study region. We stipulated that groups of metrics most sensitive to land-use effects should have the highest amount of variance explained by the joint effects of land use and environmental variation, independently of spatial structuring. Statistical analyses were repeated removing rare taxa in order to assess the effects of their inclusion in the responsiveness of each group of metrics. Traditional bioindicator metrics were more responsive to environmental variation associated with agriculture than taxa abundances and functional attributes. Furthermore, a few common taxa drove a high proportion of the variation observed in invertebrate communities, regardless of how invertebrate data were organized. Similar analytic approaches have the potential to be useful in curtailing sorting and identification efforts when developing macroinvertebrate-based biomonitoring protocols, especially in areas where information regarding the taxonomy of benthic communities is still poorly described.

Keywords Land use · Aquatic macroinvertebrates · Bioassessment · Multivariate spatial analysis ordination · Environmental variables · Taxonomic composition · Functional traits · Variance partitioning

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Introduction

Macroinvertebrate communities have been widely used to assess responses of stream and riverine ecosystems to agricultural land-use impacts (Barbour et al., 1999; Bonada et al., 2006; Buss et al., 2015). The underlying rationale for using macroinvertebrate community metrics as bioindicators of stream condition is that they predictably respond to specific environmental gradients generated by anthropogenic activity (e.g., siltation, loss of riparian vegetation, nutrient enrichment) through detectable shifts in community structure (Townsend & Hildrew, 1994; Friberg et al., 2011). However, a growing body of evidence derived from metacommunity studies demonstrates that macroinvertebrate communities are not exclusively sorted by local environmental conditions (Leibold et al., 2004; Brown et al., 2011; Tonkin et al., 2018a; Valente-Neto et al., 2018). In fact, spatial processes linked to local species pools and dispersal constraints have been shown to explain a large amount of the composition of local invertebrate assemblages (Landeiro et al., 2011; Diniz-Filho et al., 2012; Grönroos et al., 2013; Li et al., 2019).

The possible confounding factors for the development of biomonitoring tools that arise from this metacommunity perspective of macroinvertebrate communities can compound on other sources of spatial structuring which are present within modern watersheds. Agricultural land use itself is often spatially structured with higher intensity of activities in more accessible and flat piedmont areas and reduced impact in steep headwater locations (Allan et al., 2002; Silva et al., 2007). This makes it possible that land–use-related effects on macroinvertebrate communities can be confounded with other processes that are expected to naturally occur along a riverine system or a given continuous land-use patch (e.g., River Continuum Concept, Vannote et al., 1980; Riverine Ecosystem Synthesis, Thorp et al., 2006; riverine dendritic network, Tonkin et al., 2018b). Thus, if large portions of the variation of a given set of indicator metrics can be explained by spatial structuring, the influence of patch dynamics, mass effects, and neutral processes in the assembly of a local community have the potential to overshadow the effects of niche processes derived from land-use-driven environmental constraints in the aquatic biota (Tolonen et al., 2017; Zawalski et al., 2019).

The same geographical features that act as physical barriers for invertebrate dispersal might also generate environmental gradients and consequently, the same spatial processes that structure invertebrate communities might also produce the environmental variation within a given region. This intersection of spatial and environmental variability, often termed spatially structured environmental variation, might determine a significant portion of the assembly of macroinvertebrate communities at a given site (Sandin & Johnson, 2004; Feld and Hering 2007; Ding et al., 2017). Conversely, even if the structuring of local macroinvertebrate communities can be linked to environmental variation that is independent from spatial structuring, that information might be of little practical use if that variation cannot be linked to land use as a source of anthropogenic impact (Suter II, 2001; Burcher et al., 2007).

In the last decades, methods have been developed that attempt to directly assess the effects of anthropogenic impacts on the functional traits of macroinvertebrate communities (Karr, 1999; Tomanova & Usseglio-Polatera, 2007; Bello et al., 2010; Castro et al., 2018; Firmiano et al., 2021). This approach combines aspects of community composition with information about taxa specific traits to aggregate individuals into functional groups (Richards et al., 1997). A functional approach may prove better than taxonomic and traditional metrics (e.g., EPT%, Family Richness) in discriminating stream conditions because it can target traits known to be responsive to local environmental variability which act as filterers for community assemblage (Saito et al., 2015a, b). Also, functional trait approaches provide direct insight into the mechanisms controlling the structure of macroinvertebrate communities by describing relationships between specific traits and environmental factors (Dolédec et al., 2006; Bello et al., 2010; Verberk et al., 2013). It is expected that functional approaches reliance on commonality of traits rather than taxa identity makes results comparable across larger geographical extents which are less dependent on the distribution of rare taxa (Bello et al., 2010).

The inclusion or exclusion of rare taxa from bioassessment has important theoretical and practical implications and has been an important topic of scientific debate (Cao et al., 2001). From a practical standpoint, the inclusion of rare taxa increases the cost and sample processing associated with biomonitoring programs, which is at odds with the goals of rapid bioassessment (Buss & Vitorino, 2010; Hughes et al., 2010; Oliveira et al., 2011). Ideally, bioindicator metrics would be capable of detecting human impacts independent of the spatially structured variability influencing biotic communities within a specific region, and should do so while minimizing the costs of sampling, sorting, and analytic effort. Also, abundance matrices that include rare taxa contain many zeroes, creating a disproportional amount of noise in commonly used multivariate analysis (Cao et al., 2001). However, excluding rare species for purely statistical reasons might also leave out important information on rare taxa that have important conservation value. While some have argued that excluding rare taxa might cause important aspects of community variation to be overlooked, (Heino, 2013), others have presented evidence that rare macroinvertebrate taxa are structured by the same processes as common ones and that common species are good surrogates for evaluating the effects of environmental gradients on the whole community (Siqueira et al., 2012b, 2012a).

In this study, we assessed how three sets of benthic invertebrate metrics respond to agricultural land-use effects at three different spatial scales, as well as the effects of the inclusion of less common taxa metric performance. Specifically, we generated matrices containing macroinvertebrate abundances, community weighed metrics of functional characters (CWMs), as well as a multimetric index developed specifically for the study region (Oliveira et al., 2011) ,and applied redundancy analysis (RDA)-based variance partition techniques to parse out the influence of environmental variables, land use, and spatial organization on the structuring of invertebrate communities. Towards that end, we measured environmental variation through a suite of variables measured at the sampling sites. Land-use information was derived from satellite imagery and was estimated for each site as the proportion of agriculture within the watershed, reach buffer and riparian buffer scale. Spatial structuring was measured through the use of Asymmetric Eigenvector Maps (AEMs) generated from a watercourse distance matrix that represented the distribution of sites within the dendritic settings of the watershed. This study had three main objectives:

1. Describing which is the role of spatial distribution, environmental drivers and agricultural land use for changes in invertebrate communities as quantified by the three sets of metrics investigated.
2. Identifying which group of community metrics were more responsive to environmental variation caused by land use, independently of spatial processes. We contend that groups of metrics that had the highest amount of variance explained by the joined effects of agricultural land cover and environmental variables, independently of spatial ones, would be the best indicators of agricultural impacts in invertebrate communities.
3. Assessing the extent to which less abundant taxa would affect the amount of variance explained by the intersection of agriculture and environmental change across metrics, thus, providing insight into the effects of their inclusion on metric performance. In order to do so, we repeated the aforementioned analysis iteratively removing the least common taxa until the analysis failed or only two taxa were left.

Methods

Study area

We conducted this study in the Guapiaçú River basin located northeast of the city of Rio de Janeiro in the Atlantic Forest domain of Rio de Janeiro State, southeastern Brazil (Fig. 1). The Guapiaçú basin has a drainage area of approximately 442 km^2 that originates at the Serra do Mar Mountain range with generally well-preserved headwaters comprised inside two conservation units (Serra dos Órgãos National Park, and Três Picos State Park). Climate in the region varies from tropical wet forest on high-altitude locations, to tropical savannah on the piedmont. This region experiences average annual temperatures of 23.1C and 1307 mm of total rainfall. Most of the precipitation is concentrated in the late spring and early summer, with December being the wettest month (~200 mm) and July (~30 mm) the driest. The Guapiaçú basin has 54% forest cover in different states of conservation. As tributaries approach the valley floor, riparian areas are increasingly cleared for agricultural use such as cattle grazing and small plantations (Seabra et al., 2018). During this study and over the course of subsequent years, the main agricultural

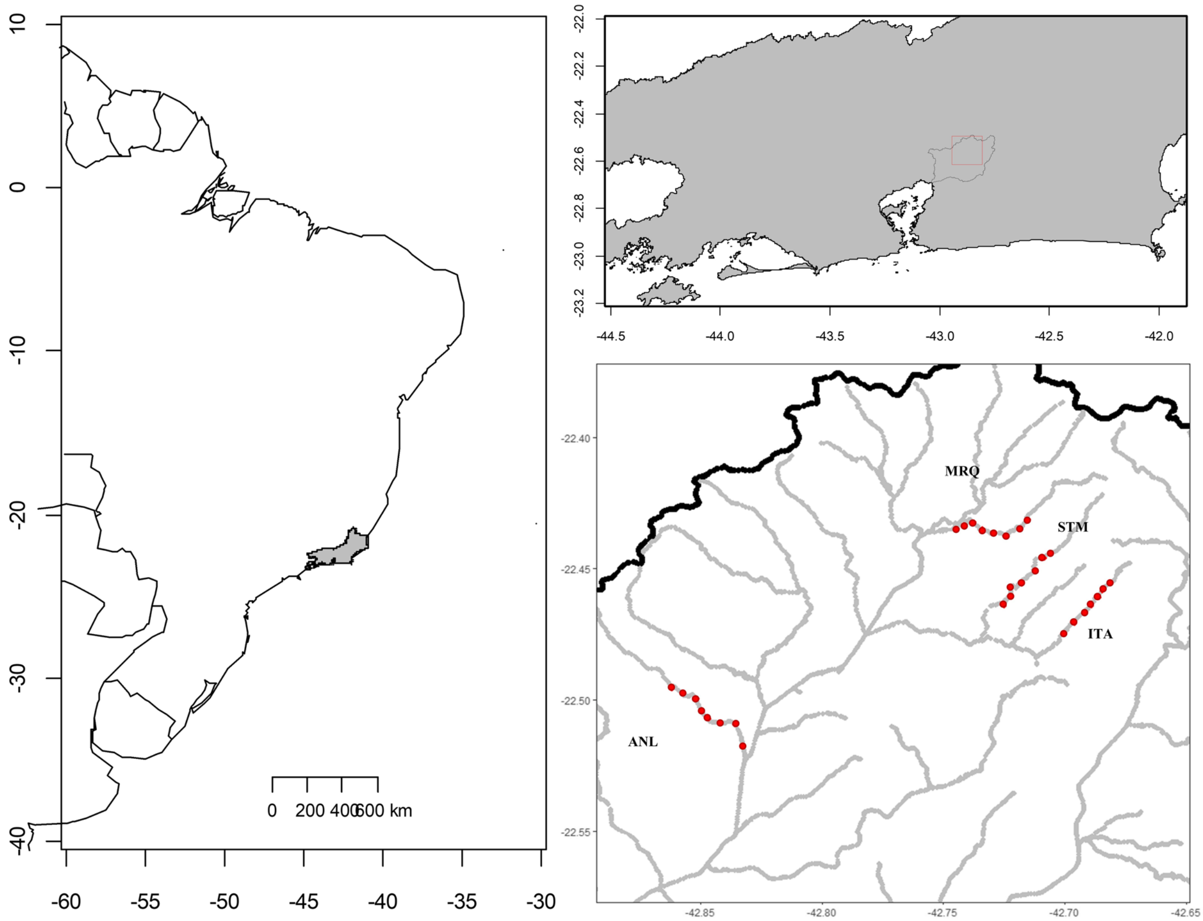


Fig. 1 Location of the Guapiaçú River Basin in Southeastern Brazil and the distribution of 30 sampling sites in the study area

activities present in the area have been mostly free-range grazing (49.8% of the land cover, Seabra et al., 2018) and small-scale agriculture (5.8%; crops are mainly cassava, corn, banana, and guava) (EMATER-RIO, 2014).

We sampled 30 sites located in 4 tributaries within the watershed (Anil—8, Itaperiti—7, Mariquita—8, and Santa Maria—7, Fig. 1). We chose these four tributaries due to the presence of at least one river section that traversed a riparian forest remnant that covered both margins of the stream. Along each tributary, we distributed sampling sites along a continuum so as to obtain samples within the preserved upstream section, the fragment and adjacent agricultural sections, spaced at least 300 m apart. We implemented this design in order to maximize the possible combinations of sub-watershed, riparian, and reach buffer agricultural land cover. Furthermore, in order to avoid the effects of local point source impacts, we selected sites located upstream from any urban or industrial locations.

Land-use estimates

We generated land use and land cover data for the Guapiaçú basin from satellite images obtained by the SPOT5 sensor for the year of 2014 through a supervised classification technique using ArcGIS software (ESRI, Redlands, CA, USA 2013). For each sampling site, we quantified land use (represented as a percentage of agricultural land cover) for three different spatial scales: sub-watershed scale (WS), riparian buffer scale (RB; 30 m wide), and a reach buffer scale (30 m wide and 150 m in length; sensu Allan, 2004).

Environmental variable measurements

At each sampling site, we measured riparian canopy cover using a spherical densiometer, with measurements taken in four directions at midstream. Measurements were taken by the same person in all sites to avoid inter-observer variation. We measured velocity in at least 7 locations per transect, or every 30 cm, using a velocity meter (Pygmy current meter, Teledyne- Gurley, Troy, 10 NY). Discharge was calculated at each transect by multiplying the mean velocity by the cross-sectional area of flow. We determined substrate size metrics (D16%, D50% and D84%) using the Wolman pebble count method (Wolman, 1954).

We recorded temperature, water oxygen concentrations, and percentage saturation every five minutes for a minimum of 36 h comprising at least two night time periods using HOBO®-U26 oxygen loggers (Onset Inc, MA, USA). Minimum oxygen concentration (as percent saturation) and temperature data were obtained from the previous dry season before macroinvertebrate sampling (2014). We measured soluble reactive phosphorus (SRP) and ammonium (NH_4^+-N) concentrations in the water samples collected and filtered using a 0.7 µm glass fiber filter (GF/F, Whatman, Maidstone, Kent, UK). We measured NH_4^+-N using the OPA fluorometric method (Trilogy fluorometer, Turner Designs, Sunnyvale, CA, USA) (Taylor et al., 2007) immediately following sample collection. Samples collected for soluble reactive phosphorous (SRP) were frozen immediately after collection, and concentrations were determined by absorbance using the molybdate-antimony colorimetric method (Murphy & Riley, 1958).

We sampled coarse particulate organic matter (CPOM) by collecting all plant material present within a meter wide transect across the stream at each sampling site and separating it into large wood, twigs, and leaves (Lamberti & Gregory, 2007). We sampled suspended fine particulate organic matter (FPOM) by filtering a known volume of water through a 2.7 µm pore filter (GF/D, Whatman, Maidstone, Kent, UK) until the filter clogged. We dried coarse and fine benthic matter in the lab until constant weight was achieved and then placed each sample in a muffle furnace for 1 h at 500 °C. After samples cooled to room temperature, the remaining material was weighed and Ash-Free Dry Mass (AFDM) was determined by difference. The ratio of organic to inorganic matter in seston was determined by dividing the AFDM by the ash mass remaining in the filter after combustion.

We sampled periphyton from five rocks collected randomly at each site. Rocks were subsequently scrubbed to remove organic material. Rock surface area was calculated from rock length–width measurements. We transported samples to the laboratory on ice and in a dark insulated container. Periphyton samples were filtered using ashed, pre-weighed glass fiber filters (GF/F, Whatman, Maidstone, Kent, UK), filters were then dried at 60 °C for 24 h, weighed, combusted at 500 °C for 1 h, and reweighed to obtain AFDM and inorganic mass. We measured periphyton chlorophyll-*a* (chl-a, hereafter) by filtering subsamples of the material through pre-combusted and pre-weighed 25-mm glass fiber filter. For each filter, we extracted chl-*a* in 10 ml of 90% ethanol and kept in the dark for 24 h prior to analysis by spectroscopy (monochrome method based on Lorenzen, 1967).

Macroinvertebrate sampling

We collected macroinvertebrates using a D-frame net with a 0.250 mm mesh. We sampled by disturbing the substrate at 20 one-meter-long segments distributed along the reach in order to proportionately include all microhabitats and substrates found. We preserved samples in the field in 70% ethanol. Before picking under a stereomicroscope, we conducted a search for large and rare taxa from the whole sample. We then picked samples using sub-sampling, by dividing the samples in 8 parts and picking at least 200 cumulative individuals from randomly selected fractions, then proceeding until that fraction was thoroughly picked. Animals found in the initial search for large and rare were added to the sample totals after sub-sampling values were extrapolated. We identified macroinvertebrates to the level of family (Merrit & Cummins 1996; Baptista et al., 2006) since previous studies have shown that level of taxonomic resolution is sufficient (Gayraud et al., 2003; Mueller et al., 2013). Adult beetles of the Elmidae family were considered a different taxon than Elmidae larvae, since adults and larvae greatly differ in anatomo-functional traits (Brown, 1987; Lloyd & Sites, 2000). Also, leaf-mining chironomids (*Stenochironomus*) were considered a separate taxonomic due to their unique functional aspects and also because previous studies have shown they are the most abundant shredders in the study region (Moulton et al., 2010; Silva-Junior & Moulton, 2011).

Macroinvertebrate community metrics

Statistical analysis was performed for the taxa that represented over 99.5% of the abundance in in all samples combined (30 taxa, see results section for more details). We compiled macroinvertebrate data using three different methods. A taxa abundance matrix was produced using the Hellinger transformed abundances (Legendre & Gallagher, 2001). The functional character community weighed means matrix (CWM) was constructed by generating a fuzzy coding matrix. Creating a fuzzy logic matrix consists of establishing, a degree of affinity with a number of predefined anatomo-functional characters for each taxon (Chevenet et al., 1994). We chose functional characters that are most correlated with the types of impacts associated with agriculture and grazing-related land-use impacts (Table 1). We intentionally excluded dispersal traits because those are often the mechanisms for spatial structuring (Finn & Poff, 2005; Brown & Swan, 2010; Saito et al., 2015b).

Animal feeding modes were included because land use is expected to cause changes in basal food resources along the impact gradient (Podraza et al., 2000; Ding et al., 2017). Respiration strategies are directly linked to both siltation or hypoxia resistance and different strategies are associated with greater or lesser resistance to this type of impact (Calapez et al., 2018; Chen et al., 2019). Functional characters related to body shape and fixation mode inform both animal flow resistance, as well as adaptation to silted environments (Lange et al., 2014; de Castro et al., 2017). The affinities assigned to each taxonomic group were based on laboratory observations and on studies that evaluated functional characters for neotropical families (Baptista et al., 2006; Tomanova & Usseglio-Polatera, 2007; Milesi et al., 2016; Serra et al., 2016). We generated affinity scores for each site using the *FD* package in R (Laliberté et al., 2015).

For each site we also calculated the 9 macroinvertebrate metrics that compose the Guapiaçú-Macacú basin Multimetric Index (GMMI, Oliveira et al., 2011). This index was developed specifically for the Guapiaçú-Macacu basin and is sensitive to various sources of anthropogenic impacts. These metrics were; the percentage of plecopteras; percentage of ephemeroptera plecoptera and tricoptera (% EPT); the percentage of shredders in the sample (% Shredders); the richness of families; the richness of trichopteran families; shannon diversity index (H); percentage of mollusks and diptera in the community; the ratio between trichopterans of the Hydropsychidae family and total trichopterans in the sample; and the ratio between chironomids and dipterans. For this study, the percentage of mollusks was not considered, due to the fact that invertebrate samples were elutriated in the field and that may have caused the number of heavier shell mollusks to be artificially reduced. That metric was replaced by the percentage of dipterans in the sample.

Table 1 Description of functional traits and trait categories used for the construction of the CWM matrix

Grouping feature	Traits
Body size (mm)	< 2.5 mm
	2.5–5 mm
	5.0–10 mm
	> 10 mm
Feeding style	Collector gatherer
	Shredder
	Scraper
	Collector filterer
	Predator
Fixation method	Silk gland
	Swimmer
	Crawler
	Burrower
	Temporarily attached
	Case builder
Body shape	Flat-streamlined
	Cylindical
Respiration	Air store
	Stigmata
	Gills
	Cutaneous
Total	

Statistical analyses

We imputed missing values in the environmental variables matrix using a principal component analysis (PCA)-based technique via the function imputePCA in the R package missMDA (Husson et al., 2016). All environmental variables were standardized and land-use-related variables were all expressed in arcsine square-root-transformed proportion of forest cover. Prior to statistical analysis, land-use and environmental variables were tested regarding variance inflation factors (VIF). Variables with VIF > 10 were excluded from further analysis. We summarized the remaining environmental variables across all sampled sites using a principal component analysis (PCA), and the first two axes were used to highlight the correlations between environmental variables.

In order to generate spatial variables that could potentially represent the spatial structuring of the macroinvertebrate communities present, we produced spatial variables that take water flow directionality into account using Asymmetric Eigenvector Maps analysis (AEM, Blanchet et al., 2008a). These spatial variables (AEMs) are eigenvectors obtained from the decomposition of the spatial variation of a matrix of connectivity between sites. AEMs with descending eigenvalues represent different possibilities of large to small-scale geographical structuring, thus, allowing to model broad to fine spatial organization when ordered by value. In this case, AEMs were generated using a watercourse distance matrix was obtained from using the coordinates of each sampling site and a watercourse shapefile for the Guapiaçú watershed using the Riverdist package in R (Tyers, 2016). We produced a directional downstream distance matrix by combining the position of each sampling site within the watershed, the direction of water flow and weighed by watercourse distances using the 'adespatial' package in R (Jombart et al., 2019). Only AEMs) that had positive values were retained for further analysis.

For each of the macroinvertebrate matrices, we used RDA-based procedures to calculate the proportion of the variance explained by the three sets of candidate predictor variables. A global RDA test that included all predictor variables was performed prior to forward variable selection, and forward selection was only performed for models in which the global model was significant ($P < 0.05$). We used a partial redundancy analysis (pRDA, Blanchet et al., 2008a, b) based technique to partition the total variation of the macroinvertebrate data that was explained by the spatial, environmental and land-use variables individually. In this procedure the variable selection was performed with a double-stopping criterion to minimize the risk of including too many predictors (Blanchet et al., 2008b), using the *ordiR2step* function of the vegan package (Oksanen et al., 2016). To minimize the influences of the number of sampling sites and number of explanatory variables, we always used adjusted R^2 values (Peres-Neto et al., 2006). We tested the significance of the fractions explained by the spatial eigenvectors (AEMs), local environmental variables, and land-use variables separately using 999 permutations at a significance level of 0.05 (Legendre & Legendre, 1998; Peres-Neto et al., 2006). The fractions of the total variance that were explained by more than one of the variable groups will be hereafter termed spatially structured environmental variation, spatially structured land-use variation, land-use-associated environmental variation, and spatially structured land-use-related environmental variation.

In order to test the influence of the inclusion of rare families in the analysis, after performing the analysis using the matrices considering all taxa, the procedure above was repeated, removing the rarest taxa at each iteration. Rarity was defined as the smallest proportion of the abundance of a given taxa in all sites grouped together (Flather & Sieg, 2007). For each run, a new set of Hellinger transformed abundances, CWM and GMMI indexes matrices were produced and the entire proceeding listed above was repeated until there only 2 taxa left. All statistical analyses were performed in the R environment (R Core Team, 2015).

Results

Environmental conditions

The studied streams consisted of well-preserved headwaters with variable amounts of agricultural land use. Downstream sites presented different degrees of impairment, with environmental variables presenting a wide range of variation (Table 2). After performing Variance Inflation tests, 15 of the original 21 environmental variables were retained for further analysis.

The first two PCA axes of the environmental variables explained 47.2% of the total variation of the data (Fig. 2). Sites impacted by land use tended to be positively ordinated along PC1 with preserved sites presenting negative values. PC1 was positively

Table 2 Environmental variables used in the present study, organized by variable types. Asterisks indicate variables retained for further analysis after variance inflation test

Variables	Short Names	Unit	Min	Max	Mean ± SD
Physical					
Canopy cover*	% Cover	%	0.0	90.7	48.2 ± 33.7
Depth*	Depth	cm	16.8	51.1	27.4 ± 9.0
Width*	Width	cm	199.7	960.0	505.8 ± 208.9
W/D ratio	W/D	–	4.1	37.6	19.9 ± 9.1
Temperature*	Temp	oC	16.6	20.4	18.3 ± 1.0
Discharge	Discharge	l/s	1.5	454.8	192.9 ± 96.9
Gravelometry					
D16*	D16	mm	< 1	70.0	14.7 ± 21.3
D50	D50	mm	< 1	120.0	56.6 ± 38.7
D84*	D84	mm	< 1	330.0	114.9 ± 95.8
Chemical					
pH*	pH	–	5.3	7.9	6.3 ± 0.7
NH_4	NH4	µg/l	1.0	17.6	4.0 ± 4.8
PO_{4*}	PO4	µg/l	8.6	24.0	15.6 ± 4.1
Minimum 24 h O_2% Sat*	Min O2	%	50.1	99.2	91.9 ± 10.4
Biological					
Seston organic mass*	Seston OM	mg/l	0.0	0.0	5.4 ± 5.3
Seston ratio (O/I)*	Seston O/I	–	0.1	26.0	4.0 ± 5.9
Periphyton organic mass	Periphyton OM	mg/cm^2	0.2	1.8	7.0 ± 4.0
Periphyton ratio (O/I)*	Periphyton O/I	–	0.2	1.1	0.5 ± 0.2
Periphyton ChlA area concentration*	Periphyton CHL	$\mu g/cm^2$	0.40	0.00	3.1 ± 1.6
Periphyton Autotrophic Index *		–	500.6	6537.8	2835.5 ± 1394.4
Coarse organic benthic matter*	CPOM	g/m^2	0.4	111.9	29.0 ± 30.3

correlated with both suspended particles concentrations ($R = 0.38$) and the proportion of organic mass in suspended material ($R = 0.41$) and negatively correlated with canopy cover ($R = -0.40$), periphyton chl-*a* concentration ($R = -0.64$) and organic to inorganic ratio ($R = 0.8$), minimum nighttime oxygen saturation values ($R = -0.76$) and small (D_{16}, $R = -0.83$) and large (D_{84}, $R = -0.73$) substrate size metrics. The ordination of sites along PC2 was mainly associated with position along the river, with headwater sites scoring high values along the axis. PC2 was positively correlated with canopy cover ($R = 0.72$), periphyton autotrophic index ($R = 0.76$), stream width ($R = 0.65$), coarse allochthonous matter area concentrations ($R = 0.66$), and pH ($R = 0.41$), while being negatively correlated to the size of the small fraction of substrate (D_{16}, $R = -0.60$), periphyton chl-*a* area concentrations ($R = -0.51$), stream temperature ($R = -0.50$) and the proportion of suspended organic matter ($R = -0.47$).

Macroinvertebrate community composition

Macroinvertebrates were distributed within 49 taxa. A total of 13,969 macroinvertebrates were picked and, after extrapolating the site abundances due to sub-sampling, 99.5% of the individuals were of 30 families or morpho groups, with 95% of the community composition being represented by 12 families, namely: Chironomidae, Leptohyphidae, Elmidae (Larvae and Adults), Baetidae, Simulidae, Hydropsychidae, Helicopsychidae, Leptophlebiidae, Hydroptilidae, Stenochironomus, and Ceratopogonidae in decreasing order of abundance (Fig. 3).

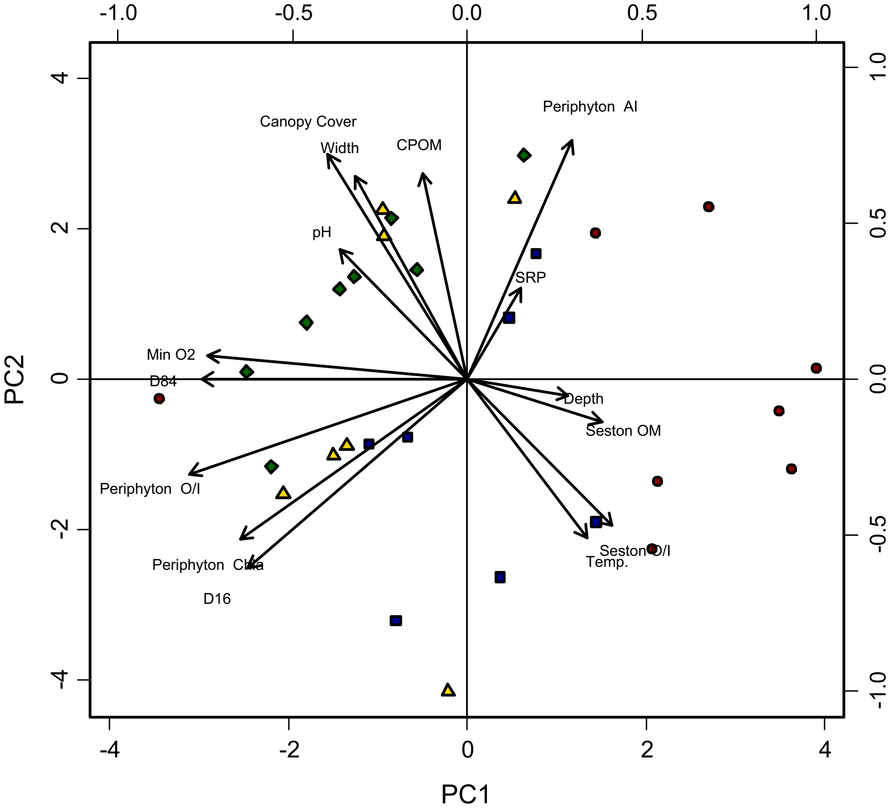


Fig. 2 Principal components analysis showing the variability within sampled sites located in the four streams sampled in the Guapiacu basin. Squares = Anil; Circles = Itaperiti, Triangles = Mariquita, Crosses = Santa Maria. Primary axes represent principal component scores. Secondary axes represent correlations of variables with principal components. See Table 1 for variable short names

Partial redundancy analysis

After performing the Asymmetric Eigenvector maps analysis, 12 positive spatial variables were retained for further analysis. Variables representing both broad scales (AEMs 1, 2 and 3) and fine spatial scales (AEMs 7, 8, 9, 10 and 11) of spatial structuring were selected across the three data matrices. The highest level of spatial structuring was found for the functional CWM, with 53% of the variation being explained by 7 spatial variables (Table 3). The macroinvertebrate abundances matrix had 26% of the variance explained by 6 spatial variables. The global model for the spatial RDA for the GMMI metrics was not significant and pRDA was not performed for that dataset. AEMs 2, 3 10 and 11 were most frequently the first selected indicating that these are the most important spatial gradients structuring the macroinvertebrate community for functional CWMs and abundances (Table 3).

The proportion of variance explained by land-use variation alone was 23%, 14% and 12% for the GMMI metrics, abundances, and functional CWMs respectively (Fig. 5A–C). All three 3 of the land-use variables tested were retained by the pRDA for at least one of the matrices. For the CWM and GMMI matrices, only one variable was retained, (RCB) which represented the presence of agriculture in the local reach scale (Table 3). All three land-use variables were retained by the abundance matrix pRDA, with the percent of agricultural land cover within the whole riparian corridor (RB) being the most important, followed by local (RCB) and whole watershed agriculture cover (WS).

Of the 15 environmental variables tested, 5 were retained by at least one of the three pRDAs (Table 3). Notably, minimum nighttime oxygen saturation was selected as the most important environmental variables across the three groups of metrics (Table 3, Fig. 4A–C). Environmental variation explained 17% of the variance present in the abundance matrix. Sites that presented intermediate levels of agricultural land use were concentrated in negative values of the second axis of the ordination. (Fig. 4A).

Taxa associated with well-preserved sites were mainly trichopterans of the Leptoceridae and

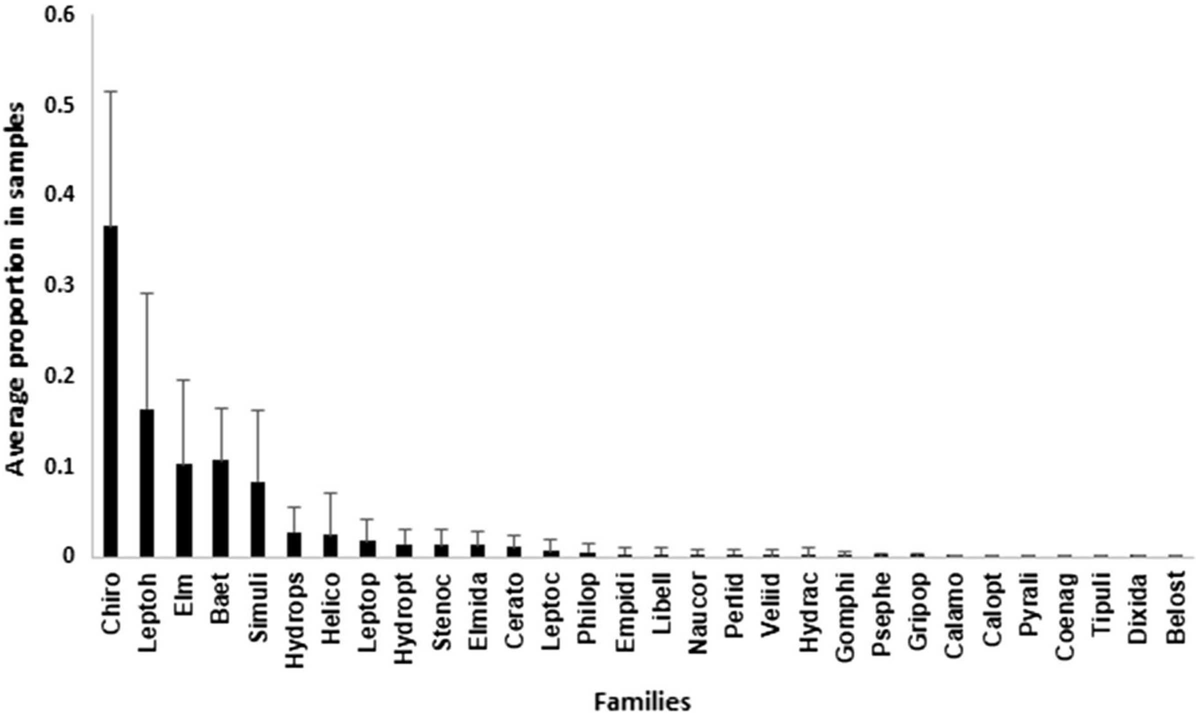


Fig. 3 Rank abundance bars representing the distribution of families in the sampled sites. Abundances are expressed as the average percentage within samples and vertical bars represent the Standard deviation. For taxa codes, see Appendix S1

Table 3 Table of selected variables for each pRDA performed for the three invertebrate data matrices

Matrix		Retained variables	Df	F	*P*
Abundance					
	Spatial	AEMs: 3,2,10,7,11,8	6	2.467	< 0.001
	Environmental	Min % O_2, Canopy Cover	2	3.901	< 0.001
	Land Use	RB30, RCB 150 × 30, WS	3	3.031	< 0.001
Functional traits					
	Spatial	AEMs: 2,3,10,11,8,9,1	7	5.611	< 0.001
	Environmental	Min % O_2, Width, Periphyton (O/I) Ratio, Temperature	4	5.694	< 0.001
	Land Use	RCB 150 × 30 m	1	5.002	0.005
GMMI metrics					
	Spatial	N/S	NA	NA	NA
	Environmental	Min % O_2, Canopy Cover	2	7.409	< 0.001
	Land Use	RCB 150X30m	1	9.644	< 0.001

Calamoceratidae families, ephemeropterans of the Leptophlebiidae family as well as both the plecopteran families found in the studied area (Gripopterigidae and Perlidae), followed by trichopterans of the Philopotamidae and Helicopsichidae families, as well as leaf-mining chironomids (Stenochironomids). Intermediate impact sites were mostly associated with the higher proportion of Hydroptilidae trichopterans and dipterans of the Empididae and Simuliidae families. Sites with higher degree of impairment presented a notable increase in water mites and non-leaf-mining chironomids, as well as an increase in dragonflies, damselflies, and hemipterans (Fig. 4B).

Environmental variation explained 39% of the variation in functional traits. The main variables structuring the affinity of functional attributes across sampled sites were minimum O_2% saturation, canopy cover, temperature and the organic to inorganic ratio of periphyton. However, the ordination of functional traits by the environmental gradient did not conspicuously separate sites according to the increase in agricultural land use in both pRDA axes (Fig. 4C).

Functional traits that were strongly correlated with the first axis of the ordination were related to the collector gatherer (positive) and filterer (negative) feeding habits, and gills respiration. Along the second axis of the ordination, the main functional traits were related to size, with animals ranging from 2.5 to 5 mm being positively correlated and animals ranging from 5 to 10 mm being negatively correlated. As a general pattern, sessile animals were associated with wider streams that maintained high canopy cover. Larger predators, collector gatherers, and burrowing animals were associated with low night-time oxygen availability while scrapers were mostly associated with sites that had low canopy cover but did not have low night-time O_2 saturation (Fig. 4D).

The GMMI matrix had 30% of the variation explained by environmental variables. Increasing amounts of local agriculture impact were related to more positive values along the first axis of the ordination. The percentage of shredders and percentage of plecopterans in the samples were largely associated with local canopy cover. Diversity, family richness, and trichopteran family richness were associated with the least impacted sites that had higher night-time O_2 saturations (Fig. 4E). Metrics associated with sites that presented the most amount of agricultural land use were the proportion of Hydropsychidae within trichopterans the percentage of dipterans in the sample and the ratio between chironomids and dipterans. The percentage of EPT in the samples tended to be associated with sites that presented intermediate levels of impairment due to agricultural land use, mostly due to the increase of the amount of grazing ephemeropterans of the Baetidae and Leptohyphidae families (Fig. 4F).

Variance partition

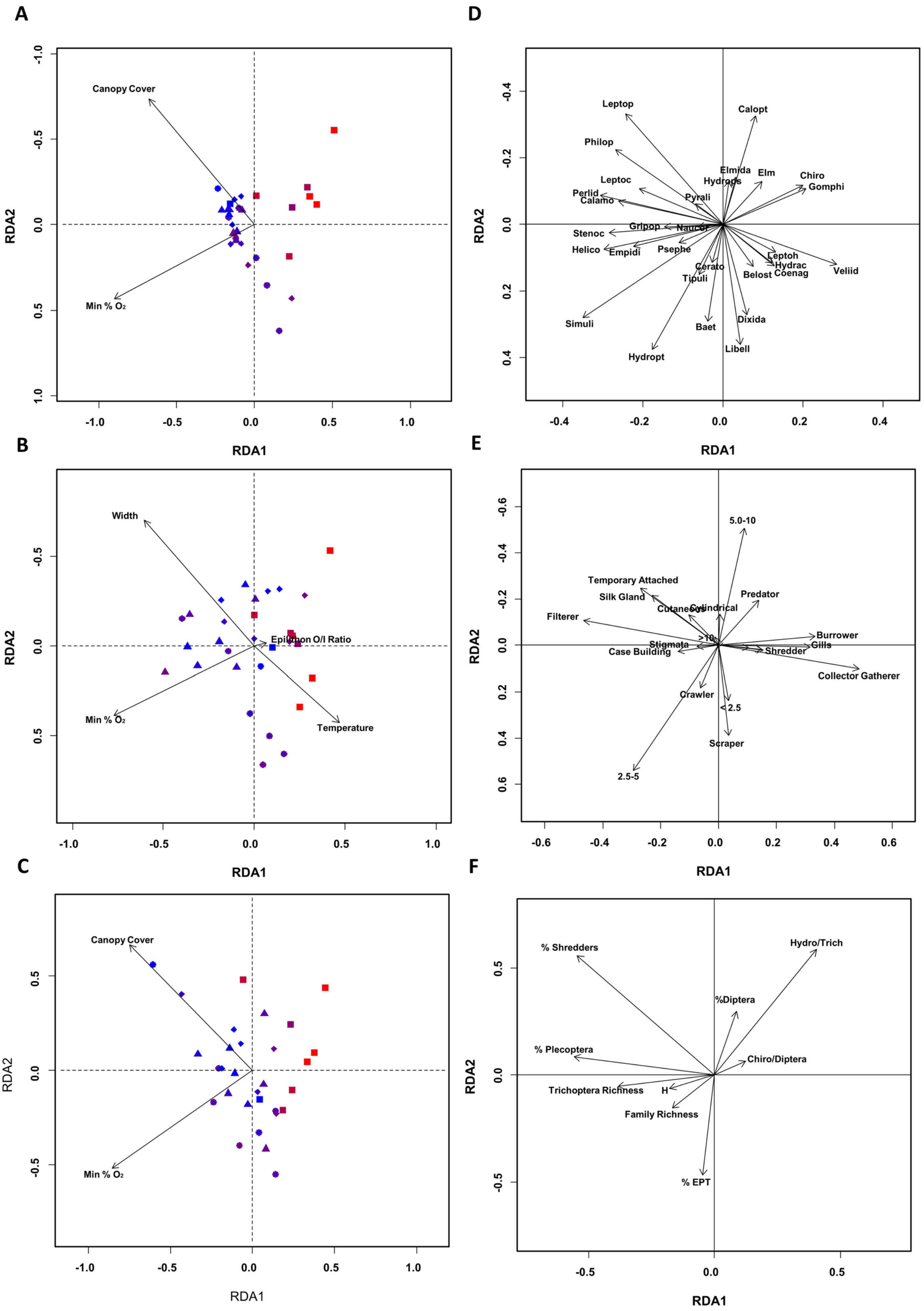
The total variation explained by spatial, land-use, and environmental variables combined was 27% for abundances, 57% for the functional CWM, and 31% for the GMMI metrics. For the three matrices, land-use and environmental variables explained a significant portion of the variation (Table 3). The abundances matrix had 8% of the variation explained exclusively by spatial factors, while pure environmental or land-use-related variables represented less than 1% of the explained variation (Fig. 5A). Although all of these fractions were statistically significant (Table 3), most of the variance was explained by the spatially structured land-use-related environmental variation fraction (12%), followed by land-use-related environmental variation and spatially structured land use (2%), (Fig. 5A).

For the functional CWM matrix including all 30 families, the largest portion of the variation explained was exclusively by spatial structuring (17%). Spatially structured environmental variation explained 28% of the variation, and the intersection among the three variable sets comprised 10% of the variation (Fig. 5B). The proportion of the variation explained by land-use, environmental variables, as well as by land-use-related environmental variation was low (3%, 0%, and > 1%, respectively).

Since the global model for spatial variables was not significant for the GMMI metrics, there was no variance explained exclusively by spatial variables or the associated fractions. The largest fraction of variance was explained by land-use-related environmental variation (22%). The pure environmental fraction explained 8% of the variation and the pure land-use-related variation explained 1% of the variation (Fig. 5C).

Rare taxa removal

The abundance matrix presented a behavior of less overall variance explained when more taxa were included in the analysis, with the highest amount (68%) being explained when considering only four taxa. When considering only two taxa, global models for all three sets of explanatory variables were not significant. The distribution of variance explained by each variable group and intersections was relatively stable between 30 and 19 taxa (Fig. 5D, see


A
Canopy Cover
Min % O₂
RDA1
RDA2
D
Leptop
Calopt
Philop
Elmida
Elm
Chiro
Gomphi
Hydrops
Leptoc
Pyrali
Perlid
Calamo
Gripop
Naucor
Stenoc
Helico
Empidi
Psephe
Leptoh
Hydrac
Coenag
Veliid
Cerato
Belost
Tipuli
Dixida
Simuli
Baet
Libell
Hydropt
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Width
Epilithon O/I Ratio
Min % O₂
Temperature
E
5.0-10
Temporary Attached
Silk Gland
Predator
Cutaneous
Cylindrical
Filterer
>10
Burrower
Stigmata
Gills
Case Building
Shredder
Collector Gatherer
Crawler
<2.5
Scraper
2.5-5
C
Canopy Cover
Min % O₂
F
% Shredders
Hydro/Trich
%Diptera
% Plecoptera
Chiro/Diptera
Trichoptera Richness
H
Family Richness
% EPT

◀**Fig. 4** Sites per environmental variable plots of redundancy analysis (RDA) showing the ordination of invertebrate metric groups regarding their ordination across the main environmental gradients for **A** = abundance, **B** = functional, **C** = GMMI. Colors indicate low (Blue) to high (Red) amount of agriculture land cover quantified at the local scale (30 × 150 Reach Buffer). **D–F** Taxonomic, functional traits and GMMI metrics ordination corresponding to the environmental gradients

Appendix 2 for a detailed report on retained variables). Between 17 and 4 taxa, the amount of variance explained increased in a steady fashion. The spatial and land-use variables retained by the pRDAs were consistent along the rare taxa removal gradient. For the environmental variables, CPOM biomass was retained for some models with a reduced number of taxa.

For the functional CWM, the amount of inertia explained tended to be lower with the removal of rare taxa. The amount and proportion of variance explained by each variable group were notably stable down to using the 7 most common taxa for the analysis (Fig. 5E). This was also true regarding the variables retained by the pRDAs. Below 7 taxa, the amount of possible functional group assignments decreased drastically and the amount of variance explained was greatly reduced, with only spatial pRDAs remaining when less than 5 taxa were considered.

For the GMMI metrics, total variance explained remained stable until the 14 most common taxa were considered. With less than 14 taxa, the global model for environmental variables was not significant until only nine taxa were included. The highest amount of variance was explained when considering only the 9 most common taxa (45%) (Fig. 5F). With 9 taxa or less, the global model for spatial variables became significant with AEMs 2, 3, 10, and 11 being retained.

Discussion

Effects of spatial processes in structuring macroinvertebrate communities

In support of similar studies (Zhang et al., 2014; Wilson & McTammany, 2016; Nicacio & Juen, 2018; Wan et al., 2018; Zawalski et al., 2019), we found evidence that stream macroinvertebrate communities are both spatially structured and filtered by local environmental conditions. The relative proportion of the variation explained by spatial structuring was similar to other studies that investigated the relative importance of space and environment in structuring macroinvertebrate communities (Landeiro et al., 2012; Ding et al., 2017; Nicacio & Juen, 2018). However, spatial structuring was marginally higher in this study for the abundances and functional CWM matrix compared to similar efforts in the South American Atlantic Rainforest domain (Siqueira et al., 2012b; Padial et al., 2014). We attribute the greater role of spatial factors in this study to our sampling design and the incorporation of directional processes. Our sampling design facilitated the detection of spatial processes because we had both low-grain and high-grain spatial variation sampling, improving our ability to detect directional processes such as the downstream drift of benthic macroinvertebrates (Diniz-Filho et al., 2012; Valente-Neto et al., 2018).

Selected spatial variables were similar across matrices, indicating that similar spatial processes were responsible for both the functional and taxonomic structuring of the communities. Other studies that explicitly compared the susceptibility of taxonomic and functional characterizations of benthic invertebrate communities to spatial structuring found similar results (Finn & Poff, 2005; Feld & Hering, 2007; Heino et al., 2007). When watercourse distances and directional effects are explicitly accounted for, this importance of spatial structuring for macroinvertebrate communities and environmental factors can be even more marked (Landeiro et al., 2011, Wan et al., 2015, Nicacio and Juen 2018, reviewed by Tonkin et al., 2018a, b). This phenomenon has also been demonstrated for Atlantic Rainforest riverine systems (Siqueira et al., 2012a, b, 2015; Colzani et al., 2013; Saito et al., 2015a, b and others). In this study, while large-scale spatial variables were often selected before small-scale variables, in global models that were global models were significant, all matrices retained at least one small-scale variable demonstrating that local scale spatial variation is also an important structuring element for these communities (Landeiro et al., 2012; Grönroos et al., 2013; Li et al., 2019).

The amount of variation explained by spatially structured land use was dependent on the spatial scale of the land-use variables that were retained by each of the three matrices. While the joint effects of spatial structuring and land use explained a large

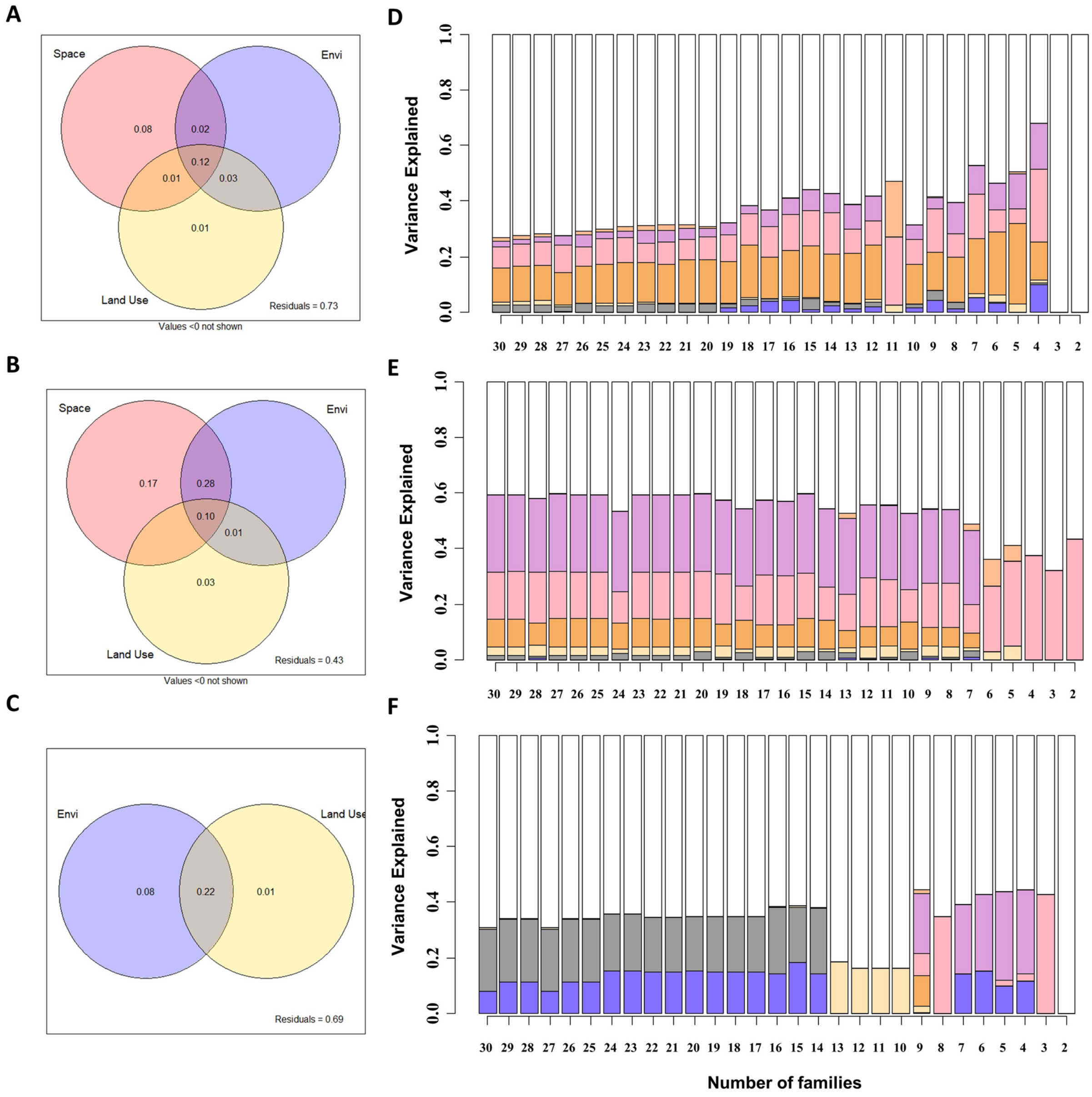

Fig. 5 Variance partition results for the dataset containing 30 families for the **A** taxonomic matrix, **B** functional traits matrix, **C** GMMI metrics and variance partition results after the removal of rare taxa for **D** taxonomic matrix, **E** functional traits matrix, **F** GMMI metrics

portion of the variation of the taxonomic composition, the local scale-related land-use variables that were retained for the CWM and GMMI matrices did not share significant amounts of explained variance with spatial structuring, indicating that local-scale agricultural land use was less prone to spatial structuring within the watershed context.

Environmental drivers of macroinvertebrate assemblages in the Guapiaçú basin

Based on the environmental variables retained by the three matrices, we can infer that the main local factors structuring the sampled communities studied were the presence of stream side forest (canopy cover), heterogeneity of habitat (stream width), and hypoxia stress (night-time oxygen saturation). Local canopy cover was selected for two of the groups of metrics and can be a surrogate of many mechanisms that have the potential to act as local filters for macroinvertebrate communities, such as light availability, primary productivity, temperature, and the supply of terrestrial organic matter to adjacent streams (Gregory et al., 1991; Naiman et al., 1997), as well as negatively affecting taxa with natural inverse phototaxis.

There was a marked differentiation between sites that had medium and high levels of adjacent agricultural land use (Fig. 4A–C). Sites that had intermediate levels of agricultural land use had a broad range of combinations between the amount of local canopy cover and variables related to local siltation impacts and habitat heterogeneity, while most of the sites that presented high amounts of agricultural land use had very low amounts of canopy cover, were severely affected by local bank erosion and substrate homogenization, and were prone to night-time hypoxia events.

Night time oxygen saturation was found to be an important environmental variable for all metrics, even when a reduced number of taxa was considered (Supplementary Material 2). In highly impacted sites with reduced canopy cover, the possible effects of high oxygen availability due to increased daytime primary productivity was generally offset by the increased nutrient availability (Silva-Junior et al., unpublished results) with one site reaching 50% oxygen saturation overnight. It is important to note that at all sampling locations, oxygen sensors were deployed in the middle of the water column. Therefore, it is possible to speculate that, in certain types of substrata such as leaf packs and well-embedded cobbles, oxygen saturations might reach even lower night-time concentrations, generating a strong local filter for taxa that are not tolerant to hypoxia events.

Responses of different macroinvertebrate metric groups to land-use impacts

The metrics that composed the Guapiaçú Multimetric Index had the highest amount of variation explained by the intersection between land-use and environmental variables and greatly outperformed the purely taxonomic and functional traits matrices regarding their responsiveness to land-use-related environmental variation and no variance explained exclusively by spatial factors after variance partition. The pronounced differentiation between sites that had medium and high amounts of adjacent land use was also observable within the macroinvertebrate community through shifts in taxonomic composition and traditional bioindicator metrics, as well as in the functional composition. However, for functional traits that variation was not as marked when land-use variation was accounted for (Fig. 4A–C).

The total variance explained for the CWM matrix was higher than compared to the other two datasets, which has been observed in similar studies that compare functional and purely taxonomic approaches (Feld & Hering, 2007; Heino et al., 2007; Li et al., 2019). For the functional and taxonomic matrices, the amount of variance explained by the intersection of the three groups of explanatory variables strongly suggests strong correlation between spatial structure, land use, and environmental variation within the study area.

Since the GMMI was developed specifically for this region, we expected these metrics to perform well with respect to their responsiveness to land-use impacts (Oliveira et al., 2011, 2019). We expected environmental variation to explain a higher proportion of the observed variation in the functional traits CWM than in the purely taxonomic matrix, elucidating the functional pathways through which land use impacts macroinvertebrate communities (Vandewalle et al., 2010, de Castro et al., 2017; Ding et al., 2017 and many others). Although the amount of variation explained by environmental variables was high for the CWM matrix (58%), the environmental gradients were almost entirely confounded with spatial variables, with only 1% of the variation being explained exclusively by land-use-associated environmental variation.

A careful consideration of these results shows that while the ordination of sites regarding their functional trait composition was somewhat successful in separating sites with high amounts of local agricultural impact from the most preserved ones, sites with intermediate levels of agricultural impact were highly variable. Highly impacted sites tended to be dominated by collector gathering chironomids, while well-preserved sites maintained a high diversity of feeding strategies. Sites with intermediate impacts were dominated by either filter feeding simuliids or grazing ephemeropterans of the families Baetidae and Leptohyphidae.

The main environmental gradient determining these alternative states appears to be local canopy cover. However, the effects of environmental variables at sites with intermediate agricultural impact and high canopy openness were highly site specific and, thus, confounding the environmental gradient with large-scale spatial structuring (AEMs 2,3). On the second axis of the ordination, the main organizing traits were related to animal size categories. We found that large taxa were associated with both severely impaired sites (e.g., belostomatidae, libellullidae, vellidae, calopterigidae) which were located on the downstream sections, as well as with well-preserved headwater sites, (calamoceratidae, grypopterigidae, and large leptophlebiidae ephemeropterans). This might have further contributed to the low amount of variability explained by land-use-related environmental variation.

There is enough evidence that using family level taxonomic resolution is sufficient for assessing anthropogenic impacts in streams (Jones, 2008; Buss & Vitorino, 2010; Mueller et al., 2013). However, since one of the main environmental gradients detected here were related to hypoxia events, we could potentially detect a clearer response to environmental drivers of the functional traits with increased taxonomic resolution, especially for chironomids. For members of this group, traits that correlate with tolerance to hypoxic events can only be accurately assessed at lower taxonomic levels, such as tribe or subfamily (Serra et al., 2016; Calapez et al., 2018). In fact, Siqueira et al., 2012b found that the variation of rare chironomid species was almost exclusively explained by environmental factors for two independent datasets obtained from studies performed within the Atlantic Rainforest region. It is important to note that that study did not consider the role of directional processes when producing spatial variables.

Effects of including Rare Taxa

The removal of rare taxa revealed a diverging pattern between the taxonomic matrix and the CWM and GMMI. In general, the amount of variation explained for the two matrices where the complexity of the data set was reduced to either a number of functional traits or impact metrics increased or remained stable with the inclusion of rare taxa. For the taxonomic abundance matrix, there was an increasingly lower proportion of overall variance explained with the inclusion of rare taxa. Feld & Hering (2007) attributed the higher amount of variance explained by a simplified functional traits matrix to be evidence of the better performance of functional traits in revealing anthropic stressors in macroinvertebrate communities and not to the purely statistical effects of that simplification. Our results show the opposite trend, with a taxonomic matrix with a reduced number of rare taxa performing equally or better than a functional traits matrix. This may point out to the fact that using a higher number of response variables, thus, increasing the amount of variance to be explained by RDA techniques does not lead to a statistically fair comparison of the performance of the use of functional traits and purely taxonomic matrices.

While our analysis was not as robust as Heino & Soininen (2010) and Siqueira et al. (2012a, b), our results also seem to indicate that common species are similar or better at indicating turnover over environmental gradients. Roughly the same variables were retained by a reduced set of common species for the three datasets. From a practical standpoint, we conclude that when summarizing the community with either CWM or the metrics that compose the GMMI, using the 15 most common taxa yielded similar or better results than when using the whole community. For the abundance matrix, using the 18 most common taxa would not detect different spatial, land-use, and environmental gradients, while the greatest amount of explained variance would be obtained when considering only the 4 most common taxa. Although from a purely statistical standpoint, the highest amount of explanation of variance is desirable, even with a reduced number of taxa, the amount of variance explained by spatial factors could not be traced back to environmental variation driven by land use. Even for the GMMI metrics, the amount of variance explained by pure spatial and spatially structured environmental variation seems to increase across matrices when only the 5–6 most abundant families remain, indicating that common species are more prone to local patch dynamics or mass effects.

Final remarks

We found that spatial processes play an important role in determining the structure of macroinvertebrate communities in the Guapiaçú basin. As a result, directional spatial processes significantly confound our ability to quantify the amount of the variation in these communities that can be traced back to land-use impacts (King et al., 2005). If spatial processes were not considered in this study, we would have concluded that environmental variables explained 16% of the variation in abundances and 39% of the variation of functional metrics when in fact there was hardly any variation explained exclusively by environmental variables for those metrics. Only recently have studies explicitly addressed directional processes in streams (Göthe et al., 2013; Padial et al., 2014; Bertin et al., 2015). In small agricultural streams, the longitudinal propagation of local impacts seems to play an important role in shaping macroinvertebrate communities (Suga & Tanaka, 2013; Feijó-lima et al. 2018a, 2018b). Combined with our current results, we contend that explicit treatment of directional processes may improve our ability to discriminate the role of spatial structuring on macroinvertebrate communities. Furthermore, by assessing the effects of land use in different scales (WS, RB, and RCB), we could identify at which spatial dimensions macroinvertebrate communities respond to anthropogenic impacts mediated by changes in environmental variables (Finn & Poff, 2005; Mykrä et al., 2007; Feld et al., 2011).

Traditional bioindicator metrics outperformed the use of taxonomic and functional affinity matrices in detecting land-use-related environmental variation. We also found that a few common taxa drive much of the variation we observed in these communities, regardless of how the data were organized. Nevertheless, this is not a statement on the overall importance of rare species and does not advise regarding the conservation values of biodiversity. On that regard, we fully endorse Siqueira et al. (2012a) statement regarding how all species within the Atlantic Rainforest should be considered threatened and of relevance for conservation efforts. The methodological framework and results presented here are only attempts to present objective criteria for metric selection for decision makers and index developers.

Land use is a stimulus that impacts stream ecosystems through multiple pathways (Allan, 2004; Burcher et al., 2007). However, not all biological variation that is detected in an agricultural watershed is necessarily land use related. We believe that the analytical approach we employed for this study is useful in parsing the effects of environmental variation that is not related to anthropogenic impacts from land-use-driven variation in invertebrate communities that explicitly points towards mechanisms mediated by environmental variables. Finally, since these responses were driven by the most abundant taxa for all metrics, similar analytic approaches have the potential to be useful in curtailing sampling, sorting, and identification efforts. We believe that these findings are of great relevance for the development of bioindicator metrics in underdeveloped and tropical regions where the knowledge about macroinvertebrate taxonomy lags behind the urgency for the development of biomonitoring techniques to assess the integrity of riverine systems.

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Data availability The datasets and R code that support the findings of this study are available from the corresponding author, RF-L, upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare.

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