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Beta diversity of aquatic invertebrates increases along an altitudinal gradient in a Neotropical mountain

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Abstract

Mountains harbor rich biodiversity and high levels of endemism, particularly due to changes in environmental conditions over short spatial distances, which affects species distribution and composition. Studies on mountain ecosystems are increasingly needed, as mountains are highly threatened despite providing ecosystem services, such as water supply for half of the human population. We aimed to understand the patterns and drivers of alpha and beta diversities of aquatic invertebrates in headwater streams along an altitudinal gradient in the second largest South American mountain range, the Espinhaço mountains. Headwater streams were selected at each 100 m of elevation along an altitudinal gradient ranging from 800 to 1400 m asl, where three substrate types per stream were sampled: leaf litter, gravel, and cobbles. Environmental variables were sampled to represent local riparian canopy cover, instream physical habitat, water quality, climatic data, and land use. Generalized linear models and mixed models were used to test relationships between altitude and the richness and abundance of invertebrates and to assess the influence of environmental variables on the same metrics. Patterns of spatial variation in aquatic invertebrate assemblages along the altitudinal gradient were assessed using multiplicative beta diversity partitioning. The richness and abundance of aquatic invertebrates decreased with increasing altitude, whereas beta diversity increased with increasing altitude. Significant differences in assemblage composition and in relative abundance of invertebrates were observed for both substrates and altitude. We thus show that the high regional beta diversity in aquatic ecosystems in the studied site is due to the high turnover among areas.

Abstract in Portuguese is available with online material.

KEYWORDS

aquatic ecosystems, elevation, macroinvertebrate assemblages, mountain ecology, rupestrian grassland, species distribution

1 | INTRODUCTION

Patterns of biological diversity along altitudinal gradients are among the most studied themes in ecology (e.g., Lomolino, 2001; Sanders & Rahbek, 2012). Mountain systems are considered natural laboratories in which altitudinal gradients can serve as natural experiments for studies on community and ecosystem responses to ongoing climatic changes (McCain & Colwell, 2011). In such systems, environmental conditions (e.g., relative humidity, precipitation, geological substrates, air temperature, and some

geophysical and climatic trends) change with increasing elevation over short spatial distances, affecting species distributions and allowing evolutionary and ecological studies to be performed (e.g., Fernandes & Price, 1988; Körner, 2007; Sundqvist, Sanders & Wardle, 2013). Ecological studies in mountains around the globe are increasing owing to the great importance of mountains in biodiversity and ecosystem services (e.g., Antonelli et al., 2018; Price, 1998; Resende, Fernandes & Coelho, 2013) but primarily because of the fragility of their ecosystems and because of threats imposed by climate change (e.g., Fernandes et al., 2018; Loarie et al., 2009; Sundqvist et al., 2013). While greater attention has been devoted to tall mountains, short, ancient, and eroded tropical mountains harbor equivalent or even greater biodiversity and high levels of endemism (Fernandes et al., 2016, 2018; Schaefer et al., 2016). In Southeast Brazil, the Espinhaço mountain chain stretches over 1200 km and 10 degrees of latitude and shelters the springs of many important rivers. This region requires profound scientific conservation and political consideration due to its unparalleled biodiversity and because it is under severe anthropogenic threat (Fernandes, Barbosa, Negreiros & Paglia, 2014; Fernandes et al., 2018, see Fernandes, 2016a for a review).

Most biological communities experience losses of diversity, biotic interactions, and ecosystem processes with increasing altitude (Fernandes et al., 2016; Grytnes & McCain, 2007; Jacobsen, 2003; Raich, Russell & Vitousek, 1997), likely due to the increasing harshness of abiotic factors and to the decrease in the available habitat area. However, not all *taxa* respond to altitude in the same way, and this pattern is even less clear in the freshwater biota (Sundqvist et al., 2013). Patterns of aquatic invertebrates' distribution along altitudinal gradients have been described in some South American regions, especially in the Andes (Jacobsen, Schultz & Encalada, 1997; Miserendino, 2001; Ramírez, Roldán & Yepes, 2004; Scheibler, Cristina Claps & Roig-Juñent, 2014), but are scarce in tropical mountains (e.g., Henriques-Oliveira & Nessimian, 2010). Local and regional factors regulate the biodiversity of stream ecosystems by filtering organisms based on their attributes (Poff, 1997). Environmental factors, such as rainfall, altitude (regional scale) and flow types, heterogeneity and substrate types (local scale), for example, are known as key components structuring aquatic invertebrate distribution and abundance in streams (Castro, Dolédec & Callisto, 2017; Heino, Muotka & Paavola, 2003; Silva, Ligeiro, Hughes & Callisto, 2014). However, the main drivers of their community assembly along tropical altitudinal gradients remain unclear.

Classical studies (e.g., Colwell, Brehm, Cardelus, Gilman & Longino, 2008; Rahbek, 1995) have mainly focused on altitudinal patterns of alpha and gamma diversities, and surprisingly little is known about the patterns and drivers of spatial variation in community composition (i.e., beta diversity) across altitudinal gradients (Tello et al., 2015; Perillo, de Neves, Antonini & Martins, 2017; Sabatini, Jiménez-Alfaro, Burrascano, Lora & Chytrý, 2018, but see Nunes et al., 2017). Generally defined as the variation in species identities among sites or times (Tuomisto, 2003; Whittaker, 1960), beta diversity has long been used to investigate changes in community composition and structural patterns along environmental, spatial and temporal gradients, and it is essential for understanding the mechanisms that influence species distribution (Anderson et al., 2011; Coelho, Carneiro, Branco, Borges & Fernandes, 2018; Jankowski, Ciecka, Meyer & Rabenold, 2009; Legendre, Borcard & Peres-Neto, 2005). Quantifying beta diversity along environmental gradients can support the proposition of landscape-wise conservation strategies for protecting biological diversity (Jankowski et al., 2009). For example, if beta diversity is high, even small impacts or alterations in parts of the environment could eliminate a significant proportion of the regional biodiversity. Beta diversity can be due to either species replacement (turnover) or nestedness, when the species at the poorest site are a strict subset of those at the richest site (Baselga, 2012). Given that these tropical montane landscapes harbor diverse fauna with many coexisting species within habitat types, it is expected that species turnover will occur (Coelho et al., 2018; Jacobsen et al., 1997; Perillo et al., 2017).

Benthic macroinvertebrates in headwater streams participate in crucial ecological processes of ecosystem functioning, including leaf litter breakdown and linking energy flow from riparian vegetation to freshwater biodiversity (Castro et al., 2016; Covich, Palmer & Crowl, 1999). Nevertheless, before deeply investigating ecological processes, it is essential to further understand the species–environment relationship (de Castro, Dolédec & Callisto, 2018). Measuring community changes along an altitudinal gradient is perhaps the first step to address relevant questions about the ecosystem functions and processes in regions that possess great environmental variation and are highly endangered (Fernandes et al., 2018).

This study aims to shed light on the patterns and drivers of alpha and beta diversities in headwater streams along an altitudinal gradient in the oldest and second largest South American mountain chain, the Espinhaço mountain range. The study area underwent several geotectonic events before reaching the present configuration, but the current altimetric conformation can be largely explained using two events: (a) the rifting process at approximately 1752 Ma (end of the Paleoproterozoic), beginning the formation of a basin in which more than 5000 m of predominantly sandstone sediments of the Espinhaço Supergroup accumulated, and (b) the closure of the basin by compressive forces with transport from east to west, which generated the Espinhaço Orogen at approximately 1250 Ma (Mesoproterozoic) (Almeida-Abreu, 1995). These events are mainly responsible for the conformation of relief above 1000 m, making them very old areas from a biogeographic perspective. These mountains comprise a mosaic of vegetation types, including savannas, dry woodlands, montane vegetation, and moist forests (see Fernandes et al., 2016; Silveira et al., 2016), and the Serra do Cipó (in the southern portion of Espinhaço) offers nearly pristine streams for ecological studies. This study is the first to determine the effect of altitude (along a gradient of 800–1400 m asl) on alpha and beta diversities of aquatic macroinvertebrates. We also assess the influence of different substrates on the richness, abundance and composition of aquatic invertebrates along the altitudinal gradient.

Finally, we attempt to discriminate the main drivers of biodiversity at different spatial scales, including land use, riparian vegetation integrity, instream physical habitat, and water quality. We expected a decrease in abundance and alpha diversity of aquatic invertebrates with increasing altitude, following the common pattern of diversity decline with increasing altitude, and an increase in beta diversity along the altitudinal gradient in the region (e.g., Fernandes & Price, 1988; Araújo & Fernandes, 2003; Perillo et al., 2017, for a review see Fernandes, 2016a).

2 | METHODS

2.1 | Study area

This study is part of the Brazilian Long-Term Ecological Research Program (PELD-Site 17 CRSC). One headwater stream (second and third orders at a 1:100,000 scale, *sensu* Strahler, 1957) was selected at each 100 m of elevation along an altitudinal gradient ranging from 800 to 1400 m asl, totaling seven sampling sites (Figure 1). The streams are located in rupestrian grassland vegetation (*campo rupestre* in Portuguese) in Serra do Cipó, a montane, grassy–shrubby vegetation mosaic with rocky outcrops of quartzite in the southern part of the Cadeia do Espinhaço (Espinhaço Mountain Range), southeastern Brazil (for details of the vegetation, see Fernandes, 2016a; Mota et al., 2018). The Cadeia do Espinhaço is a predominant quartzitic mountain chain that extends for ca. 1200 km across the states of Minas Gerais and Bahia, separating the Atlantic Forest and Cerrado (savanna) biomes (Fernandes, 2016b). The region has a highland tropical Cwb Köppen climate, with two well-defined seasons: a wet season from October to March and a dry season from April to September; it also has a 1500 mm mean annual rainfall and a mean annual temperature of 20°C (Fernandes et al., 2016). All sampled streams presented well-oxygenated clearwater, as well as riverbeds composed of rocks, cobbles, gravel and sand, with leaf pack accumulations and silt deposited in pool areas.

2.2 | Field data collection

Sites were sampled in May 2017. At each stream (hereafter called stream sites), a 25 m long stretch subdivided into six equidistant transects was determined (Martins, Ligeiro, Hughes, Macedo & Callisto, 2018). Three substrate types were sampled in each stream: leaf litter, gravel (>2–64 mm diameter), and cobbles (>64–250 mm). These substrates were selected because they are the most representative

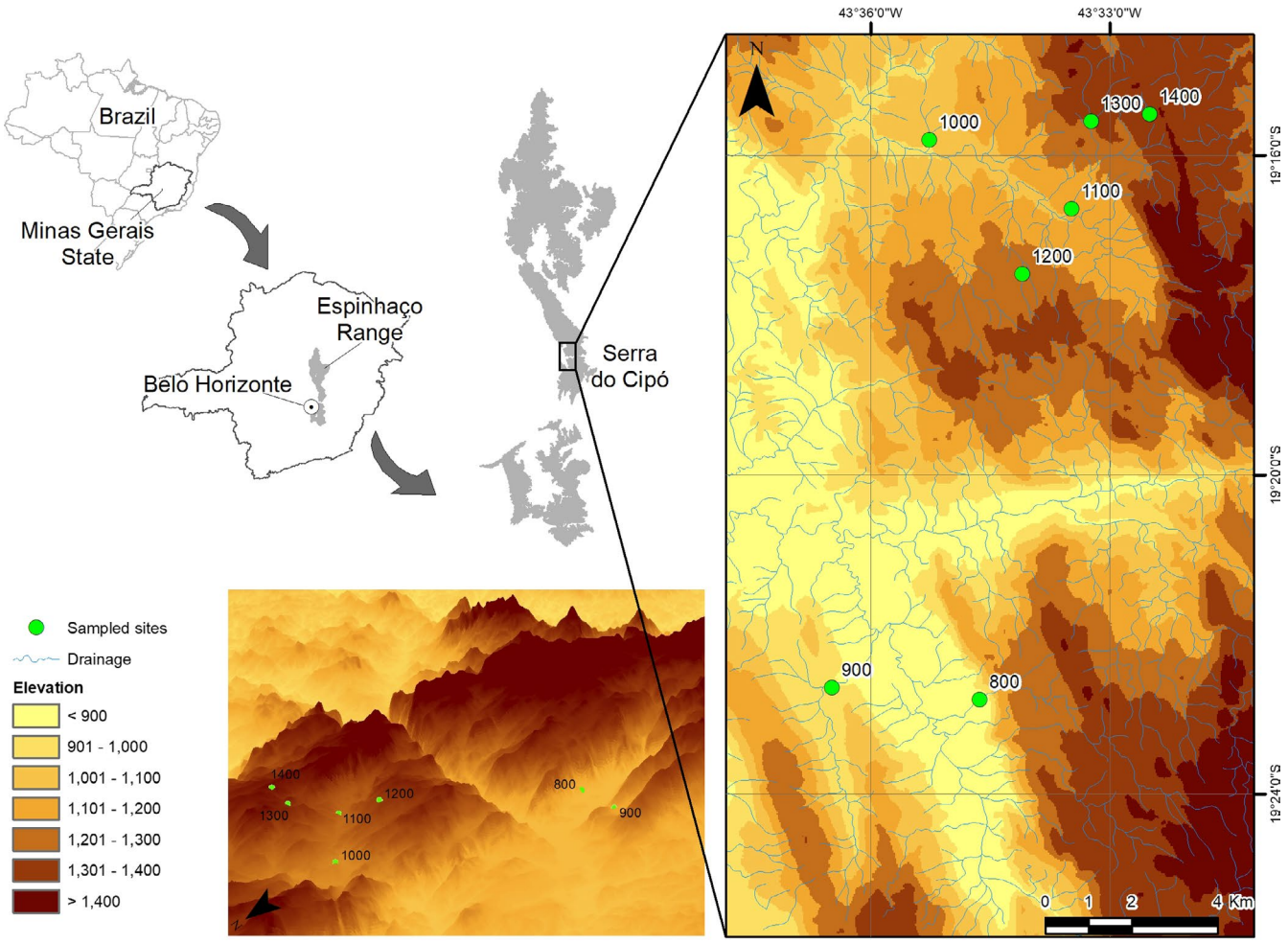


FIGURE 1 Elevational map of the study area with the locations of the seven sampling sites in Serra do Cipó, Minas Gerais State, Brazil

of the streams in this region (Ligeiro, Melo & Callisto, 2010). Three subsample units were taken with a Surber sampler (0.09 m² area and 500 μm mesh size) per substrate type per site, totaling 63 samples. Thus, stream sites were our replicates. After collection, samples were washed in the field to remove organic particulates and substrates, placed in individual plastic jars and preserved with 70% alcohol. In the laboratory, macroinvertebrates were sorted, identified, and counted under a stereomicroscope. Ephemeroptera, Plecoptera, and Trichoptera (EPT) individuals were identified to the genus level, and other individuals were identified to the family level using taxonomic keys (Dominguez, Molineri, Pescador, Hubbard & Nieto, 2006; Hamada, Nessimian & Querino, 2014; Mugnai, Nessimian & Baptista, 2010).

Environmental variables at each site were described in terms of local riparian canopy cover, instream physical habitat (i.e., habitat hydromorphology, substrate size, and flow type), water quality, and climatic data. We assessed land use and cover for each stream catchment by manually interpreting high-resolution satellite images (0.6–5 m spatial resolution, Google 2018) together with Landsat multispectral satellite images to more accurate results (Macedo et al., 2014) and identified four natural vegetation covers (woodland, grasslands, rupestrian grasslands, and rock outcrops). Due to natural fluctuations in climate (i.e., drier or rainier years in relation to the historical background) and because of the seasonal influence on the physical habitat stability, we calculated mean annual rainfall and mean annual temperature for the three previous months, the previous year, and the two previous years before sampling each stream site. The climatic data were obtained from seven meteorological monitoring stations (Onset HOBO® U30 data logger) located adjacent to each sampling site (i.e., one station at each 100 m elevation) and extrapolated to each stream site by cokriging interpolate procedures and using an elevation digital model (SRTM model; ~30 m spatial resolution) as a covariate (Alvares, Stape, Sentelhas, de Moraes Gonçalves & Sparovek, 2013). We also calculated stream morphometric variables through the SRTM model by using GIS procedures (e.g., distance to source, catchment area, and slope). Water quality was characterized by measuring temperature, electrical conductivity, pH, turbidity, and dissolved oxygen concentration (APHA 2005). Physical habitat characteristics were measured based on the protocol developed by the US Environmental Protection Agency (Peck et al., 2006; USEPA, 2013) as adapted and validated for streams of the Brazilian Cerrado (Callisto, Hughes, Lopes & Castro, 2014) and mountaintop grasslands (Martins et al., 2018). All site variables were calculated according to Kaufmann, Levine, Robison, Seeliger and Peck (1999).

A total of 270 variables were initially recorded. In a first step, we eliminated those variables that had more than 90 percent zero values, low variability (<0.2), and high correlation with each other ($r > |0.8|$). For highly correlated variables, we retained the most ecologically meaningful ones. Those procedures yielded a set of 18 metrics. To reduce the number of environmental variables, as well as to maintain the number of variables at 3–4 (due to our sample size), a principal component analysis (PCA) was conducted on the 18 remaining metrics. The first axis synthesized 99.9 percent of the variability, and we selected the four metrics with the highest scores (i.e., spring distance, 24 months rainfall, water pH, and substrates > 16 mm) along that axis for the analyses.

2.3 | Data analyses

The taxonomic richness and the abundance of aquatic invertebrate families and EPT genera were analyzed for each stream (altitude) and substrate type. A generalized linear mixed-effects model (GLMM) was run to test for the relationships between the observed taxonomic richness and abundance of aquatic invertebrates with altitude. For those analyses, we used the identity of each site (i.e., altitude) as a random effect and Poisson distribution in the *lme4* package. We then applied an ANOVA on the model created to observe whether the effect was statistically significant.

We examined patterns of spatial variation in aquatic invertebrate assemblages among stream sites along the altitudinal gradient by using the beta diversity partitioning method of Baselga (2010); see also Legendre (2014). The Jaccard dissimilarity coefficient (based on species presence/absence) was calculated and used as a measure of beta diversity. Taxonomic richness in each stream was used as a measure of alpha diversity. In additive partitioning, alpha diversity represents the diversity within each stream, beta diversity the diversity among streams of different altitudes, and gamma diversity the diversity of the entire gradient analyzed. Values for alpha and beta diversity were calculated using the sampled taxonomic richness of the seven sites at different altitudes.

Permutational multivariate analysis of variance (PERMANOVA) was performed to test differences in taxonomic composition along the altitudinal gradient between substrate types and the interaction between them. We used nonmetric multidimensional scaling (NMDS) to plot results from a Bray–Curtis dissimilarity matrix on log-transformed abundance data.

Finally, to assess the influence of the selected environmental metrics on richness and abundance of aquatic invertebrates, generalized linear models (GLMs) were constructed using altitude, distance to spring, water pH, percent of substrates > 16 mm, and 24-month rainfall as response variables. A model selection procedure using backward elimination was applied. We used R v3.2.2 (R Core Team, 2015) for all analyses. We performed residual analyses for all models and checked for the distribution of errors, over-dispersion of the data and spatial autocorrelation of residuals. Diversity partitioning and ANOVAs were conducted using the *vegan* package (Oksanen et al., 2016). Beta diversity decomposition was undertaken using the *betapart* package (Baselga, Orme, Villeger, Bortoli & Leprieur, 2013) and GLMMs using the *lme4* package (Bates, Mächler, Bolker & Walker, 2015).

3 | RESULTS

A total of 7821 specimens, distributed into 59 families, were collected. Most taxa were rare, with 79 percent of the taxa having

abundances of <1 percent. The dominant families were Chironomidae (4700 individuals), Leptophlebiidae (662 individuals), Elmidae (409 individuals), and Libellulidae (233 individuals). EPT was composed of 1627 specimens (20.8% of the total), distributed in 19 families and 51 genera. Similarly to families, most genera were rare, with 59 percent of the EPT genus having abundances of <1 percent.

Family richness ($\chi^2 = 8.26$, $df = 1$, $N = 7$, $p = 0.004$) and abundance ($\chi^2 = 5.37$, $df = 1$, $N = 7$, $p = 0.020$) of aquatic invertebrates decreased with altitude. EPT genera richness ($\chi^2 = 4.93$, $df = 1$, $N = 7$, $p = 0.026$), but not abundance ($\chi^2 = 1.44$, $df = 1$, $N = 7$, $p = 0.228$), also decreased with increasing altitude. The mean richness of invertebrate families at the 800 m site was 16.7 ± 1.39, whereas at the 1400 m site, the mean richness was 9.66 ± 2.17 (Figure 2a). The mean abundance of invertebrate families at the 800 m site was 137.7 ± 47.1, whereas at the 1400 m site, the mean abundance was 85.1 ± 58.9 (Figure 2b). When considering the effects of different substrates (i.e., leaf litter, cobbles, and gravel), there was no significant difference in family richness ($\chi^2 = 1.01$, $df = 2$, $N = 7$, $p = 0.603$), while abundance was higher in leaf packs ($\chi^2 = 22.21$, $df = 1$, $N = 7$, $p < 0.001$). The richness and abundance of EPT genera did not differ significantly between the three substrates.

The NMDS ordination based on the Bray–Curtis dissimilarity matrix on abundance data showed that leaf litter had a different taxonomic composition of aquatic invertebrate families in comparison with cobbles and gravel substrates (Figure 3). Although 36 taxa (61% of the total) occurred on all substrates, 23 taxa showed a marked frequency for two substrates (18%) or one substrate type (20%). This difference is more pronounced when considering the altitude separately. Although there was no difference in the richness among the substrates or in the interaction between substrate and altitude,

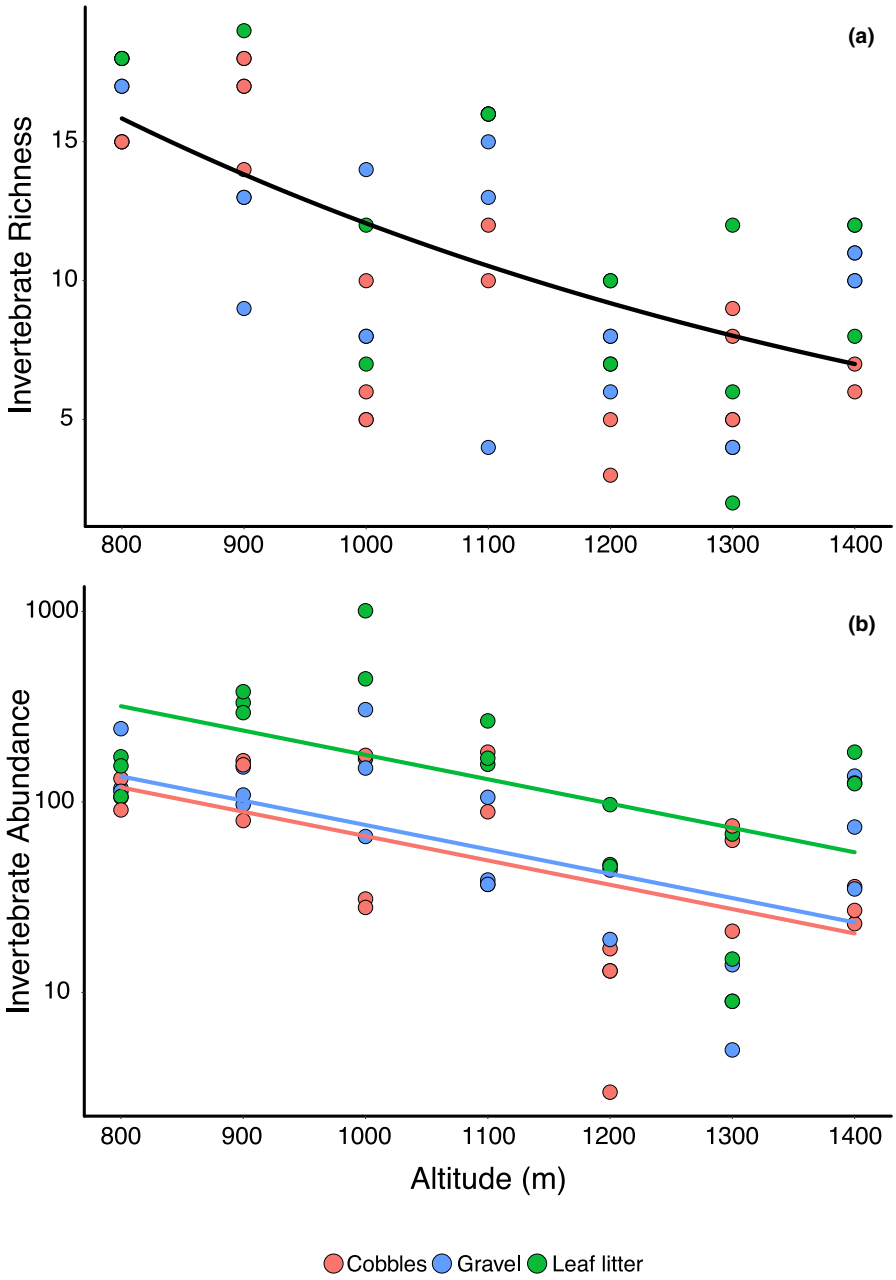


FIGURE 2 Richness (a) and abundance (b) of macroinvertebrate families in the different substrates (leaf litter, gravel, and cobbles) along an elevation gradient in Serra do Cipó, Brazil

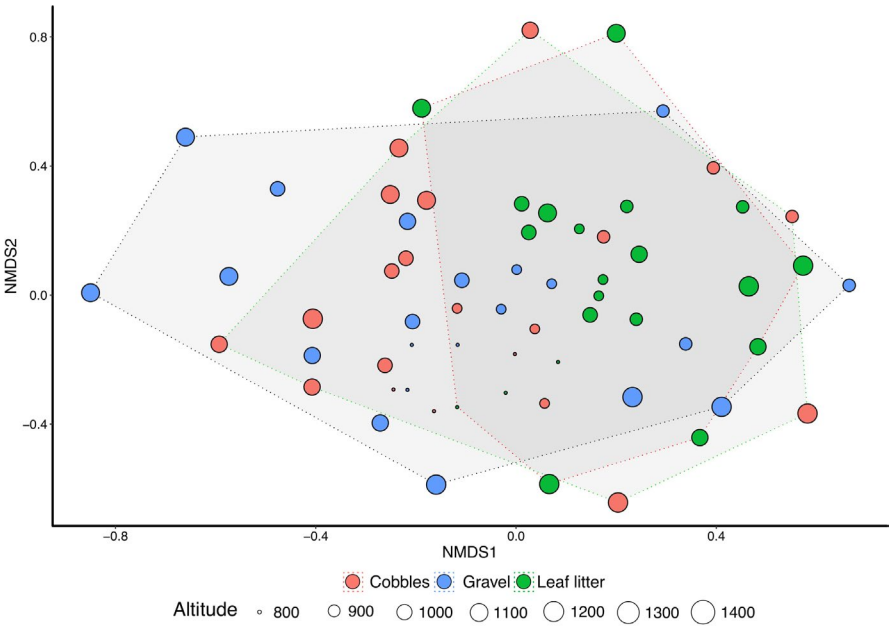


FIGURE 3 Nonmetric multidimensional scaling analyses of invertebrate assemblages among substrates and along the altitudinal gradient in Serra do Cipó, Brazil

PERMANOVA revealed significant differences in assemblage composition and in the relative abundance for both substrates (Family *pseudo-F* = 2.45, *df* = 2, $p < 0.001$; EPT genera *pseudo-F* = 1.54, *df* = 2, $p < 0.001$) and altitude (Family *pseudo-F* = 8.85, *df* = 1, $p < 0.001$; EPT genera *pseudo-F* = 3.35, *df* = 1, $p < 0.001$) (Figure 4a,b). As expected, beta diversity increased with increasing altitude ($F_{1,5} = 8.7$, $p = 0.03$, $R^2 = 0.56$), having a lower value at 800 m and a higher value at 1400 m asl (Figure 5). The reduction in taxonomic richness with increased altitude characterizes species turnover (93 ± 3.6%). Analyzing only EPT genera, we did not find a significant relationship between beta diversity and altitude ($F_{1,5} = 0.98$, $p = 0.37$).

For the stepwise GLM regression procedures constructed using altitude, distance to spring, water pH, percent of substrates > 16 mm, and 24-month rainfall as response variables, the reduced model for invertebrates family and EPT genera richness included only altitude as a predictor variable ($\chi^2 = 5.37$, *df* = 1, $N = 7$, $p = 0.04$; $\chi^2 = 13.53$, *df* = 1, $N = 7$, $p < 0.001$, respectively). For abundance, none of the models constructed was statistically significant. Using Moran's I, we did not find evidence of spatial autocorrelation.

4 | DISCUSSION

The results corroborate the prediction that the richness of aquatic invertebrates along a tropical altitudinal gradient decreases with increasing altitude while beta diversity increases in an opposite trend. This greater contribution of beta diversity to regional diversity means that more species are added to the community, owing to differences in composition between sites of different altitudes. These data showed that aquatic ecosystems in Serra do Cipó present high accumulated diversity, caused by differences among areas, along with high species turnover. Studies of terrestrial invertebrates in the area [e.g., termites (Nunes et al., 2017), dung beetles (Nunes, Braga, Figueira, de Neves & Fernandes, 2016), and bees and wasps (Perillo et al., 2017)] show the same trend as that reported here.

Despite a relatively small elevational range (600 m), aquatic macroinvertebrate richness and abundance declined with altitude in Serra do Cipó, following the pattern observed in the same region for other biological groups, such as woody plants, dung beetles, ants, gall insects, and termites (Fernandes et al., 2016), and in other South American regions for aquatic invertebrates (Jacobsen, 2003; Jacobsen et al., 1997; Scheibler et al., 2014). Jacobsen (2004) found that the local family richness of macroinvertebrates in Ecuadorian streams decreased linearly with altitude. On the other hand, Henriques-Oliveira and Nessimian (2010) did not find a decrease in the richness of aquatic invertebrates studying a gradient (~1500 m) in a Brazilian Atlantic Forest. These authors postulated that their results could be associated with a greater human influence at lower altitudes, with high anthropogenic pressure in relation to land use and the state of riparian vegetation. In our study, all sites are located in protected areas, and sites at lower altitudes (800 and 900 m) are located within the Serra do Cipó National Park, with very low influence of human activities. On the other hand, the lack of any trend in the study by Henriques-Oliveira and Nessimian (2010) could be caused by the lack of significant variation in the forest environment along the altitudinal gradient. In the savanna ecosystem studied by us, there are strong differences in the vegetation along the altitude (see Mota et al., 2018), which could influence the trends.

Although total family richness was not different among the substrate types, the composition of aquatic communities was strongly influenced by substrate type. This pattern was even more evident in the sites at higher altitudes (1200–1400 m), where the number of shared taxa among the three substrates was lower than at lower altitudes (Venn diagrams in Figure 5). The importance of substratum type for the composition of stream macroinvertebrate assemblages is widely recognized in the literature by regulating habitat complexity,

food availability, and refuge against predation or flow disturbance (Buss, Baptista, Nessimian & Egler, 2004; Milesi, Dolédec & Melo, 2016; Mykrä, Heino & Muotka, 2007; Vinson & Hawkins, 1998). For instance, the abundance of aquatic invertebrate families was higher on leaf packs, possibly because this substrate provides greater food resources and shelter against predators for the fauna compared to gravel and cobble substrates.

The beta diversity of aquatic invertebrate families increased with altitude elevation, contributing more to regional diversity than to local diversity. Although beta diversity of EPT genera did not show a significant result, we observed a consistent trend with family results. For trees, beta diversity has been reported to generally decline with increasing latitude and altitude (Kraft et al., 2011; Tello et al., 2015), but for aquatic invertebrates, the opposite was observed by Jacobsen et al. (1997) when studying a gradient of altitude in the Andes. The higher beta diversity at higher altitudes could also be caused by reduced dispersal of adult insects due to a colder and windier climate and to large topographic barriers (Clarke, Macnally, Bond & Lake, 2008; Finn, Khamis & Milner, 2013; Jacobsen, 2003), among other factors. The decrease in community similarity—and the increase in beta diversity—may be caused either by a decrease in environmental similarity with distance (e.g., altitudinal gradient) or by limits to dispersal and niche width differences among taxa (Nekola & White, 1999). In a study in southeastern Brazil, Saito, Soininen, Fonseca-Gessner and Siqueira (2015) suggest that a decrease in similarity among communities may be due to a historical imprint caused by dispersal limitation over time instead of to closely related species having similar niches. Thus, the dispersal ability of species and their local abiotic conditions can act as filters, leading to differences in species composition between areas and increasing turnover along the studied gradient (da Luz et al., 2018). The high number of endemisms at Serra do Cipó may explain the turnover of species. However, the study of dispersal among aquatic insects is challenging due to difficulties

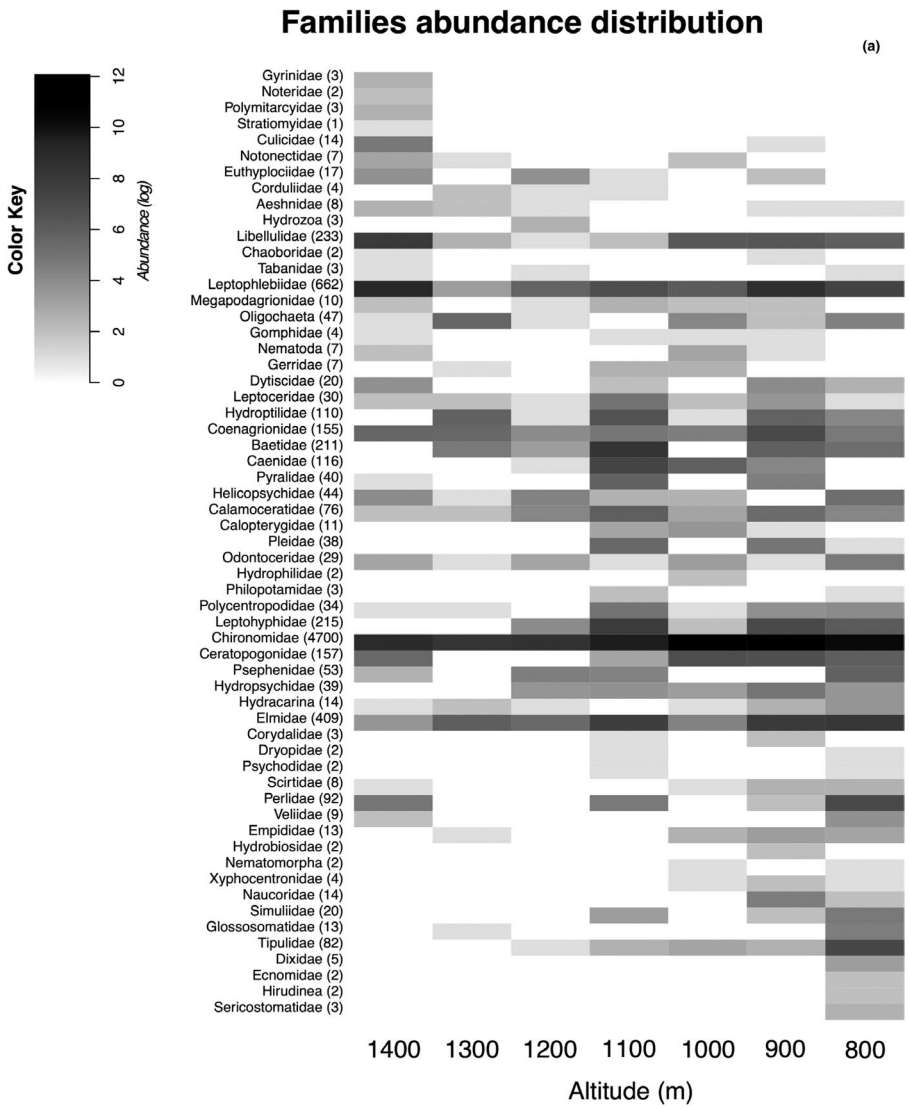
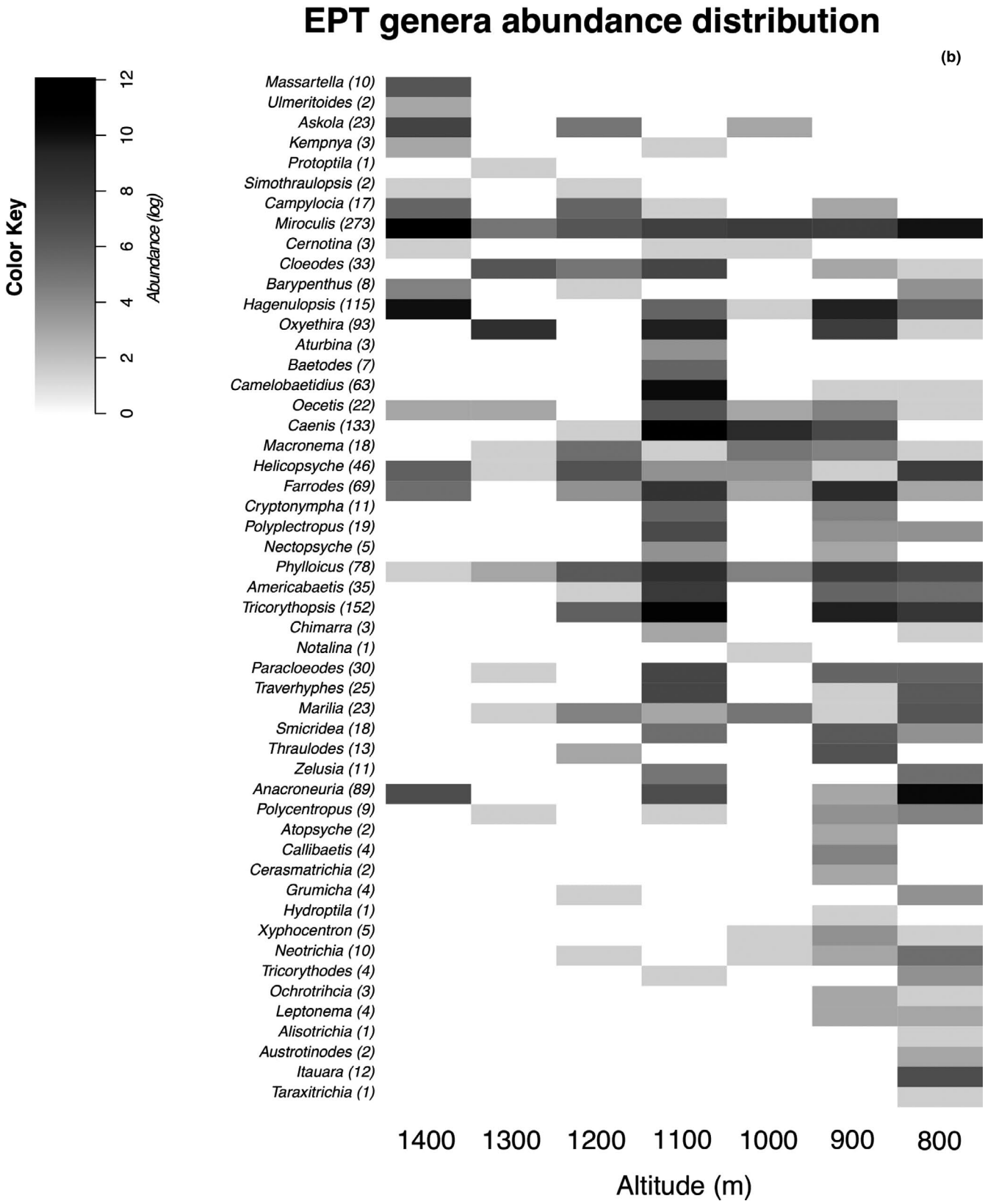


FIGURE 4 Heatmap showing the distribution and total abundance (numbers in parentheses) of each family (a) and EPT genera (b) of aquatic invertebrates along the altitudinal gradient in Serra do Cipó, Brazil

FIGURE 4 Continued



in obtaining observation data (Bilton, Freeland & Okamura, 2001), leaving this question to be studied in detail in the future through methods such as the use of DNA barcodes (e.g., Baird & Hajibabaei, 2012; Emilson et al., 2017).

The importance of altitude *per se* in influencing aquatic invertebrates' richness along the altitudinal gradient compared to the other environmental metrics is probably a result of a multitude of factors acting in synergy. Taxon richness along geographical gradients may

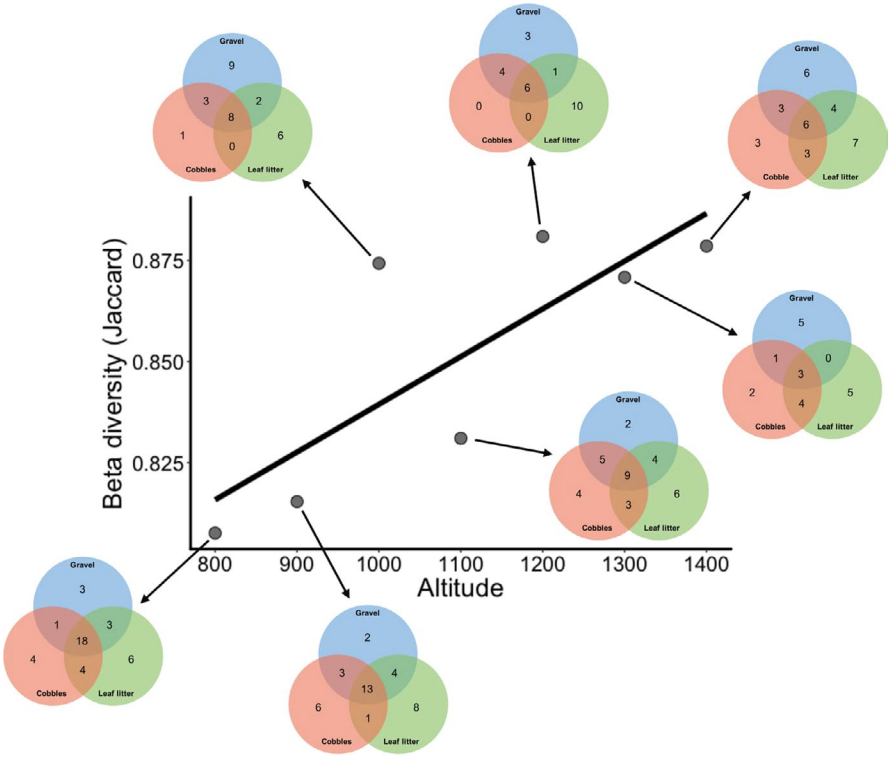


FIGURE 5 Beta diversity values (Jaccard index) along the altitudinal gradient of Serra do Cipó and taxonomic richness in each substrate by altitude (Venn diagrams)

be influenced by contemporary environmental and biological factors and by historical or evolutionary factors (Fernandes & Price, 1992; Jacobsen, 2003; Polato et al., 2018). The age of the ancient Espinhaço mountain range (1250 Ma) and the climatic stability of its geological formation during the past few thousand years (Silveira et al., 2016) may have led to fine-tuned adaptations of the flora and fauna (Fernandes, 2016b). These mountains have recently been called snow-free mountains, reinforcing the stability mentioned above (Streher, Sobreiro, Morellato & Silva, 2017). In higher elevational ranges with harsher environmental conditions, such as low temperatures and snow, some authors have reported different environmental filters for aquatic biota (e.g., Jacobsen et al., 1997; Polato et al., 2018; Scheibler et al., 2014).

Although Brazil encompasses one of the most important biodiversity hotspots in the world, very few studies involving altitudinal gradients have been carried out in that country (e.g., see Fernandes et al., 2016 and references herein). The results presented here show that despite the limited altitudinal range of Serra do Cipó, there is a distinct modification in the faunal community in relation to composition and abundance along the gradient. Because most of the diversity of the aquatic invertebrates along the Serra do Cipó altitudinal gradient is a result of the high dissimilarities between the headwater streams, conservation and management actions should invest in protecting the highest possible number of headwater streams in the region. Each stream damaged by human activities can mean the loss of aquatic species in the whole region (Callisto, Gonçalves & Ligeiro, 2016).

Studies addressing biodiversity in mountainous regions have largely overlooked the consideration of such a small range gradient in very geologically old montane systems (Old, Climatically Buffered, Infertile Landscapes - OCBILs, Hopper, Silveira & Fiedler, 2016). Understanding such fine-tuned changes of the aquatic diversity in such systems is a major change, as recent human-induced climate changes are more likely to affect these areas first; therefore, it will be possible to detect those changes earlier. In this area, species will have very compact home ranges, being more sensitive to global changes; thus, even small changes in habitat conditions are likely to produce profound changes in biological communities. This is especially true in tropical areas (Barlow et al., 2018), where there is a widespread increase in the effects of human activities that, apart from climatic changes, have been producing several other global change drivers (e.g., land use and land cover, biogeochemical cycles, eutrophication of urban streams, and invasive species; Steffen et al., 2015). Thus, despite the small ranges of their altitudinal gradients, these areas are crucial for our understanding for three reasons: (1) They are more prone to suffer first from global change drivers, (2) due to their old evolutionary history, they have fine-tuned adaptations that respond at a much finer scale than large-ranged, young mountainous systems, and (3) they have been neglected by the scientific community so far, despite being spread around the world. Studying such effects from the perspective of aquatic invertebrates (composition, richness, abundance, and multiscale diversity), we think we were among the first to link geological, ecological, and ecosystemic levels with the very recent changes in the Anthropocene. Our contribution to the study of freshwater biodiversity lies in the understanding of how water transports all these multifactorial drivers across the human-dominated landscape.

We are aware of the limitations of our study, particularly those regarding the small number of sampled sites. We carried out this sampling to be comparable with a Brazilian long-term (11-year) ecological research study at the same sites (Fernandes et al., 2016), altitudes, and regions. As suggested by Ligeiro et al. (2010), efficient diversity studies should concentrate sampling in different microhabitats and stream sites. Despite these limitations, this study presents a first assessment of the patterns of alpha and beta diversities in headwater streams along an altitudinal gradient in the oldest and second largest South American mountain chain. To improve the knowledge of dynamics and ecological processes in aquatic ecosystems in ancient and eroded mountains, future studies should evaluate how human activities change aquatic biota distribution and incorporate measures of organic matter processing and secondary production as indices of stream ecosystem function to complement structural measures in stream health monitoring.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.38fh0mc (Castro, Callisto, Solar, Macedo & Fernandes, 2019).

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REFERENCES

Almeida-Abreu, P. A. A. (1995). O supergrupo Espinhaço da Serra do Espinhaço Meridional (Minas Gerais): O rifte, a bacia e o orógeno. *Revista Geonomos*, *3*, 1–18. https://doi.org/10.18285/geonomos.v3i1.211

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes Gonçalves, J. L., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, *22*, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., … Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, *14*, 19–28. https://doi.org/doi.wiley.com/10.1111/j.1461-0248.2010.01552.x

Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., … Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience*, *11*, 718–725. http://www.nature.com/articles/s41561-018-0236-z.

Apha (2005). *Standard methods for the examination of water and wastewater* (21st ed.). Washington, DC: American Public Health Association/American Water Works Association/Water Environment Federation.

Araújo, L. M., & Fernandes, G. W. (2003). Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats. *Lundiana*, *4*, 103–109.

Baird, D. J., & Hajibabaei, M. (2012). Biomonitoring 2.0: a new paradigm in ecosystem assessment made possible by next-generation DNA sequencing. *Molecular Ecology*, *21*, 2039–2044. https://doi.org/doi.wiley.com/10.1111/j.1365-294x.2012.05519.x

Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., … Graham, N. A. J. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, *559*, 517–526. http://www.nature.com/articles/s41586-018-0301-1.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*, 1223–1232. https://doi.org/doi.wiley.com/10.1111/j.1466-8238.2011.00756.x

Baselga, A., Orme, D., Villeger, S., Bortoli, J. D., & Leprieur, F. (2013). *Betapart: Partitioning beta diversity into turnover and nestedness components*. R Packag. version 1.3 15782. Retrieved from http://cran.r-project.org/package=betapart.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bilton, D. T., Freeland, J. R., & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, *32*, 159–181. http://www.annualreviews.org/doi/10.1146/annurev.ecolsys.32.081501.114016.

Buss, D. F., Baptista, D. F., Nessimian, J. L., & Egler, M. (2004). Substrate specificity, environmental degradation and disturbance structuring macroinvertebrate assemblages in neotropical streams. *Hydrobiologia*, *518*, 179–188. https://doi.org/10.1023/B:HYDR.0000025067.66126.1c

Callisto, M., Gonçalves, J. F., & Ligeiro, R. (2016). Water resources in the Rupestrian Grasslands of the Espinhaço Mountains. In G. W. Fernandes (Ed.), *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 87–102). Cham, Switzerland: Springer International Publishing. http://link.springer.com/10.1007/978-3-319-29808-5_5.

Callisto, M., Hughes, R. M., Lopes, J. M., & Castro, M. A. eds. (2014). *Ecological conditions in hydropower basins*. Serie Peixe Vivo 3. Belo Horizonte, Brazil: Companhia Energética de Minas Gerais.

Castro, D. M. P., Callisto, M., Solar, R. R. C., Macedo, D. R., & Fernandes, G. W. (2019). Data from: Beta diversity of aquatic invertebrates increases along an altitudinal gradient in a Neotropical mountain. Dryad Digital Repository. https://doi.org/10.5061/dryad.38fh0mc

Castro, D. M. P., Carvalho, D. R., Pompeu, P. S., Moreira, M. Z., Nardoto, G. B., & Callisto, M. (2016). Land use influences niche size and the assimilation of resources by benthic macroinvertebrates in tropical headwater streams. *PLoS ONE*, *11*, e0150527. http://dx.plos.org/10.1371/journal.pone.0150527.

Castro, D. M. P., Dolédec, S., & Callisto, M. (2017). Landscape variables influence taxonomic and trait composition of insect assemblages in Neotropical savanna streams. *Freshwater Biology*, *62*, 1472–1486. https://doi.org/doi.wiley.com/10.1111/fwb.12961

de Castro, D. M. P., Dolédec, S., & Callisto, M. (2018). Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*, *84*, 573–582. http://linkinghub.elsevier.com/retrieve/pii/S1470160X17305988.

Clarke, A., Macnally, R., Bond, N., & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: A review. *Freshwater Biology*, *53*, 1707–1721. https://doi.org/doi.wiley.com/10.1111/j.1365-2427.2008.02041.x

Coelho, M. S., Carneiro, M. A. A., Branco, C. A., Borges, R. A. X., & Fernandes, G. W. (2018). Species turnover drives β-diversity patterns across multiple spatial scales of plant-galling interactions in mountaintop grasslands. *PLoS ONE*, *13*, e0195565. https://dx.plos.org/10.1371/journal.pone.0195565.

Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*, 258–261. http://www.sciencemag.org/cgi/doi/10.1126/science.1162547.

Covich, A. P., Palmer, M. A., & Crowl, T. A. (1999). The role of benthic invertebrate species in freshwater ecosystems. *BioScience*, *49*, 119. https://academic.oup.com/bioscience/article-lookup/doi/10.2307/1313537.

Dominguez, E., Molineri, C., Pescador, M. L., Hubbard, M. D., & Nieto, C. (2006). Ephemeroptera of South America. In J. Adis, J. R. Arias, G. Rueda-Delgado, & K. M. Wantzen (Eds.), *Aquatic Biodiversity of Latin America* (Vol. 2, 646 pp). Moscow, Russia: Pensoft.

Emilson, C. E., Thompson, D. G., Venier, L. A., Porter, T. M., Swystun, T., Chartrand, D., … Hajibabaei, M. (2017). DNA metabarcoding and morphological macroinvertebrate metrics reveal the same changes in boreal watersheds across an environmental gradient. *Scientific Reports*, *7*, 12777. http://www.nature.com/articles/s41598-017-13157-x.

Fernandes, G. W. (Ed.) (2016a). *Ecology and conservation of mountaintop grasslands in Brazil*. Cham, Switzerland: Springer International Publishing.

Fernandes, G. W. (Ed.) (2016b). The megadiverse Rupestrian Grassland. In *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 3–14). Cham, Switzerland: Springer International Publishing. http://link.springer.com/10.1007/978-3-319-29808-5_1.

Fernandes, G. W., Almeida, H. A., Nunes, C. A., Xavier, J. H. A., Cobb, N. S., Carneiro, M. A. A., … Beirão, M. V. (2016). Cerrado to Rupestrian Grasslands: Patterns of species distribution and the forces shaping Them along an altitudinal gradient. In G. W. Fernandes (Ed.), *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 345–377). Cham, Switzerland: Springer International Publishing. http://link.springer.com/10.1007/978-3-319-29808-5_15.

Fernandes, G. W., Barbosa, N. P. U., Alberton, B., Barbieri, A., Dirzo, R., Goulart, F., … Solar, R. R. C. (2018). The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. *Biodiversity and Conservation*, *27*, 2587–2603. http://link.springer.com/10.1007/s10531-018-1556-4.

Fernandes, G. W., Barbosa, N. P. U., Negreiros, D., & Paglia, A. P. (2014). Challenges for the conservation of vanishing megadiverse rupestrian grasslands. *Nature Conservation*, *12*, 162–165. http://linkinghub.elsevier.com/retrieve/pii/S1679007314000097.

Fernandes, G. W., & Price, P. W. (1988). Biogeographical gradients in galling species richness - Tests of hypotheses. *Oecologia*, *76*, 161–167. https://doi.org/10.1007/BF00379948

Fernandes, G. W., & Price, P. W. (1992). The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia*, *90*, 14–20. https://doi.org/10.1007/BF00317803

Finn, D. S., Khamis, K., & Milner, A. M. (2013). Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography*, *22*, 40–51. https://doi.org/doi.wiley.com/10.1111/j.1466-8238.2012.00766.x

Grytnes, J. A., & McCain, C. M. (2007). Elevational trends in biodiversity. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (pp. 1–8). Elsevier Inc.

Hamada, N., Nessimian, J. L., & Querino, R. B. (2014). (Eds.). *Insetos aquáticos na Amazônia brasileira: Taxonomia, biologia e ecologia*. Manaus, Brazil: Editora INPA.

Heino, J., Muotka, T., & Paavola, R. (2003). Determinants of macroinvertebrate in headwater diversity streams : regional and local influences. *Journal of Animal Ecology*, *72*, 425–434. https://doi.org/10.1046/j.1365-2656.2003.00711.x

Henriques-Oliveira, A. L., & Nessimian, J. L. (2010). Aquatic macroinvertebrate diversity and composition in streams along an altitudinal gradient in Southeastern Brazil. *Biota Neotropica*, *10*, 115–128. http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1676-06032010000300012&lng=en&tlng=en.

Hopper, S. D., Silveira, F. A. O., & Fiedler, P. L. (2016). Biodiversity hotspots and Ocbil theory. *Plant and Soil*, *403*, 167–216. http://link.springer.com/10.1007/s11104-015-2764-2.

Jacobsen, D. (2003). Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv für Hydrobiologie*, *158*, 145–167. http://www.ingentaselect.com/rpsv/cgi-bin/cgi?ini=xref&body=linker&reqdoi = 10.1127/0003-9136/2003/0158-0145.

Jacobsen, D. (2004). Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology*, *49*, 1293–1305. https://doi.org/10.1111/j.1365-2427.2004.01274.x

Jacobsen, D., Schultz, R., & Encalada, A. (1997). Structure and diversity of stream invertebrate assemblages : the influence of temperature with. *Freshwater Biology*, *38*, 247–261. https://doi.org/10.1046/j.1365-2427.1997.00210.x

Jankowski, J. E., Ciecka, A. L., Meyer, N. Y., & Rabenold, K. N. (2009). Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology*, *78*, 315–327. https://doi.org/doi.wiley.com/10.1111/j.1365-2656.2008.01487.x

Kaufmann, P. R., Levine, P., Robison, E. G., Seeliger, C., & Peck, V. D. (1999). *Quantifying physical habitat in wadeable streams*. EPA/620/R-99/003. Washington, DC: U.S. Environ. Prot. Agency, 130.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*, 569–574. http://linkinghub.elsevier.com/retrieve/pii/S0169534707002819.

Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., … Myers, J. A. (2011). Disentangling the drivers of diversity along latitudinal and elevational gradients. *Science*, *333*, 1755–1758. http://www.sciencemag.org/cgi/doi/10.1126/science.1208584.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*, 1324–1334. https://doi.org/10.1111/geb.12207

Legendre, P., Borcard, D., & Peres-Neto, P. R. (2005). Analyzing beta diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs*, *75*, 435–450. https://doi.org/10.1890/05-0549

Ligeiro, R., Melo, A. S., & Callisto, M. (2010). Spatial scale and the diversity of macroinvertebrates in a Neotropical catchment. *Freshwater Biology*, *55*, 424–435. https://doi.org/doi.wiley.com/10.1111/j.1365-2427.2009.02291.x

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055. http://www.nature.com/articles/nature08649.

Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, *10*, 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

da Luz, G. R., da Mota, G. S., Spadeto, C., Tolentino, G. S., Fernandes, G. W., & Nunes, Y. R. F. (2018). Regenerative potential of the soil seed bank along an elevation gradient of rupestrian grassland in south-eastern Brazil. *Botany-Botanique*, *96*, 281–298. http://www.nrcresearchpress.com/doi/10.1139/cjb-2017-0162.

Macedo, D. R., Hughes, R. M., Ligeiro, R., Ferreira, W. R., Castro, M. A., Junqueira, N. T., … Callisto, M. (2014). The relative influence of catchment and site variables on fish and macroinvertebrate richness in Cerrado biome streams. *Landscape Ecology*, *29*, 1001–1016. https://doi.org/10.1007/s10980-014-0036-9

Martins, I., Ligeiro, R., Hughes, R. M., Macedo, D. R., & Callisto, M. (2018). Regionalization is key to establish reference conditions for neotropical savanna streams. *Marine & Freshwater Research*, *69*, 82–94. https://doi.org/10.1071/MF16381

McCain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, *14*, 1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

Milesi, S. V., Dolédec, S., & Melo, A. S. (2016). Substrate heterogeneity influences the trait composition of stream insect communities: an experimental in situ study. *Freshwater Science*, *35*, 1321–1329. https://www.journals.uchicago.edu/doi/10.1086/688706.

Miserendino, M. L. (2001). Macroinvertebrate assemblages in Andean Patagonian rivers and streams: Environmental relationships. *Hydrobiologia*, *444*, 147–158. https://doi.org/10.1023/A:1017519216789

Mota, G. S., Luz, G. R., Mota, N. M., Silva Coutinho, E., das Dores Veloso, M., Magalhães, G. W. Fernandes., & Nunes, Y. R. F. (2018). Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. *Flora*, *238*, 32–42. http://linkinghub.elsevier.com/retrieve/pii/S0367253017331663.

Mugnai, R., Nessimian, J. L., & Baptista, D. F. (2010). Manual de Identificação de Macroinvertebrados Aquáticos do Estado do Rio de Janeiro. Entomol. y Vectores 1 edição: 126.

Mykrä, H., Heino, J., & Muotka, T. (2007). Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography*, *16*, 149–159. https://doi.org/10.1111/j.1466-8238.2006.00272.x

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, *26*, 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Nunes, C. A., Braga, R. F., Figueira, J. E. C., de Neves, F. S., & Fernandes, G. W. (2016). Dung beetles along a tropical altitudinal gradient: Environmental filtering on taxonomic and functional diversity. *PLoS ONE*, *11*, e0157442. http://dx.plos.org/10.1371/journal.pone.0157442.

Nunes, C. A., Quintino, A. V., Constantino, R., Negreiros, D., Reis Júnior, R., & Fernandes, G. W. (2017). Patterns of taxonomic and functional diversity of termites along a tropical elevational gradient. *Biotropica*, *49*, 186–194. https://doi.org/doi.wiley.com/10.1111/btp.12365

Oksanen, A. J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2016). vegan: Community Ecology Package. In R package version, 2.4-1.

Peck, D. V., Herlihy, A. T., Hill, B. H., Hughes, R. M., Kaufmann, P. R., Klemm, D. J., … Cappaert, M. R. (2006). *Environmental monitoring and assessment program – surface waters western pilot study: Field operations manual for wadeable streams. - EPA 600/R-06/003*. Washington, DC: U.S. Environmental Protection Agency, Office of Research and Development.

Perillo, L. N., de Neves, F. S., Antonini, Y., & Martins, R. P. (2017). Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient D (Ed.). Doucet. *PLoS One*, *12*, e0182054. http://dx.plos.org/10.1371/journal.pone.0182054.

Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, *16*, 391–409. https://www.journals.uchicago.edu/doi/10.2307/1468026.

Polato, N. R., Gill, B. A., Shah, A. A., Gray, M. M., Casner, K. L., Barthelet, A., … Zamudio, K. R. (2018). Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 12471–12476. http://www.pnas.org/lookup/doi/10.1073/pnas.1809326115.

Price, M. F. (1998). Mountains: Globally important ecosystems. *Unasylva*, *49*, 3–12.

Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography*, *18*, 200–205. https://doi.org/doi.wiley.com/10.1111/j.1600-0587.1995.tb00341.x

Raich, J. W., Russell, E., & Vitousek, P. M. (1997). Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai. *Ecology*, *78*, 707–721.

Ramírez, J. J., Roldán, G., & Yepes, G. A. (2004). Altitudinal variation on the numerical structure and biodiversity of the taxocenosis of Ephemeroptera in the south, north, and central regions of the Department of Antioguia, Colombia. *Acta Limnologica Brasiliensia*, *16*, 329–339.

Resende, F., Fernandes, G., & Coelho, M. (2013). Economic valuation of plant diversity storage service provided by Brazilian rupestrian grassland ecosystems. *Brazilian Journal of Biology*, *73*, 709–716. https://doi.org/10.1590/S1519-69842013000400005

Sabatini, F. M., Jiménez-Alfaro, B., Burrascano, S., Lora, A., & Chytrý, M. (2018). Beta-diversity of central European forests decreases along an elevational gradient due to the variation in local community assembly processes. *Ecography*, *41*, 1038–1048. https://doi.org/doi.wiley.com/10.1111/ecog.02809

Saito, V. S., Soininen, J., Fonseca-Gessner, A. A., & Siqueira, T. (2015). Dispersal traits drive the phylogenetic distance decay of similarity in Neotropical stream metacommunities. *Journal of Biogeography*, *42*, 2101–2111. https://doi.org/doi.wiley.com/10.1111/jbi.12577

Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, *35*, 1–3. https://doi.org/doi.wiley.com/10.1111/j.1600-0587.2011.07338.x

Schaefer, C. E. G. R., Corrêa, G. R., Candido, H. G., Arruda, D. M., Nunes, J. A., Araujo, R. W., … Neri, A. V. (2016). The physical environment of Rupestrian Grasslands (Campos Rupestres) in Brazil: Geological, geomorphological and pedological characteristics, and interplays. In G. W. Fernandes (Ed.), *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 15–53). Cham, Switzerland: Springer International Publishing. http://link.springer.com/10.1007/978-3-319-29808-5_2.

Scheibler, E. E., Cristina Claps, M., & Roig-Juñent, S. A. (2014). Temporal and altitudinal variations in benthic macroinvertebrate assemblages in an Andean river basin of Argentina. *Journal of Limnology*, *73*, 76–92.

Silva, D. R. O., Ligeiro, R., Hughes, R. M., & Callisto, M. (2014). Visually determined stream mesohabitats influence benthic macroinvertebrate assessments in headwater streams. *Environmental Monitoring*

and Assessment, *186*, 5479–5488. http://link.springer.com/10.1007/s10661-014-3797-3.

Silveira, F. A. O., Negreiros, D., Barbosa, N. P. U., Buisson, E., Carmo, F. F., Carstensen, D. W., … Lambers, H. (2016). Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil*, *403*, 129–152. http://link.springer.com/10.1007/s11104-015-2637-8.

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., … Sorlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, *347*, 1259855–1259855. http://www.sciencemag.org/cgi/doi/10.1126/science.1259855.

Strahler, A. N. (1957). Quantitative analysis of watershed geomorphology. *EOS. Transactions of the American Geophysical Union*, *38*, 913–920. https://doi.org/10.1029/TR038i006p00913

Streher, A. S., Sobreiro, J. F. F., Morellato, L. P. C., & Silva, T. S. F. (2017). Land surface phenology in the tropics: The role of climate and topography in a snow-free mountain. *Ecosystems*, *20*, 1436–1453. http://link.springer.com/10.1007/s10021-017-0123-2.

Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. *Annual Review of Ecology Evolution and Systematics*, *44*, 261–280. http://www.annualreviews.org/doi/10.1146/annurev-ecolsys-110512-135750.

R Core Team (2015). *R: A Language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Tello, J. S., Myers, J. A., Macía, M. J., Fuentes, A. F., Cayola, L., Arellano, G., … Jørgensen, P. M. (2015). Elevational gradients in β-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS ONE*, *10*, e0121458. http://dx.plos.org/10.1371/journal.pone.0121458.

Tuomisto, H. (2003). Dispersal, environment, and floristic variation of western Amazonian Forests. *Science*, *299*, 241–244. http://www.sciencemag.org/cgi/doi/10.1126/science.1078037.

USEPA - United States Environmental Protection Agency (2013). *National rivers and streams assessment 2013-2014: Field operations manual – Wadeable. EPA-841-B-12-009b*. Washington, DC: USEPA - United States Environmental Protection Agency.

Vinson, M. R., & Hawkins, C. P. (1998). Biodiversity of stream insects: Variation at local, basin, and regional scales. *Annual Review of Entomology*, *43*, 271–293. http://www.annualreviews.org/doi/10.1146/annurev.ento.43.1.271.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*, 407–407. https://doi.org/doi.wiley.com/10.2307/1948435

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