

# Which metrics drive macroinvertebrate drift in neotropical sky island streams?

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## ABSTRACT

Despite long-standing interest, the mechanisms driving aquatic macroinvertebrate drift in tropical streams remain poorly understood. Therefore, the objective of this study was to evaluate which environmental metrics drive macroinvertebrate drift in neotropical sky island streams. We evaluated whether altitude, the abundance of food resources, and variations in water quality influenced macroinvertebrate drift density, diversity, richness, and functional feeding groups. An hypothesis was developed to test whether increased altitude, lower food availability (particulate organic matter), and discharge would increase the density, taxonomic richness, and diversity of drifting invertebrates. Nine headwater stream sites were sampled in the rainy and dry seasons in the Espinhaço Meridional Mountain Range (EMMR) of southeast Brazil. Samples were collected using drift nets deployed from 5:00 p.m. to 8:00 p.m. The abundance of food resources was assessed through estimates of coarse (CPOM) and fine (FPOM) particulate organic matter, and primary producers. CPOM availability was an important explanatory variable for Gathering-Collectors and Scrapers. Altitude was important for Shredders and Predators, and Filtering-Collectors were linked to water discharge, suggesting that functional group drift masses were linked to different ecosystem components. Water temperature, conductivity, dissolved oxygen, current velocity, FPOM biomass and microbasin elevation range exerted little influence on macroinvertebrate drift. Regarding taxa composition, this study also found that Baetidae and Leptohyphidae (Ephemeroptera) and Chironomidae and Simuliidae (Diptera) were the most abundant groups drifting.

## 1. Introduction

Drift is the downstream transport of aquatic macroinvertebrates in the water column and represents an important behavior of organisms that inhabit river and stream bottoms (Brittain and Eikeland, 1988; Waters, 1972). This ecological process has been studied with a focus on the association of drift with abiotic and biotic factors (Naman et al., 2016). Those factors include diel periodicity (Mendoza et al., 2018), seasonal variations (Ramírez and Pringle, 2001; Castro et al., 2013b), current velocity (Castro et al., 2013a; Schülting et al., 2016), physical habitat

structure (Enefalk and Bergman, 2016), resource availability (Siler et al., 2001), intra- and inter-specific competition, and predation (Leung et al., 2008).

Drift is important for the structure and functioning of lotic ecosystems because it facilitates the dispersal of invertebrates and the recolonization of available downstream habitats (Ríos-Touma et al., 2012). In addition, drifting invertebrates are important food resources for vertebrate and invertebrate predators (Leung et al., 2008), an important part of the downstream transport of matter and energy from autochthonous sources (Clarke et al., 2008; Jiang et al., 2011), and useful tools for assessing

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environmental impacts on aquatic ecosystems (Callisto et al., 2020).

The downstream transport of allochthonous inputs from riparian vegetation and nutrients are important determinants of food relationships in headwater streams (Erdozain et al., 2021). Leaf deposits accumulated on the streambed as leaf patches represent temporary areas where the biodiversity of aquatic macroinvertebrates is high (biodiversity hotbeds, *sensu* Ligeiro et al., 2020). Similarly, instream primary production and algal biomass are often critically important nutrient sources for headwater stream macroinvertebrates (Kiffer et al., 2018a; Lau et al., 2009). Variation in the availability of food resources in these environments is an important factor in structuring benthic macroinvertebrate assemblages (Richardson, 1991).

The azonal Campo Rupestre is an ancient, widespread Neotropical biome and the second largest mountain range in South America (Miola et al., 2021). Although the headwaters in the isolated and naturally fragmented sky islands of the Campo Rupestre are nutrient-impovertished and a climate refuge (Fernandes et al., 2020), there is little information about how drift of Campo Rupestre aquatic macroinvertebrates is related to altitude, food supply, and water chemistry. Therefore, seeking a deeper understanding of the ecological factors that shape headwater biota in the Campo Rupestre sky islands, we sought to fill some gaps regarding multi-taxa monitoring and ecosystem functioning as they affect drifting macroinvertebrates.

Despite long-standing interest, the mechanisms driving the drift of aquatic macroinvertebrates in tropical streams remain poorly understood and there are several non-exclusive assumptions. (i) Stream

macroinvertebrates leave patches actively and passively (Brittain and Eikeland, 1988). (ii) Altitude and elevation ranges are important factors structuring benthic macroinvertebrate assemblages (Callisto et al., 2021; Castro et al., 2019; Gueuning et al., 2017). (iii) Hydraulic characteristics are more important than site water quality (e.g., pH, redox, DO) (Gibbins et al., 2007). (iv) Drift may be density-dependent because of resource competition (Hammock and Wetzel, 2013). Based on these assumptions, the objective was to evaluate which environmental metrics drive macroinvertebrate drift in neotropical sky island stream sites. The hypothesis that was tested in this study was that physical habitat variables and organic matter availability have more impact on drift richness and density than water quality parameters, predicting that water discharge, catchment altitude and slope, organic matter availability and related variables will comprise most of the significant variables explaining drift.

## 2. Methodology

### 2.1. Study area and sampling design

Headwater streams in the rupestrian fields (rocky fields, “Campos Rupestres” in Portuguese) are common on eastern Brazilian mountain-tops. The concept of “sky islands” was adopted to describe neotropical montane Campos Rupestres that are steep and geologically stable (Callisto et al., 2021), i.e., OCBIL (old, climatically buffered, infertile landscapes; Hopper, 2009) systems. The sky islands are biodiversity hotspots in the neotropical savanna (Fernandes et al., 2020) and they

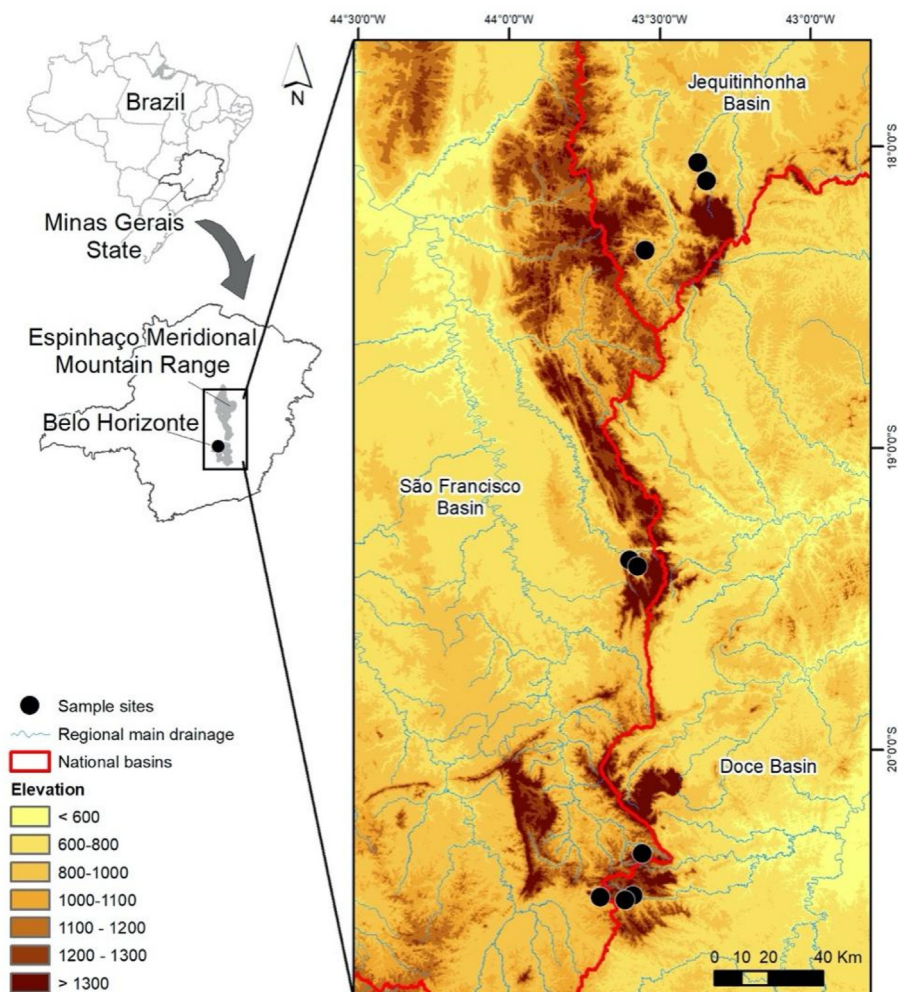


Fig. 1. Map of the Espinhaço Meridional Mountain Range stream site locations.

contain streams in three river basins along the Espinhaço Meridional Mountain Range (EMMR). The EMMR is part of a UNESCO Biosphere Reserve in eastern Brazil, which supports headwaters of the Rio São Francisco (to the west), Rio Doce (to the east) and Rio Jequitinhonha (to the northeast) in the state of Minas Gerais. The studied streams integrate the landscapes across the sky islands (Agra et al., 2019; Hynes, 1975), serving as riparian meta-ecosystems (Callisto et al., 2019) and as ecological belts across the landscape interconnecting stream riparian vegetation and facilitating aquatic insect dispersal (Firmiano et al., 2021). The sky island streams in the EMMR are also natural laboratories for evaluating biological assemblages and ecosystem responses to climate change (Callisto et al., 2019, 2021; Castro et al., 2019; Silveira et al., 2019).

This study was conducted in nine sky island stream sites in the EMMR (Fig. 1). The region's climate is tropical altitude (Cwb), marked by dry winters from April to September, and rainy summers from October to March. The annual average temperature varies between 17.5 and 18.5 °C and the average annual precipitation between 1450 and 1600 mm (Callisto et al., 2021; Castro et al., 2019). The EMMR has shallow and rocky soils, with frequent quartzite outcrops. Its vegetation consists of unique rocky fields grasslands and shrublands, Cerrado (Neotropical Savanna), and gallery forests that vary with elevation, longitude and latitude (Silveira et al., 2016).

Nine second-order stream sites were selected through use of an *ad hoc* selection process based on access, level of riparian vegetation conservation and minimum anthropogenic disturbance. The sites were distributed within a matrix of natural native vegetation, had over 70% canopy cover, ranged in altitude from 760 to 1320 m AMSL, and had similar morphological and water quality characteristics (Table 1). Nine headwater stream sites were selected based on previous benthic macroinvertebrate assessments (e.g. Callisto et al., 2021). Each site was sampled twice—once in the 2012 dry season (May–June), and once in the 2012 rainy season (November–December) to capture the natural variability of the highly seasonal allochthonous organic matter input of the streams (Tonin et al., 2017).

## 2.2. Water quality and catchment variables

Temperature (°C), electrical conductivity ( $\mu\text{S}\cdot\text{cm}^{-1}$ ), pH, and total dissolved solids (ppm) were measured *in situ* using a multi-parameter probe (YSI 6600 m). Turbidity (NTU) and redox (water and sediment) were measured with a Digimed turbidimeter and redox meter, respectively. Chlorophyll-a ( $\text{mg}\cdot\text{L}^{-1}$ ) and dissolved oxygen concentrations ( $\mu\text{g}\cdot\text{L}^{-1}$ ) were determined at the laboratory from water samples following standard methods (APHA, 2005). Water samples and measurements were always obtained at each site at the same time of day (around 10 a.m.). It was assumed that those isolated sky island headwater sites with minimal human pressure influence had little or no diel water chemistry variation.

**Table 1**  
Water quality, physical habitat and potential food variables in the sky island sites.

Variables	Metric type	Description	Mean (min-max)
Temperature	Water quality	Water temperature (°C)	19.45 (16.1–23.0)
pH	Water quality	Water pH	6.28 (4.96–7.46)
Conductivity	Water quality	Water electrical conductivity ( $\mu\text{S}/\text{cm}$ )	19.43 (0.83–58.6)
Redox <sub>H<sub>2</sub>O</sub>	Water quality	Water potential redox (mV)	197.83 (3–380)
Redox <sub>sedim</sub>	Water quality	Sediment potential redox (mV)	147 (–282–407)
Turbidity	Water quality	Water turbidity (NTU)	3.93 (0.76–21.6)
Dissolved oxygen	Water quality	Water dissolved oxygen concentration ( $\text{mg}\cdot\text{L}^{-1}$ )	8.20 (5.85–9.40)
Water chlorophyll-a concentration	Chlorophyll a Potential food	( $\text{mg}\cdot\text{L}^{-1}$ )	0.81 (0–3.19)
Fine particulate organic matter	FPOM Potential food	( $\text{mg}\cdot\text{L}^{-1}$ )	0.051 (0–0.33)
Coarse particulate organic matter	CPOM Potential food	( $\text{mg}\cdot\text{L}^{-1}$ )	0.07 (0–0.49)
Discharge	Physical habitat	Volume of water moving down a stream per second ( $\text{m}^3\cdot\text{s}^{-1}$ )	0.059 (0.029–0.101)
Current velocity (mean)	Physical habitat	Current velocity ( $\text{m}\cdot\text{s}^{-1}$ )	0.21 (0.11–0.31)
Site altitude	Physical habitat	Site altitude (m)	1012 (728–1386)
Catchment slope (mean)	Physical habitat	Catchment slope (m)	19.37 (7.4–25.4)
Elevation (range)	Physical habitat	Catchment elevation range (m)	378 (70–606)

Instantaneous discharge and current velocity were measured using a flow meter at a cross-section having nonturbulent or near-laminar flow in each stream site (Peck et al., 2006).

Site altitude (m), mean catchment slope (m), and elevation range (m) were determined using GIS procedures and a SRTM model (~30 m spatial resolution; USGS, 2015).

## 2.3. Suspended particulate organic matter

To collect drifting suspended coarse and fine organic matter (CPOM and FPOM), three double drift nets were installed at each site, one with 1 mm mesh, one with 40  $\mu\text{m}$  mesh, and both with 0.3  $\text{m}^2$  openings, which remained in place for up to 30 min to avoid clogging. The nets were deployed at the same times as macroinvertebrate sampling. The material collected in the nets was used as a proxy for the amount of organic matter available at each site (Tamaris-Turizo and Rodríguez, 2015). The samples were fixed in the field with 70% ethanol and returned to the laboratory for processing. In the laboratory, the samples were screened, and the material dried in an oven at 60 °C for 72 h then ignited in a muffle furnace at 550 °C for 4 h to determine the ash-free dry weight. The density of drifting organic matter was expressed as mass of organic matter per unit volume of filtered water ( $\text{mg}\cdot\text{m}^{-3}$ ).

## 2.4. Macroinvertebrate drift sampling

Macroinvertebrate samples were collected using three drift nets with an area of 0.16  $\text{m}^2$  and a 250  $\mu\text{m}$  mesh at each site. The nets were deployed at dusk from 5:00 p.m. to 8:00 p.m. — a period considered as the peak in the density of organisms in the drift that occurs during twilight hours (Castro et al., 2013b, a). The nets were positioned to sample the entire wetted stream width. The average velocity of the water column ( $\text{m}\cdot\text{s}^{-1}$ ) was measured with a flow meter (model Global Water FP101/201) at the beginning and end of each sampling event. The total volume of filtered water sampled by each drift net ( $\text{m}^3$ ) was calculated by multiplying the net area by the average water speed by the sampling time. In this way it was possible to calculate the population density of invertebrates in each sample ( $\text{ind}\cdot\text{m}^{-3}$ ). All analyses were performed based on the density of organisms in the drift ( $\text{ind}\cdot\text{m}^{-3}$ ), and taxonomic richness was estimated as the total number of different taxa found in each sample.

The drift samples were fixed in the field with 4% formaldehyde. In the laboratory, invertebrates were identified to family with the help of taxonomic keys (Merritt and Cummins, 1996; Mugnai et al., 2010; Roldán-Pérez, 1988). The invertebrates were also classified into functional trophic groups (filtering-collectors, gathering-collectors, predators, scrapers, shredders) following Cummins et al. (2005), Tomanova et al. (2006) and Ramírez and Gutiérrez-Fonseca (2014) (Supplementary Material Table S1).

## 2.5. Data analyses

Each site's explanatory variables (i.e. water quality, physical habitat, catchment; Table 1), and response variables (i.e. taxonomic richness, total invertebrate density, and shredder, filtering-collector, gathering-collector, scraper, and predator densities) were tested for possible seasonal differences using a *t*-test. No significant differences were found between dry and rainy seasons, so all the samples for each sampling site were pooled.

To test which environmental variables had the most influence on invertebrate drift, all 15 explanatory environmental variables were used in a model selection approach (Burnham and Anderson, 2002). The biological response variables were used in generalized linear models (GLM's) with a Gamma distribution, where the response variables in each of the GLM's were the total drift density, drift richness, gathering-collector density, filter-feeder density, shredder density, scraper density, or predator density. Models were then constructed based on all possible additive variable combinations that may have influenced the invertebrate drift structure. Importantly, a null model (i.e. the intercept-only model) was also included in each of the model sets. Both model sets were compared independently using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002). Candidate models were ranked based on their AICc scores and log-likelihood (LogL)  $R^2$  adjusted for number of predictors, cumulative Akaike weights (wi), and the difference between the given, and best-fitting model ( $\Delta i$ ) was calculated for each model (Burnham and Anderson, 2002a). The best-fitting model was determined by the lowest AICc score (a  $\Delta i$  value of 0.0); however, a  $\Delta i$  of  $<2$  was also considered to have substantial support (Burnham and Anderson, 2002). This strategy resulted in a balanced model set for each analysis, which allowed us to calculate the cumulative AICc weights for each variable (Burnham and Anderson, 2002). Statistical analyses were carried out using the MuMIn

package (Bartón, 2019) in R 3.6.1 (R Development Core Team, 2018).

Distance-based redundancy analysis (db-RDA) was used to verify the relationships between macroinvertebrate drift composition and the explanatory environmental variables (Legendre and Anderson, 1999). The analysis was based on a Bray-Curtis dissimilarity matrix of macroinvertebrate data. Highly correlated variables (Spearman's  $r > 0.6$ ) were removed. Density data were Hellinger transformed and environmental variables were standardized prior to analysis. The significance of the full model of db-RDA was first examined using the anova function in the R package vegan. Because the model was significant, the function forward.sel was implemented in the R package adespatial to select the most significant factors for each explanatory variable. Adjusted  $R^2$  (Adj.  $R^2$ ) of contributions were selected based on the constrained ordinations. All analyses were performed in R using the vegan package (Oksanen, 2015).

## 3. Results

### 3.1. Macroinvertebrate drift

In total, 11,085 individuals and 54 invertebrate taxa (Supplementary Material Table S2), were found represented by Insecta (Trichoptera, Ephemeroptera, Plecoptera, Odonata, Hemiptera, Coleoptera, Megaloptera, Lepidoptera, Diptera), Annelida (Oligochaeta), and Platyhelminthes (Turbellaria). The total density of individuals had a mean of  $0.87 \text{ ind}\cdot\text{m}^{-3}$  (Table S2). Only 8 taxa occurred with relative densities above 1%, with a predominance of Baetidae (31.3%), Chironomidae (27.5%), Simuliidae (20.7%), Leptohyphidae (3.4%), Hydropsychidae (3.3%), Dixidae (3.2%), Elmidae (3.0%) and Leptophlebiidae (1.2%) (Fig. 2 and Table S2). The largest proportion of organisms in the drift was represented by gathering-collectors (36.1%), followed by scrapers (32.8%), filtering-collectors (25.1%), predators (5.1%) and shredders (0.9%).

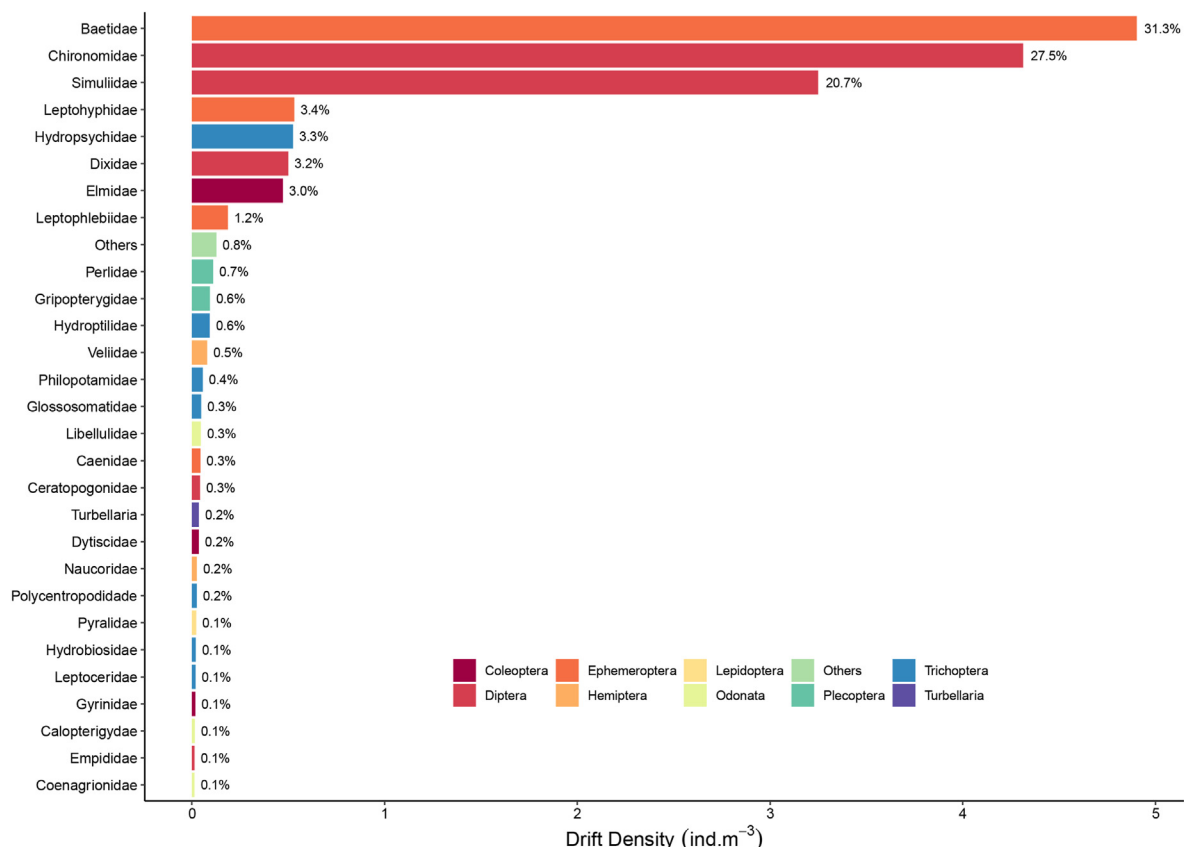


Fig. 2. Total macroinvertebrate density and relative abundance from the sky island sites.



### 3.2. Macroinvertebrate drift versus environmental predictor variables

The best supported AICc model to predict drift richness was Site Altitude + Discharge + pH + water redox (Table 2), where all those metrics had a positive relation with richness (Fig. 3c–f). The best model for total drift density was CPOM + Turbidity (Table 2), with both metrics having a negative relation with total density (Fig. 3a and b). For the functional feeding groups, the best model for gathering-collectors density was CPOM + catchment slope + turbidity (Table 2), where slope had a positive relation and CPOM and turbidity a negative relation (Fig. 3g–i). The best model for filtering-collectors density included only discharge in a positive, but weak relationship (Fig. 3j; Table 2). For shredders, the best model was pH + site altitude in a positive relation (Fig. 3k–l). For scrapers, the best model was CPOM + Turbidity with a negative relation for both (Fig. 3m–n). Finally, the best model for predator density was pH + site altitude (Table 2), where both metrics had a positive relation (Fig. 3o–p). All models, except that for filtering-collector density, explained 59–89% of the biotic indicator variability, indicating moderate to high explanatory power.

Distance-based redundancy analysis explained 32.3% of the invertebrate drift composition and environmental variables (Fig. 4). The first and second axes were significant and accounted for 28.5% of the constrained variance (Adj.  $R^2 = 0.187$ ). The first axis accounted for 17.9% of the variance and the second axis for 10.6% of the variance. Discharge ( $F = 2.55$ ), water redox ( $F = 2.13$ ) and pH ( $F = 1.99$ ) had significant influences on the composition of drifting macroinvertebrate assemblages.

## 4. Discussion

The hypothesis was not corroborated, because total taxa richness in the drift was explained by equal numbers of water quality and physical habitat variables. Additionally, both food and water quality variables explained total drift density and water quality variables were important for explaining the drift densities of four of the five functional groups analyzed.

In many headwater streams, primary production is limited by riparian vegetation shading (Graça, 2001; Vannote et al., 1980). Consequently, allochthonous organic matter in the forms of CPOM and FPOM is often the main source of energy and nutrients for macroinvertebrate assemblages in those streams (Cummins et al., 2005; Kiffer et al., 2018b). Differences in drift densities may be associated with the available particulate organic matter and differences in system primary productivity (Waringer, 1992) because the exchange of organic matter affects lotic ecosystem function (Vannote et al., 1980). The densities of drifting macroinvertebrates have been reported to increase in response to reduced food availability (Katano et al., 2017; Siler et al., 2001). This study corroborates this pattern, considering that a negative relationship between drift densities of macroinvertebrates and CPOM was observed, where drift density decreased with increasing CPOM availability. This may be a consequence of a density-dependence resulting from resource

competition, favoring the drifting of organisms. Allochthonous organic matter is considered the main energy source for heterotrophic organisms in shaded headwater streams (Vannote et al., 1980; Kiffer et al., 2018b) and increased food drift may be a proxy for the quantity of food in the system. The more food available in the stream, the more is present in the drift. So, increased food drift means increased food in the stream and less competition for food, leading to fewer drifting organisms.

The mean macroinvertebrate densities in the drift was  $0.87 \text{ ind m}^{-3}$ , which is lower than the drift densities found in temperate streams (Benke et al., 1986; Schreiber, 1995). These results corroborate other studies in the neotropics that reported low drift densities (i.e.,  $<1 \text{ ind m}^{-3}$ ) (Callisto and Goulart, 2005; Lobón-Cerviá et al., 2012). The low drift densities may be explained partly by the low productivity of EMMR streams (Callisto and Goulart, 2005; Galdean et al., 2001). The different results between site altitude and catchment elevation range can also be explained by the regional characteristics of the EMMR. Site altitude varied considerably among sampling sites, whereas catchment elevation range varied little among sites, indicating that the EMMR geography shows little variation at this spatial extent (Fernandes et al., 2020).

A high proportion of scrapers in comparison to the other feeding groups was observed in the drift (32%), but it was not related to primary producers (chlorophyll-a). This might result from the food requirements of this group, which drives individuals to actively drift downstream (Katano et al., 2017). Most of the stream sites have riparian vegetation that shades the streams and limits local primary production (Vannote et al., 1980). Because primary production is suboptimal, it forces the drift of aquatic organisms that are dependent on this type of resource.

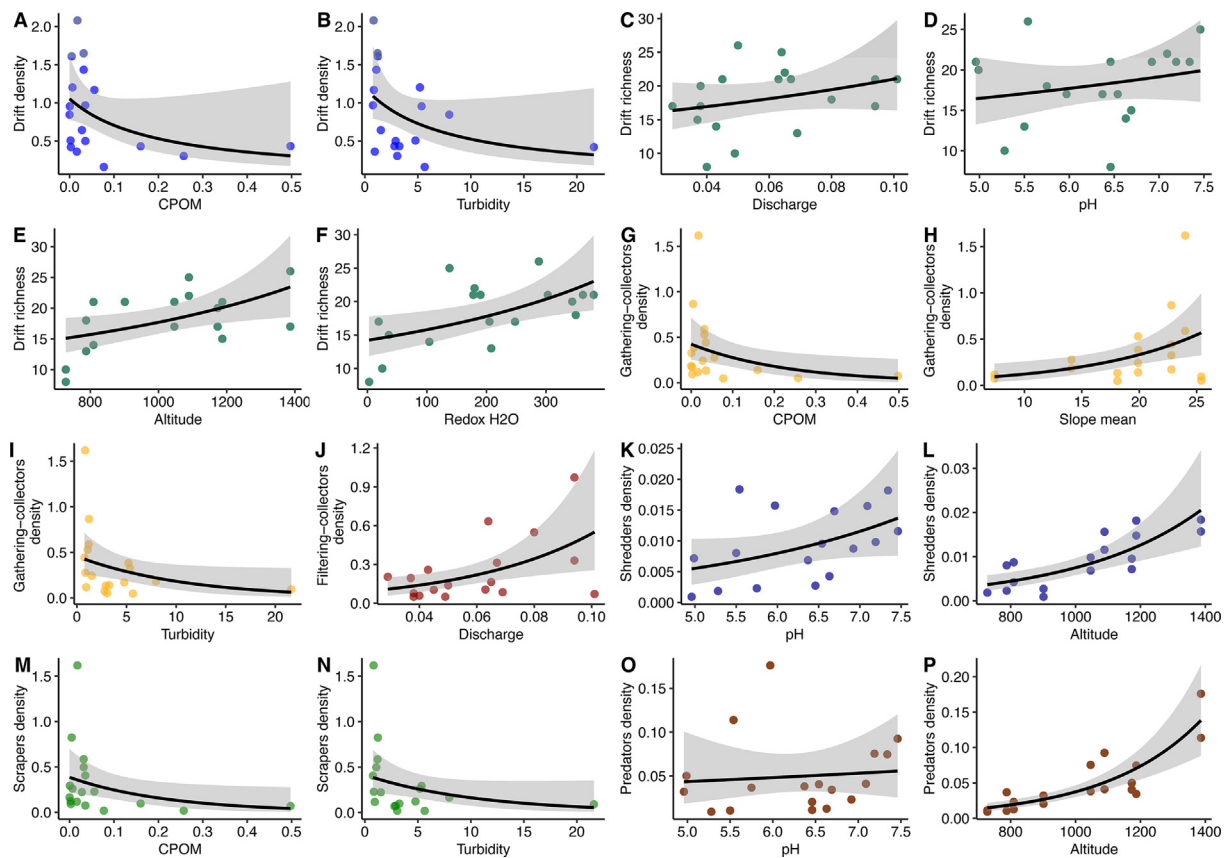
The density of shredders was 0.9% and their abundance in the drift was mostly related to pH and site altitude. The scarcity of shredders has been reported in several other tropical stream studies (Bojsen and Jacobsen, 2003; Moretti et al., 2007) in contrast to studies in temperate streams, which is a key difference between temperate and tropical streams (Boyer et al., 2015). A possible explanation for this pattern is that the chemical composition of foliage in tropical riparian forests makes them less palatable than leaves in temperate regions, as a way to reduce pressure from herbivory (Boyer et al., 2015). Despite the abundance of CPOM in tropical Asian streams, Li and Dudgeon (2008) observed that shredding invertebrates did not make use of this resource, with FPOM being the main component of their diets. Other studies confirm this result (Chará-Serna et al., 2012; Ferreira et al., 2015; Tomanova et al., 2006) and showed that suspended FPOM is an important food resources for downstream invertebrates (Callisto and Graça, 2013; Mollá et al., 2006). In this study, CPOM drift was most strongly linked with both gathering-collector and scraper densities, suggesting that it was mostly serving as a substrate for decomposing organisms, most likely fungi (Ferreira et al., 2015; Gessner et al., 1999; Graça et al., 2015).

This study focused on niche theory, which emphasizes deterministic processes by highlighting the role of niche differences (e.g., abiotic selection and biotic interactions). The latter are particularly important in tropical systems (Brown, 2014). There was no data for assessing the

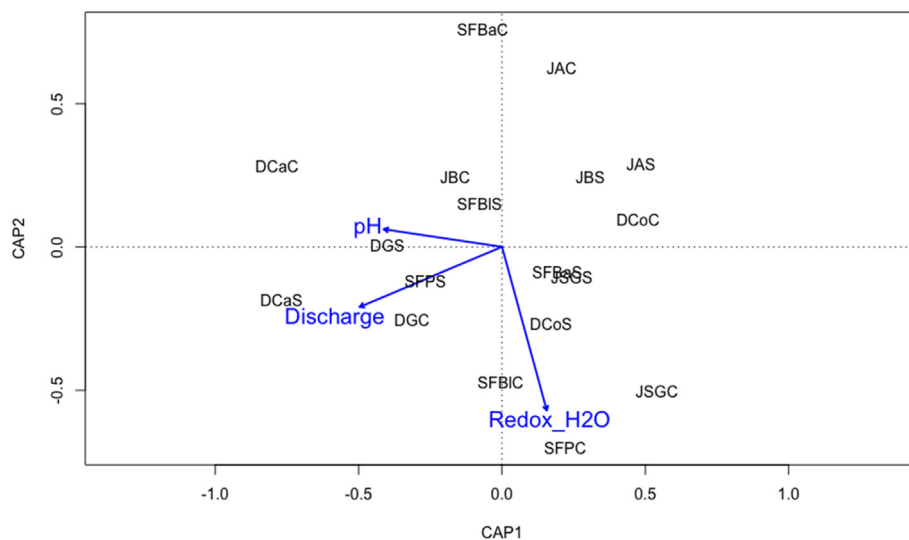
**Table 2**

Regression statistics, loglikelihood (LogL) and Akaike's information criterion corrected for small sample sizes (AICc) for generalized linear models of invertebrate drift response variables versus environmental predictor variables. The number of model parameters (k), cumulative Akaike weights (wi), adjusted percent  $R^2$  values and the difference between the given and best fitting model ( $\Delta i$ ) are presented for each candidate model.

Metric	Model	k	logL	AICc	Delta AIC	Weight	adjR <sup>2</sup>
Density	CPOM + Turbidity	4	-6.89	24.9	0	0.649	0.59
	CPOM + Slope + Turbidity	5	-5.55	26.1	1.23	0.351	0.69
Richness	Altitude + Discharge + pH + redox	6	-37.18	94	0	0.58	0.85
	Altitude + Conductivity + Discharge + pH + redox	7	-34.74	94.7	0.69	0.41	0.89
Gathering collectors	CPOM + Slope + Turbidity	5	-66.31	147.6	0	1	0.82
Filtering collectors	Discharge	3	-71.83	151.4	0	0.109	0.28
Shredders	Altitude + pH	4	-5.45	22.2	0	1	0.78
Scrapers	CPOM + Slope + Turbidity	5	-67.8	150.6	0	1	0.75
	Altitude + pH	4	-33.02	77.1	1.4	0.263	0.75
	Altitude + pH + Temperature	5	-31.29	77.6	1.86	0.208	0.80



**Fig. 3.** Relationships between environmental metrics and drift variables. The dark line indicates predicted values; dots indicate observed values, and the gray band indicates 95% confidence intervals.



**Fig. 4.** Distance-based redundancy analysis ordination for drift invertebrate density and water quality and food variables. Vectors indicate the 3 environmental variables that explained most of the variability in the drift composition.

neutral theory (Hubbell, 2009), which holds the view that stochastic processes associated to random dispersal, colonization and mortality are the major forces in regulating assemblage composition. However, it is presumed that both niche and neutral theories are at play in sky island streams (Wennekes et al., 2012; Whitfield, 2002).

Finally, this study found that water quality was an important factor for all but one drift variable (filterer-collector density), indicating its importance for drift processes in EMMR streams. Local environmental

variables were shown to be the most important factor for the structuring of benthic macroinvertebrate assemblages in previous studies in Neotropical Savanna streams (Callisto et al., 2021; Firmiano et al., 2021; Linares et al., 2021).

## 5. Conclusions

The results presented here show that multiple types of environmental

conditions (food, water quality, physical habitat) play essential roles in the drift processes for benthic macroinvertebrate assemblages in sky island streams, highlighting their importance for supporting biodiversity. These results also suggest that drift is linked negatively with organic matter transport dynamics. It is therefore suggested that future studies should look further into this link because it is the opposite of what has been usually reported in the literature, and may be driven by the sky islands occurrence in OCBIL ecosystems. Such ecosystems share characteristics that often differ markedly from those characterizing young, often disturbed, fertile landscapes (Hopper, 2009), and are therefore more likely have important implications for terrestrial and lotic ecosystem management in OCBIL landscapes.

## Ethical statement

Nothing to declare.

## Authors contributions

**Marcos Callisto:** Conceptualization, Methodology, Writing – original draft, review & editing. **Diego M.P. Castro:** Methodology, Writing – review & editing. **Marden S. Linares:** Methodology, Writing – review & editing. **Laryssa K. Carvalho:** Methodology, review & editing. **José E. L. Barbosa:** Methodology, review & editing. **Robert M. Hughes:** Writing – review & editing.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watbs.2022.100077>.

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