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Land use and local environment affect macroinvertebrate metacommunity organization in Neotropical stream networks

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Abstract

Aim: Changes in land use and cover (hereafter land use) affect freshwater ecosystems at different spatial scales. We tested the effects of land use on the dispersal capacity of stream macroinvertebrates through local and regional processes.

Location: In all, 183 Brazilian headwater stream sites, located in the Neotropical Savanna with variable land use and covering a total area of 46,394 km^2.

Methods: We used multiple regression models for distance matrices to identify the relative importance of environmental and landscape characteristics to explain community dissimilarity of stream macroinvertebrates with different mobility traits. As predictors, we calculated four distance metrics: environmental distance describing the dissimilarity in local conditions, the network distance accounting for distances across the drainage system and two distances measuring landscape resistance to dispersal (topographic and land use). We classified macroinvertebrates in dispersal groups according to their dispersal abilities (flying and drifting) and life story traits (voltinism, adult life span and body size). We tested the effects of these distances on all taxa and on the different dispersal groups, to explore whether biological traits would result in different metacommunity patterns.

Results: Our hierarchical clustering analysis identified five macroinvertebrate dispersal groups. The dispersal group 1 was mainly composed by aquatic obligate taxa, dispersal group 2 by taxa with low drift propensity, dispersal group 3 represented taxa with high directional flight capacity, dispersal group 4 included taxa with medium drift propensity and dispersal group 5 represented taxa with high drift propensity. We found that environmental distance and land use distance were the most important predictors explaining community dissimilarity for most of the dispersal groups.

Main conclusion: The metacommunity patterns found in this study suggest that environmental filtering was the most important community assembly mechanism at a local scale, whereas land use could constrain dispersal at the regional scale. Understanding these processes is crucial to meet conservation and restoration goals, especially in biodiversity hotspots. Our results reinforce the importance of considering entire catchments for preserving stream health and aquatic biodiversity and indicate the need for a much more integrative research between terrestrial and aquatic ecology.

1 | INTRODUCTION

Freshwater ecosystems such as rivers and streams are among the most impacted by human activities (IPBES, 2019). Human populations tend to disproportionality live near these ecosystems, greatly modifying the surrounding landscape and compromising ecosystem health (Sala et al., 2000). Where humans dominate, natural vegetation is replaced by anthropogenic land uses such as agriculture, silviculture, livestock grazing and urbanization. Changes in land use and cover (hereafter land use) affect freshwater ecosystems at different spatial scales (Stendera et al., 2012). So far, scientific attention has focused on the local scale effects of land use on freshwater ecosystems, that is, the relationship between land use and habitat modification (Martinuzzi et al., 2014). At this scale, land use can degrade riparian zones and instream habitats in different ways (Dala-Corte et al., 2020; Simião-Ferreira et al., 2018; Siqueira et al., 2015). For example, the loss of riparian vegetation causes biological changes such as the replacement of habitat specialist species by opportunistic and generalist ones (Castro et al., 2018; Heino, 2013; Siqueira et al., 2015), the reduction of organic matter inputs (Tiegs et al., 2019) and an increase in fine sediment inputs linked to streambed siltation (Feld et al., 2018). At the regional scale, land use fragments natural landscapes (Baguette et al., 2013) and streams occurring in those landscapes can be highly isolated (Urban et al., 2006; Zeller et al., 2012). For instance, Carlson et al. (2016) demonstrated altered dispersion of stream macroinvertebrates with aerial phases in streams surrounded by agriculture. Thereby, land use can significantly modify the movement of organisms across the landscape (i.e. dispersal), affecting regional freshwater biodiversity (Johnson et al., 2013).

Metacommunity ecology provides an ideal theoretical and methodological framework to explore how land use can shape regional freshwater biodiversity by modifying dispersal rates (Heino et al., 2017; Johnson et al., 2013). Different metacommunity studies have shown that the exchange of species between local communities can be significantly influenced by landscape configuration. For example, in river networks, geographical barriers such as mountains can limit the dispersal of stream macroinvertebrates with an adult aerial phase (Brown & Swan, 2010; Kärnä et al., 2015). At the same time, the fragmentation of the river network by droughts can force flying insects to disperse away from the river corridor to find suitable habitats for oviposition. For instance, Cañedo-Argüelles et al. (2015) showed that aridification led to increased overland dispersal of aquatic macroinvertebrates, which used available water bodies (e.g. pools) as stepping stones to disperse from one stream to another. Thereby, it is reasonable to expect that land use will have an impact on metacommunity organization through the modification of the landscape resistance to dispersal, defined as the degree of restriction to dispersal by the landscape (Heino et al., 2017; Johnson et al., 2013; Zeller et al., 2012). For example, the replacement of forests by agricultural fields could affect adult insects' dispersal rates through changes in physical barriers and habitat availability (Carlson et al., 2016; French & McCauley, 2019). On the contrary, the dispersal of obligate aquatic species (e.g. gastropods, crustaceans) and species with weak flying abilities should be less affected by land use at the regional level because their movements are restricted to the river network (Petersen et al., 2004; Sarremejane et al., 2020). Understanding the links between land use and freshwater biodiversity at the regional scale is urgent because it can help us to assess the anthropogenic impacts on subsidies between aquatic and terrestrial ecosystems (Carlson et al., 2016) and to plan biodiversity conservation across ecosystem boundaries (Beger et al., 2010; Leonard et al., 2017).

Here, our aim was to assess the effects of natural and anthropogenic factors on species sorting and dispersal-related mechanisms of stream macroinvertebrate metacommunities. We used neotropical streams as model systems because they are under increasing threats from human landscape alterations (Azevedo-Santos et al., 2019; Castro et al., 2018; Siqueira et al., 2015). Brazil is a country of continental dimensions that houses high freshwater biodiversity in different biomes and ecoregions (Agostinho et al., 2005). Among the Brazilian biomes, the Neotropical Savanna is constantly threatened by natural vegetation conversion into large agricultural landscapes (Simião-Ferreira et al., 2018; Strassburg et al., 2017). According to previous studies (e.g. Brown & Swan, 2010; Cañedo-Argüelles et al., 2015), we expected that both local environmental conditions and landscape configuration would shape macroinvertebrate metacommunities. We hypothesized that land use should have an effect on metacommunity organization by modifying the landscape structure, increasing the landscape resistance to dispersal, and that this effect would be dependent on the dispersal abilities of the organisms. For example, we expected strong flyers (e.g. Odonata) to
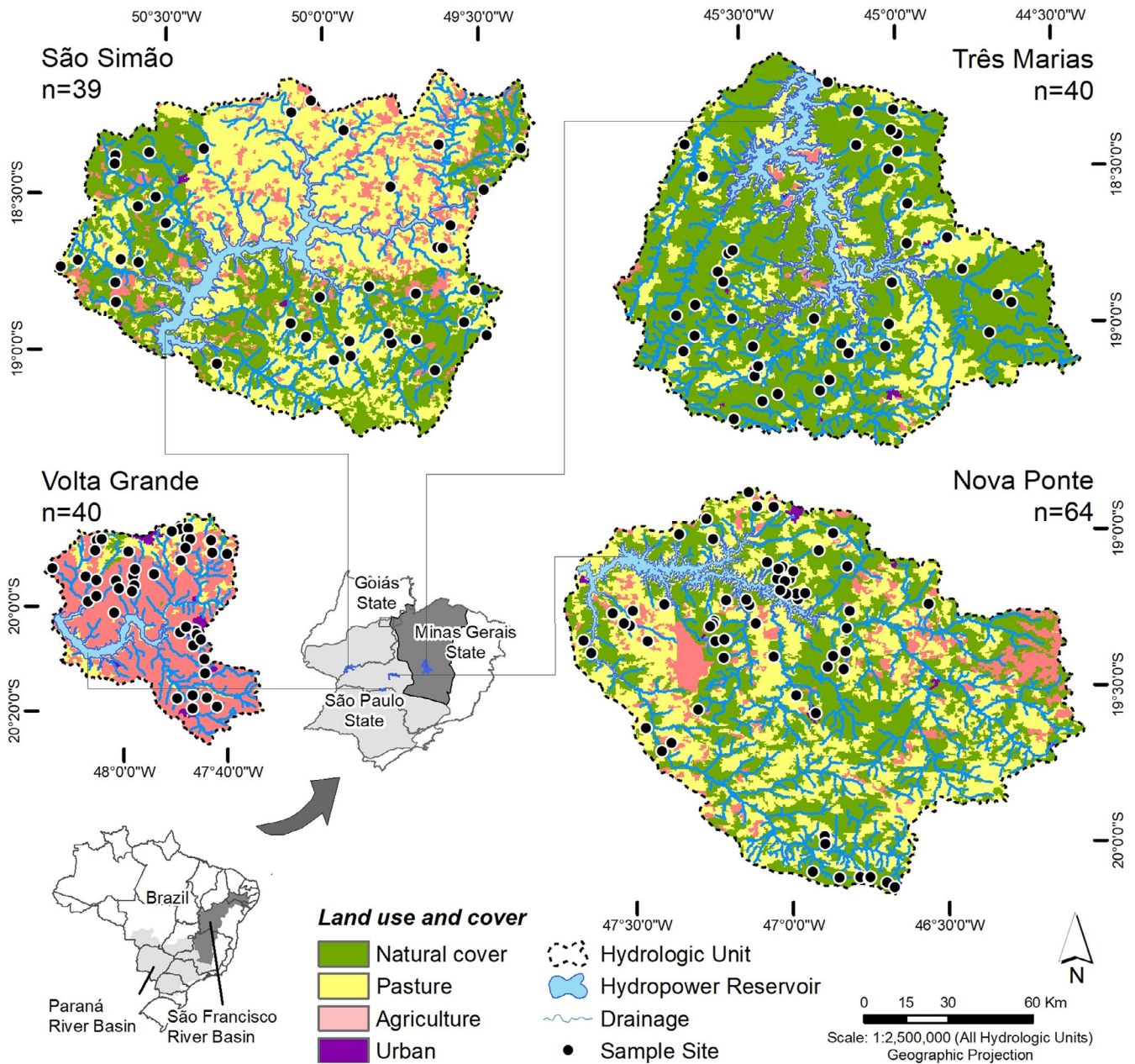
FIGURE 1 Stream site locations in the four hydrologic units in the Neotropical savanna (N = 183)

be more influenced by land use than aquatic obligate species (e.g. Gastropoda).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area was located in the Brazilian Neotropical Savanna (Cerrado biome), a global biodiversity hotspot (Myers et al., 2000) with both natural and anthropogenic land uses, the latter mainly related to agriculture and urbanization (Strassburg et al., 2017). Although soils exhibit high acidity, high aluminium concentrations, and low

nutrient concentrations, large-scale row cropping and livestock grazing have been established through use of chemical mitigation (Klink & Machado, 2005; Strassburg et al., 2017). The Brazilian Neotropical Savanna has a dry season from April to September, and a rainy season from October to March, with air temperatures ranging from 22° to 27°C and an average annual rainfall of 1,500 mm (Klink & Machado, 2005).

2.2 | Sampling sites

We sampled 183 headwater stream sites (first to third orders; Strahler, 1957). Sites were defined at a 1:100,000 scale and selected using a spatially dispersed random survey design (Stevens

TABLE 1 Trait, trait categories and trait coding sources. Explanations justify the rationale behind trait selection

Trait	Trait category	Explanation	Trait coding source
Directional flight capacity	Aquatic obligate Low Medium High	Organisms with high directional flight capacity can overcome dispersal barriers searching for suitable sites to reproduction.	Poff et al. (2006); Saito et al. (2015)
Drift propensity index	1–80	Aquatic forms with high drift propensity can disperse to long distances and colonize downstream sites.	Rader (1997)
Adult life span	Very short (<1 week) Short (<1 month) Long (>1 month)	Longer adult life span is linked to higher chance to disperse.	Poff et al. (2006)
Body size (cm)	<1 cm 1–1.5 cm >1.5 cm	Bigger organisms have larger dispersal structures (e.g. wings for insects, legs for crustaceans), and are therefore stronger dispersers.	Saito et al. (2015)
Voltinsm	Univoltine strategy (<1 generation/year) Multivoltine strategy (>1 generation/year)	Multivoltine species present more generations, therefore have more chances to disperse.	Poff et al. (2006); Saito et al. (2015)

& Olsen, 2004). We sampled 141 randomly selected sites and 42 hand-picked sites to ensure that both minimally disturbed and highly disturbed sites were represented. Sites were located in four different hydrologic units, located upstream to four major hydropower reservoirs (sensu Seaber et al., 1987): Três Marias (TM; $n = 40$) in the Upper São Francisco River basin; and Volta Grande (VG; $n = 40$), São Simão (SS; $n = 39$) and Nova Ponte (NP; $n = 64$) in the Upper Paraná River basin (Figure 1). The hydrological units comprised a total geographical area of 46,394 km^2 (NP = 15,358; SS = 13,950; TM = 13,613; VG = 3,473). One sample per site was collected in September from 2010 to 2013 (TM: 2010; VG: 2011; SS: 2012; NP: 2013), ensuring that samples were all taken during the dry season (Silva et al., 2017; Stevens & Olsen, 2004). The hydrologic units covered a wide land use gradient ranging from natural cover, pasture, agriculture and urban areas (Figure 1).

We determined the length of each stream site to be sampled by multiplying 40 times its mean wetted width, with a minimum length sampled of 150 m. We divided each site into 11 equally spaced transects. At each transect, we collected macroinvertebrates using a D-net following a systematic zig-zag pattern along the site to obtain a multi-habitat composite sample (Peck et al., 2006). Based on this standardized protocol, we obtained a total sampled area of 0.99 m^2 per site. We fixed the samples in the field with 10% formalin, and brought them to the laboratory, where 155 macroinvertebrate taxa were sorted and identified to family (except non-insect taxa to Bivalvia, Decapoda, Nematoda and Oligochaeta) and genus (Ephemeroptera, Plecoptera and Trichoptera, EPT) levels. Collected organisms included seven non-insect taxa (e.g. Mollusca and Annelida), 66 insect families (e.g. Odonata and Coleoptera) and 82 genera belonging to the Ephemeroptera, Plecoptera and Trichoptera. Compared to other better-studied biogeographical regions, the current knowledge of Neotropical macroinvertebrates does not allow identifying most taxa to species (Heino et al., 2018). Therefore, we

opted to consider all those different taxonomic levels in our analyses to capture the viable diversity in our dataset.

In each site, we first characterized water quality. For this, we measured electrical conductivity (μS/cm), water temperature (°C), pH and total dissolved solids (mg/L) using a YSI multi-probe. We also measured dissolved oxygen (mg/L), turbidity (NTU), total phosphorus (mg/L), and total nitrogen (mg/L) in the laboratory following Standard Methods (APHA, 2005; see Appendix S1). We then assessed physical habitat heterogeneity following a protocol developed by the US-EPA (Peck et al., 2006). From this protocol, we calculated a set of 24 habitat metrics (Table S1) that are described in Kaufmann et al. (1999; 2009). Those metrics included information on channel morphology, riparian structure, anthropogenic disturbance, discharge, flow type and substrate type. Thus, they captured both natural variability and anthropogenic stressors.

2.3 | Macroinvertebrate traits data

For each of the 155 taxa, we characterized five macroinvertebrate traits related with taxon capacity to disperse in aquatic and terrestrial habitats. Trait information was obtained from available databases (Poff et al., 2006; Rader, 1997; Saito et al., 2015) and expert knowledge (Table 1; Appendix S2, and Acknowledgments). These traits are useful surrogates of organismal dispersal capacity and included adult life span, voltinism (number of generations per year), body size, directional flight capacity and drift propensity (Sarremejane et al., 2020). We classified each taxon as very short (<1 week), short (<1 month) or long (>1 month) adult life span as described in Poff et al. (2006). For voltinism, we categorized the taxa as univoltine (<1 generation/year) or multivoltine (>1 generation/year) based on Poff et al. (2006) and Saito et al. (2015). We categorized each taxon into one of three body size classes: small (<1 cm), medium

(1–1.5 cm) or large (>1.5 cm) according to Saito et al. (2015). The directional flight capacity trait was compiled from Poff et al. (2006) and Saito et al. (2015), and we considered four different categories: aquatic obligate, low, medium or high directional flight capacity. Finally, we used the drift propensity index proposed by Rader (1997) as a surrogate of downstream dispersal of aquatic forms. This index is based upon several organism characteristics and behaviours like propensity to intentional drift, abundance in drift, and if the taxa are buried or exposed. The index ranges from 1 (weak drift propensity) to 80 (strong drift propensity).

2.4 | Environmental, network and landscape resistance distance matrices

We calculated four distance metrics: one related to local environmental conditions (environmental distance), one related to the network drainage (network distance) and two related to the landscape resistance to dispersal (topographic and land use distances).

We calculated environmental distance as the Euclidean distance between each pair of sites of selected local environmental variables to represent different dimensions of local environmental conditions acting as environmental filters in each HU separately. The environmental variables were divided into six categories: variability of riparian vegetation, channel morphology, bed substrate, flow type, shelter to fauna (e.g. large wood in channel) and water quality variables (Table S1). Prior to calculating the Euclidean distance, we excluded the variables highly correlated within each HU to avoid multicollinearity among them (r Pearson > |0.7|). We retained a total of 27 variables based on their ecological meaning (Table S2). For instance, in the Nova Ponte HU, the composite riparian vegetation index (RCOND) was correlated to brush and small wood (pct_brs). We retained the pct_brs because it reflected the instream shelter availability to organisms. As the selected environmental variables had different units and ranges of variation, we first standardized their units (mean = 0, and $SD = 1$) to avoid biases when constructing the Euclidean distance (Valentin, 2012).

Network distance refers to the shortest distance between each pair of sites following the stream network within each hydrological unit. The network distance was extracted from 1:100,000 scale digital maps from the Brazilian Geographical and Statistical Institute using the Network Analyst extension in ARCGIS 10.5 (Johnston et al., 2001).

We also used ARCGIS to generate spatial raster files and calculate the two landscape resistance distances between sites. The raster files used to calculate the topographic and land use distances were generated using cost surface analysis with 250-m pixel size. We used each raster file as input in the CIRCUITSCAPE program (McRae, 2006). CIRCUITSCAPE is based on electronic circuit theory to estimate effective landscape resistance (McRae et al., 2013). The resistance pairwise values refer to the sum of resistances of individual pixels considering all possible pathways connecting between community pairs within the raster file as the total area used

to estimate the landscape resistance (McRae, 2006). We describe the meaning of each distance below.

Topographic distance assumes that terrain surface affects the dispersal of macroinvertebrates, with concave areas facilitating dispersal because of greater likelihood of water bodies and fewer topographic barriers (Cañedo-Argüelles et al., 2015). Therefore, we considered that relatively low-elevation pixels facilitate dispersal, whereas relative high-elevation pixels decrease dispersal probability. We calculated the topographic distance based on slope difference between sites. The slope was calculated from the maximum rate of change in elevation in every grid cell, based on NASA Shuttle Radar Topographic Mission – SRTM terrain model (USGS, 2005) elevation raster and was calculated as a percentage.

Land use distance assumes that dispersal probability decreases with certain land uses, like a gradient of anthropogenic pressures (Carlson et al., 2016; Urban et al., 2006) or barriers to dispersal (Baguette et al., 2013; Zeller et al., 2012). We calculated the land use distance based on an adapted land use index (CDI) described in Ligeiro et al. (2013) to assign a resistance value of each type of land use and cover within each pixel. This index was calculated following the formula: CDI = 4 × % urban areas + 2 × % agricultural areas + % pasture areas. Therefore, the CDI increases as land use intensification increases. Here we applied the same logic to weight the observed land uses on study area: × % natural vegetation; 2 × % pasture, 2 × % reservoir, 2 × % *Eucalyptus* plantation; 4 × % agriculture; and 8 × % urban areas. This modification was necessary to avoid attributing a zero value to natural vegetation. The land use information was retrieved from the Brazilian land use and land cover map (IBGE, 2015). Analogously to the topographic distance, we considered that low CDI index pixels facilitate dispersal, whereas high CDI index pixels decrease dispersal probability.

2.5 | Hierarchical clustering analysis

We simultaneously evaluated how macroinvertebrate traits related to dispersal would affect metacommunity patterns based on the compilation of traits described above. We log-transformed the drift propensity index before conducting the analyses. Many macroinvertebrates have life cycles that depend on both terrestrial (flying) and aquatic (mainly, drift) dispersal routes. Aquatic forms disperse downstream by drift, whereas females disperse upstream by directional flight searching for oviposition sites (Altermatt, 2013; Brittain & Eikeland, 1988; Petersen et al., 2004). We used a cluster analysis to classify the taxa considering both dispersal routes aiming to account for the total effect of dispersal mechanisms on community dissimilarity. First, we built a matrix with all pairwise dissimilarities among taxa based on their traits. We produced this matrix based on the modified Gower index (Pavoine et al., 2009), which can handle heterogeneous and fuzzy-coding traits. From this matrix, we produced a dendrogram using Ward's clustering and a principal coordinate analysis (PCoA) to visualize how the groups are dispersed in the functional space (Pavoine et al., 2009; Figure S1).

To identify the optimal number of dispersal groups, we used a distance-based version of multivariate analysis of variance (Anderson, 2001) that determines the quality (goodness-of-fit) of a cluster in detecting aggregation patterns in the Gower dissimilarity matrix. We evaluated clusters that aggregated taxa into 2–10 dispersal groups using both goodness-of-fit and the marginal increment of goodness-of-fit when adding a new dispersal group, along with the ecological interpretation and coherence of each dispersal group. After exploring these results, we retained a clustering with five dispersal groups as the optimum solution (Figure S3), considering that goodness-of-fit starts to saturate clustering with more dispersal groups, which provided only a small increment of quality at the cost of yielding some additional dispersal groups with unclear ecological meaning.

2.6 | Metacommunity pattern analysis

To explore the effects of environmental conditions (i.e. species sorting) and network and different landscape resistance distances (i.e. dispersal mechanisms), we ran multiple regression models for distance matrices (MRM) for each hydrological unit separately (Lichstein, 2007), using the 'Ecodist' R package (Goslee & Urban, 2007). MRM is similar to multiple regression analysis but, in this case, the predictors are distance or dissimilarity matrices, and the coefficient's significance is assessed by permutation tests (1,000 permutations). Using environmental, network, topographic and land use distances as predictors, we ran different models to explain community dissimilarity for all taxa (i.e. combined taxa), and for taxa within each dispersal group (e.g. only for the taxa belonging to group 1). For each of these community matrices, we removed rare taxa (relative frequency <3%; Valente-Neto et al., 2017) and square-root-transformed abundance values, before calculating Bray–Curtis dissimilarities (one for each dispersal group). Finally, to quantify the importance of each predictor, we performed a variance partition analysis using the 'hier.part' R package (Walsh & Nally, 2013). All statistical analyses were carried out using R software (R Development Core Team, 2019). Code to reproduce these analyses is available in Appendix S3.

3 | RESULTS

3.1 | Macroinvertebrate dispersal groups

Our hierarchical clustering analysis identified five macroinvertebrate dispersal groups that yielded the most coherent aggregation for the studied taxa (Table 2; Appendix S2) based on median trait values (Table 3), for a total of 155 observed taxa and 105 used in the analysis. Dispersal group 1 included aquatic obligate taxa and also flying taxa with moderate directional flight capacity, low drift propensity (index = 15), very short adult life span, multivoltine strategy

and small body size (<1 cm). Typical taxa of dispersal group 1 are composed by Mollusca (except Thiaridae), some Diptera, Annelida, Nematoda and Planariidae taxa. Dispersal group 2 was represented by taxa with moderate directional flight capacity, low drift propensity (index = 10), long adult life span, univoltine strategy and medium body size (1–1.15 cm). The dispersal group was exclusively composed by Coleoptera, Heteroptera and Neuroptera. Dispersal group 3 included taxa with high directional flight capacity, low drift propensity (index = 14), long adult life span, univoltine strategy, and large body size (>1.5 cm), and it comprised all Odonata except Calopterygidae. Dispersal group 4 included taxa with moderate directional flight capacity, moderate drift propensity (index = 24), short adult life span, multivoltine strategy and large body size. This dispersal group included the largest taxa diversity being represented by taxa belonging to the orders Ephemeroptera, Trichoptera, Heteroptera, Diptera and Lepidoptera, and by two aquatic obligate taxa (Decapoda and Thiaridae) that presented large drift propensity and medium body size. Finally, dispersal group 5 represented taxa with moderate directional flight capacity, high drift propensity (index = 44), short adult life span, univoltine strategy and large body size (>1.5 cm). This dispersal group was composed by different Trichoptera, Ephemeroptera, all Plecoptera, Megaloptera and Calopterygidae (Odonata).

3.2 | Effects of local and regional process on metacommunity patterns

Generally, environmental and land use distances showed the greatest number of significant associations with community dissimilarity across HUs (Table 4). Environmental distance was significantly associated with changes in community dissimilarity in all HUs when considering all taxa. When the dispersal groups were considered individually, only dispersal group 4 was significantly related to the environmental distance in all HUs. Land use distance was significantly associated with changes in community dissimilarity in NP and TM when considering all taxa. When the dispersal groups were analysed individually, dispersal group 1 was significantly related to land use distance in most HUs, except for SS. Network distance was only significantly for dispersal group 3 in NP. Finally, topographic distance did not significantly explain community dissimilarity.

The relative importance of each distance to explain community dissimilarity depended on the dispersal capacity of the taxa (Figure 2). On average, considering all dispersal groups and HUs, environmental (52 ± 25%) and land use (27 ± 23%) distances showed the highest mean relative importance. When averaging the values across HUs, the mean relative importance of environmental distance varied from 42% for dispersal group 1, to 60% to dispersal group 5. Land use showed a broad range of values (from 10% for dispersal group 3 to 45% for dispersal group 1). The network distance showed the lowest average values, ranging from 4% (for dispersal group 4) to 20% (for dispersal group 3). Finally, the relative importance of topographic distance ranged from 8% (for all taxa and dispersal group 1) to 25% (for dispersal group 3).

TABLE 2 Results of the hierarchical clustering of macroinvertebrate taxa based on traits

Dispersal group	Taxa	
1	Mollusca	Ancylidae, Bivalvia, Hydrobiidae, Lymnaeidae, Physidae, Planorbidae
	Diptera	Ceratopogonidae, Chaoboridae, Chironomidae, Culicidae, Dixidae, Dolichopodidae, Ephydridae, Muscidae, Psychodidae, Scatopsidae, Stratiomyidae
	Anellida	Hirudinea, Oligochaeta
	Nematoda	Nematoda
	Tricladida	Planariidae
2	Coleoptera	Chrysomelidae, Curculionidae, Dryopidae, Dytiscidae, Elmidae, Gyrinidae, Hydraenidae, Hydroscaphidae, Limnichidae, Lutrochidae, Noteridae, Psephenidae, Ptilodactylidae, Salpingidae, Scirtidae
	Heteroptera	Gelastocoridae, Hebridae, Helotrephidae, Naucoridae, Notonectidae, Pleidae, Saldidae, Veliidae
	Neuroptera	Sisyridae
3	Odonata	Aeshnidae, Corduliidae, Dicteriadidae, Gomphidae, Libellulidae, Megapodagrionidae, Perilestidae, Polythoridae, Pseudostigmatidae
	Heteroptera	Belostomatidae, Nepidae
	Coleoptera	Hydrophilidae
4	Mollusca	Ampullaridae
	Ephemeroptera	Baetidae, Caenidae, Leptohyphidae, Leptophlebiidae
	Trichoptera	Calamoceratidae, Ecnomidae, Helicopsychidae
	Odonata	Coenagrionidae
	Heteroptera	Corixidae, Gerridae, Mesoveliidae
	Crustacea	Decapoda
	Diptera	Empididae, Syrphidae, Tabanidae, Tipulidae
	Lepdoptera	Pyralidae
	Mollusca	Thiaridae
5	Trichoptera	Anomalopsychidae, Glossosomatidae, Hydrobiosidae, Hydroptilidae, Leptoceridae, Odontoceridae, Philopotamidae, Polycentropodidae, Xiphocentronidae
	Odonata	Calopterygidae
	Megaloptera	Corydalidae, Sialidae
	Ephemeroptera	Ephemeridae, Euthyplociidae, Polymitarcyidae
	Plecoptera	Gripopterygidae, Perlidae

4 | DISCUSSION

Overall, environmental distance was the most important predictor of community dissimilarity in the Neotropical savanna streams in all of the studied HUs. This corroborates the importance of species sorting to determine local community composition through the process of environmental filtering (Heino et al., 2015), in agreement with other studies from temperate (Brown & Swan, 2010), boreal (Kärnä et al., 2015) and Mediterranean regions (Sarremejane et al., 2017). Local communities are the result of many ecological processes at both regional and local scales, as the species need not only to be able to disperse to a certain location but also to find local suitable conditions to become established (Leibold et al., 2004). In our study, the environmental distance reflected both natural variability (e.g. river basin geology) and human impacts (e.g. siltation and water quality alteration; Kaufmann et al., 1999; Macedo et al., 2018). Thereby, the high importance of environmental filters is not surprising, as both natural and anthropogenic environmental factors are strong drivers of macroinvertebrate communities in the Neotropical savanna (Castro et al., 2019). The higher importance of

TABLE 3 Median trait values for macroinvertebrate dispersal groups according to hierarchical clustering

Trait	Group 1	Group 2	Group 3	Group 4	Group 5
Flight capacity	Medium	Medium	High	Medium	Medium
Drift propensity index	15	10	14	24	44
Adult life span	Very short	Long	Long	Short	Short
Voltinism	Multivoltine	Univoltine	Univoltine	Multivoltine	Univoltine
Body size (cm)	<1	1–1.5	>1.5	1–1.5	>1.5

TABLE 4 Results of the multiple regression models (MRM) for each hydrological unit (HU): Nova Ponte (NP), São Simão (SS), Três Marias (TM) and Volta Grande (VG) relating biological dissimilarity for all taxa and each dispersal group of macroinvertebrates to environmental (ENV), topographic (TOP), land use (LAND) and network (NET) distances. The intercepts, slopes, significance, F-values and explained variance (R^2) of the MRM are also shown for each group

HU	Dispersal group	Intercept	ENV	TOP	LAND	NET	F	R^2
NP	All taxa	0.60	0.02[**]	0.01	0.03[**]	0.01	126.22	0.20
	1	0.38	0.02	0.01	0.04[**]	0.00	62.76	0.11
	2	0.56[**]	0.02	0.00	0.08[***]	−0.02	133.10	0.21
	3	0.63	0.00	−0.01	0.00	0.09[*]	55.96	0.10
	4	0.69	0.04[**]	0.01	0.04[**]	0.01	116.67	0.19
	5	0.76	0.06[***]	0.03	0.04[*]	0.01	219.14	0.30
SS	All taxa	0.59	0.04[**]	0.02	0.01	−0.02	26.77	0.13
	1	0.54	0.07[**]	0.04	0.02	−0.03	24.61	0.12
	2	0.59	0.04	0.05	0.01	−0.02	13.74	0.07
	3	0.44	0.06[**]	0.01	−0.02	0.00	19.01	0.09
	4	0.65	0.04[*]	0.01	0.02	−0.01	14.60	0.07
	5	0.54	0.03[**]	0.02	0.00	−0.01	15.39	0.08
TM	All taxa	0.56	0.04[**]	−0.01	0.03[**]	−0.01	51.34	0.21
	1	0.29	0.03[*]	−0.02	0.03[*]	0.00	30.95	0.14
	2	0.61	0.06[*]	−0.03	0.03	−0.01	14.90	0.07
	3	0.47	0.05[**]	−0.03	0.03	0.01	26.06	0.12
	4	0.58	0.02[*]	−0.03	0.03	0.00	21.14	0.10
	5	0.74	0.06[**]	−0.02	0.03	0.00	26.67	0.12
VG	All taxa	0.58	0.05[*]	−0.02	0.03	−0.01	44.29	0.19
	1	0.46	0.03	−0.04	0.09[*]	−0.04	48.68	0.20
	2	0.38	0.04	−0.02	0.01	−0.02	13.89	0.07
	3	0.51	0.04	−0.03	0.02	0.03	26.14	0.12
	4	0.60	0.08[**]	−0.02	0.03	0.00	52.45	0.21
	5	0.67	0.02	−0.02	0.04	−0.01	15.62	0.07

Note: Pseudo-p:

[*]$p < 0.05$;

[**]$p < 0.01$;

[***]$p < 0.001$.

environmental distance in SS and TM can be attributed to a higher variance of local physical habitat variables compared to the other two HUs (Callisto et al., 2019). On the other hand, in NP, which has the highest gradient of anthropogenic pressures among the HUs (Ligeiro et al., 2013), most dispersal groups did not show a significant relationship with the environmental distance. This might suggest that the effect of environmental distances on community dissimilarity might be more related with natural variability than with anthropogenic drivers.

We also found a significant effect of land use on macroinvertebrate metacommunities, suggesting that the modification of the landscape structure associated with land uses (e.g. replacement of trees by pasture) can affect the dispersal of stream macroinvertebrates. This result was clearer in NP, which has the widest land use gradient among the studied HUs (Macedo et al., 2018). This wide gradient of land uses created a patchy landscape of areas with low and high landscape resistance that could have increased the ecological importance of dispersal corridors (Carlson et al., 2016). On the other extreme, the VG and
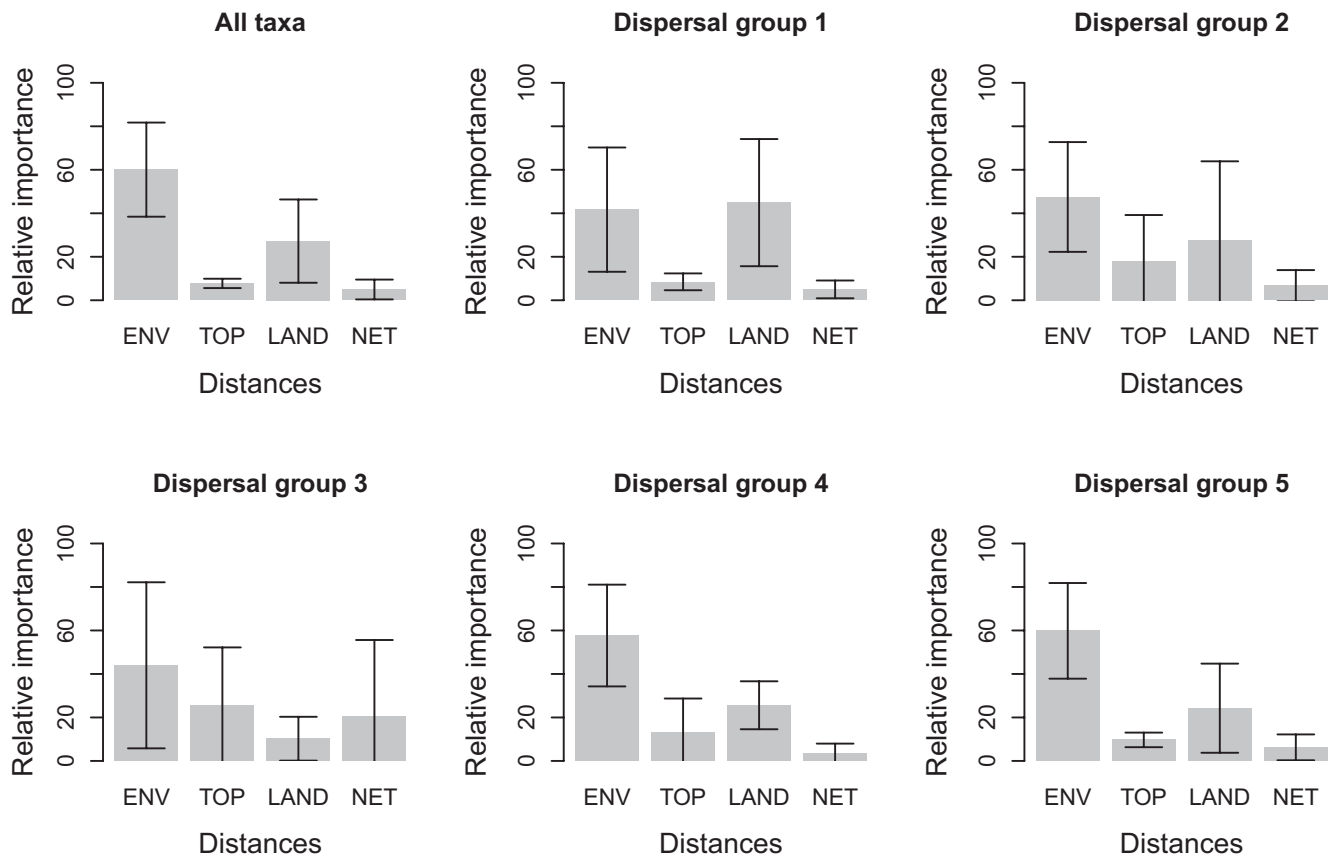
FIGURE 2 Relative contribution to overall explained variance by environmental (ENV), topographic (TOP), land use (LAND) and network (NET) distances for all HUs, shown for all taxa and each dispersal group of macroinvertebrates. For each distance, mean is shown by the grey bars and standard deviation is shown by the narrow black bars

TM were mostly homogeneous HUs at the landscape level (Macedo et al., 2018), the former due to being dominated by anthropogenic land uses, the latter due to being mostly covered by natural vegetation. In both cases, the land use distance had little importance for the distribution of the dispersal groups. These results suggest that the importance of land use for the dispersal is proportional to its variation in the studied landscape (Zeller et al., 2012).

The influence of land use depended on the dispersal abilities of the taxa (Sarremejane et al., 2020). The dispersal group that was most significantly affected by land use was dispersal group 1 (composed mainly by aquatic obligates), whereas Odonata (mostly enclosed in dispersal group 3) was not significantly affected by land use in any of the HUs. The importance of land use distance for dispersal group 1 could be related with most taxa composing the dispersal group being considered as resistant to anthropogenic disturbances (Hawkes, 1998), thereby presenting distribution ranges linked to anthropogenic land uses (Junqueira et al., 1998). Anthropogenic altered ecosystems present ecological conditions that exclude sensitive species, reducing competition for resources and allowing resistant taxa to achieve high densities (Silva et al., 2017). As these taxa are resistant to anthropogenic disturbances, anthropogenic altered landscapes would relax the competition with sensitive taxa and, therefore, be chosen as preferential dispersal corridors (Johnson et al., 2008).

The lack of a significant effect of land use on Odonata is surprising because a previous study (French & McCauley, 2019) showed that the conversion of forests to agricultural fields facilitated the dispersal of some dragonfly species. Another possible explanation is that the dispersal of Odonata between streams was not limited within each HU given their strong flying capacities. The importance of land use on taxa with medium directional flight capacity (e.g. Diptera, Coleoptera, Ephemeroptera and Trichoptera in dispersal groups 1, 2, 4 and 5) could be partly explained by the tendency of land use to increase the landscape resistance to aerial dispersal (Zeller et al., 2012). In particular, anthropogenic land uses result in open areas that impose ecological and physiological restrictions to flight dispersal by increasing their morbidity and mortality risks (Cote et al., 2017; De Marco et al., 2015). These risks include high wind speeds, high air temperatures, predator exposure and low humidity discouraging the organism to disperse distant from their original stream courses (Carlson et al., 2016; Cote et al., 2017).

Network distance had a weak influence on macroinvertebrate community dissimilarity, being only significant for the dispersal group 3 in NP. This contradicts previous studies recognizing stream networks as preferential dispersal route for macroinvertebrates (Brown & Swan, 2010; Petersen et al., 2004). This could be related with environmental filters masking the effect of network structure on the communities (Johnson et al., 2013; Urban et al., 2006).

Topographic distance did not significantly explain macroinvertebrate dissimilarity. This is most likely due to the low topographic variation found in the study area region (stream sites minimum and maximum altitudes: NP: 766–1,400, SS: 330–845, TM: 525–1,044, VG: 456–974 m a.s.l.). Other studies conducted in landscapes lacking strong land use gradients demonstrated that topography was important for metacommunity organization in arid (1,720–2,360 m.a.s.l.; Cañedo-Argüelles et al., 2015), Mediterranean (60–1,750 m.a.s.l.; Sarremejane et al., 2017) regions, as well as the Himalayan mountains (2,492–2,926 m.a.s.l.; Tonkin et al., 2017). Thus, our results suggest that land use could be more important than topography for stream macroinvertebrate metacommunity organization in areas with low topographical variation (Simião-Ferreira et al., 2018).

We acknowledge that the goodness-of-fit values of MRM models were relatively low for all groups (R^2: 0.07–0.30), meaning that a large portion of community dissimilarity remained unexplained. This was already expected given that local communities structure are the result of multiple ecological processes that were not measured (Vellend, 2010). Other stream macroinvertebrate metacommunity studies found similar results, explaining only a small portion of community variance (Cañedo-Argüelles et al., 2015; Valente-Neto et al., 2017).

In conclusion, our results suggest that both the aquatic environment and the terrestrial connectivity are important to explain macroinvertebrate community variation in Neotropical headwater streams under a land use gradient. According to our results, macroinvertebrate metacommunities in Neotropical stream metacommunity could be explained both by land use constraining organism dispersal at regional scale and by environmental filters operating at the local scale. Understanding how those processes limit dispersal is particularly crucial to meet conservation and restoration goals, especially in biodiversity hotspots wherein many species have yet to be formally described. In addition, our results reinforce the importance of considering entire catchments for preserving stream health and aquatic biodiversity, and indicate the need for a much more integrative research between terrestrial and aquatic ecology.

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DATA AVAILABILITY STATEMENT

Authors confirm that all relevant data are included in the article and/or its supplementary information files.

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BIOSKETCH

Kele R. Firmiano is a freshwater ecologist interested in how anthropogenic pressures affect biodiversity in Neotropical freshwater ecosystems, using aquatic macroinvertebrates as biological models. This study is the result of a research partnership between Brazil and Spain initiated during her PhD research visit at the University of Barcelona.

Author contributions: K.R.F., D.R.M., M.S.L. and M.C. elaborated the research design, collected and processed the data. D.R.M. calculated network and landscape resistance distances. K.R.F., M.C-A., C.G-.C. and N.B. conducted the statistical analysis. All authors wrote the paper and approved the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.