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Original Article

Influence of local and landscape environmental factors on alpha and beta diversity of macroinvertebrates in Andean rivers

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Abstract: Research on macroinvertebrate community structure in Andean rivers has been oriented towards describing patterns of alpha and gamma diversity by taking into account environmental predictors at local spatial scales (e.g., micro- and mesohabitats). However, the patterns of beta diversity and the importance of landscape-scale variables have been evaluated to a lesser extent. The objective of this study was to describe the patterns of alpha and beta diversity of benthic macroinvertebrates in the Andean rivers of the Orinoco basin and their relationship with local and landscape environmental variation. A stratified random sampling of macroinvertebrates was carried out at 40 sites (comprising an altitudinal range of between 500 and 2900 m.a.s.l.), local and landscape variables were measured. Our results showed that the variation of alpha diversity was influenced by local and landscape variables, which are directly and indirectly related to the contribution of sediments, substrate composition and flow velocity, providing a heterogeneity of habitats. Global beta diversity was explained by the combined effect of local and landscape variables. Regarding the beta diversity phenomena, turnover was predominant

while nestedness presented a minor contribution and both were explained in greater proportion by local descriptors and some landscape variables, specifically those of a geomorphological nature. Our results concur with the view of an environmental and spatial hierarchy within the river habitat and highlight the influence of multiple scales on macroinvertebrate diversity. The above suggests that both local and landscape scales must necessarily be considered for environmental management and the conservation of Andean lotic ecosystems.

Keywords: Andean lotic systems; Andean agroecosystems; Instream habitat; Landcover; Turnover; Nestedness

1 Introduction

The study of the factors that influence community structure at local (e.g., local abiotic variables and interspecific interactions) and landscape scales (e.g., regional climate and land use) has become increasingly relevant, as it is useful for understanding patterns of biodiversity (Grönroos et al. 2013; Hill et al. 2017) and could be used in

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restoration and management plans for aquatic ecosystems (Palmer et al. 2005; Langer et al. 2016). The influence of multiscale environmental factors has been estimated for different components of aquatic diversity, in particular, this relationship has been studied in more detail for the alpha component (α) or local diversity (Hill et al. 2017; Castro et al. 2019; Roa-Fuentes et al. 2022; Bacca et al. 2023). In contrast, the beta (β) component has attracted interest more recently (Epele et al. 2019; Roa-Fuentes et al. 2019; Bacca et al. 2023). Beta diversity (β) describes the variation of communities between habitats, differing in at least two structuring phenomena: turnover and nestedness (Baselga 2010). Regarding turnover, the compositional difference between biological communities is due to the substitution of some species for others; while nestedness refers to a variation in richness that occurs when there is a non-random loss of some species, while others persist (Baselga 2010). Both turnover and nestedness are driven by environmental filters and/or spatial factors, and are considered to be the determining mechanisms of beta diversity (Baselga 2010; Liu et al. 2021).

The influence of factors at different spatial scales on alpha and beta diversity has been studied to a lesser extent for aquatic macroinvertebrates and mostly in subtropical regions (Gutiérrez-Cánovas et al. 2013; Brendonck et al. 2014). For instance, Krynak et al. (2019) found that taxonomic beta diversity in an agricultural landscape was mainly due to turnover with spatial variables explaining the greatest variation, while nestedness was associated with local scale habitat factors. In this sense, Andean rivers and streams constitute strategic ecosystems given their habitat heterogeneity and dynamism at various spatial scales, from the local scale (e.g., size and type of substrate, channel morphology, hydraulic features) to that of the landscape (e.g. land use/vegetation cover, watershed geomorphology), and this can be seen reflected in the diversity patterns of aquatic macroinvertebrates (Da Silva Pereira et al. 2017; Vimos-Lojano et al. 2017).

In recent decades, research into benthic macroinvertebrate diversity in Neotropical montane systems, including the Andean, has focused on describing altitudinal patterns of alpha and gamma diversity and their response to variation in the proportions of vegetation cover, mesohabitat, and microhabitat; while the beta diversity phenomena

have been little examined, despite the fact that there are governmental entities which grant applications for this in the regional conservation plans (Jacobsen 2003; Galeano-Rendón and Mancera-Rodríguez 2018; Castro et al. 2019; Villamarín et al. 2020). For example, Epele et al. (2019) in Argentine Patagonia, identified that the main drivers of alpha and beta diversity were the local abiotic factors followed by climate descriptors; and species turnover contributed to a greater extent to beta diversity. Likewise, Callisto et al. (2021) found that both local and landscape variables explained beta diversity and that turnover was higher than nestedness. Therefore, this study describes the alpha and beta diversity patterns of benthic macroinvertebrates and their relationship with local and landscape environmental factors in Andean rivers of the upper Orinoco River Basin, comprising an altitudinal range of between 500 and 2900 m.a.s.l. The following hypotheses are proposed: H1, local variables will be better predictors of aquatic macroinvertebrate diversity than landscape variables (Hill et al. 2017), and H2, turnover will be the dominant influencing phenomenon of beta diversity (Soininen et al. 2017).

2 Materials and Methods

2.1 Study area

This study was carried out in the Garagoa river basin (GRB), located in the Cordillera Oriental (eastern mountain range) of Colombia, in the Upper Orinoco River Basin. The GRB has a drainage area of 250,663 ha (2,507 km²) (IDEAM 2013; CORPOCHIVOR 2018) (Fig. 1). A mountainous landscape predominates in the region, with the dominant vegetation cover being agricultural, including permanent and temporary crops, pasture areas and heterogeneous agricultural zones (66.94%), whereas forest cover and semi-natural areas represent a smaller percentage (31.56%) (CORPOCHIVOR 2018). The average annual temperature is between 13°C in the highlands and 19°C in lowlands, with precipitation ranging between 500 and 4000 mm per year (CORPOCHIVOR 2018).

2.2 Macroinvertebrate sampling

A total of 40 sites were sampled between March

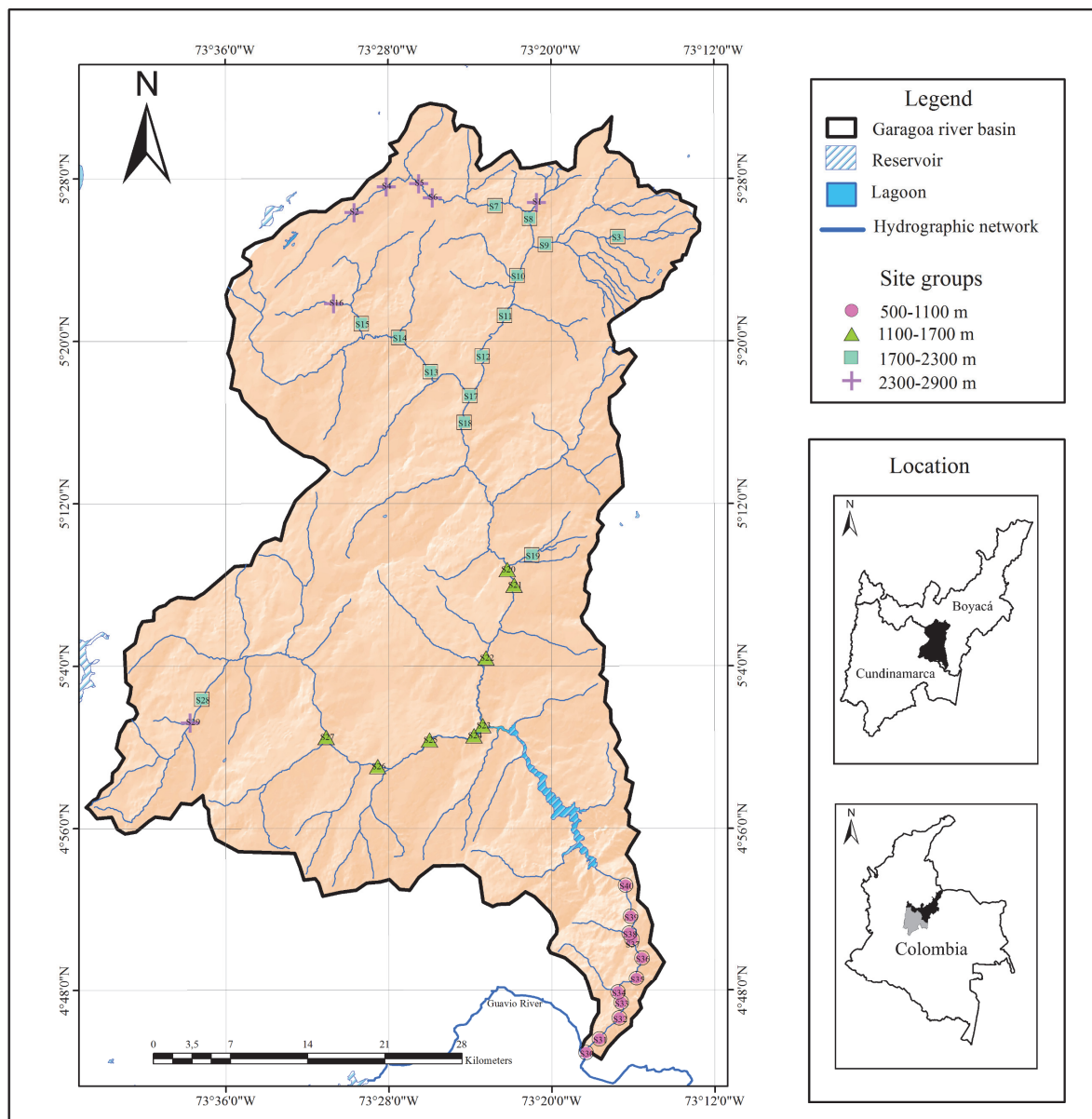


Fig. 1 Map of the study area and locations of sample sites (grouped into four zones: 500-1100 m.a.s.l., 1100-1700 m.a.s.l., 1700-2300 m.a.s.l., 2300-2900 m.a.s.l.) in the Garagoa river basin, upper Orinoco River basin, Colombia.

and June 2021, which corresponds to the transition between the lowest and highest rainfall (CORPOCHIVOR 2018). For the selection of sites, the environmental heterogeneity and a homogeneous spatial distribution in the GRB were considered (Fig. 1). The sampling sites are located in an altitudinal range of between 500 and 2900 m.a.s.l. To facilitate their distinction, they were grouped into four zones (Barrera et al. 2023): zone 1, with nine sites (500-1100 m.a.s.l.); zone 2, with eight sites (1100-1700 m.a.s.l.); zone 3, with fourteen sites (1700-2300 m.a.s.l.) and zone 4, with seven sites (2300-2900

m.a.s.l.). At each site, a 100 m long transect was delimited and a stratified random sampling of macroinvertebrates was carried out, taking into account the different types of meso- and microhabitats (Motta-Díaz and Vimos-Lojano 2020). Samples were collected using a Surber net (area of 900 cm², 0.3 mm mesh), removing the substrate for one minute and conducting three repetitions per site. The samples were preserved and stored in plastic bottles with 70% ethanol. For the taxonomic identification of macroinvertebrates down to the lowest possible taxonomic level (usually genus)

specialized literature was used (Pennak 1989; Epler 2001; Merritt and Cummins 2008; Domínguez and Fernández 2009; Hamada et al. 2018), as well as consulting specialists, using a stereoscope Zeiss STEMI 305. The identified material was deposited in the Limnological Collection (UPTC-L) at the Universidad Pedagógica y Tecnológica de Colombia (Catalog number M-291 to M-554). Additional information on the data set is provided in Barrera et al. (2022, 2023).

2.2.1 Environmental variables

(1) Local-scale variables. At each sampling site, in situ habitat characterization was carried out taking into account physical and chemical variables, including water temperature (°C), conductivity (µS/cm), oxygen saturation (%) and pH - using a portable multiparameter meter (Reference HI 98194 HANNA Brand)-, hardness (mg/L CaCO₃), alkalinity (mg/L HCO₃) and nitrates (mg/L NO₃-N) - using Aquamerck Kits (Appendix 1). For the mesohabitat types, a visual estimate of the proportions was made for each of the following categories: rapid (high velocity, turbulent flow), riffle (high velocity, and laminar flow), glide (low velocity, laminar flow) and pool (null or low speed) (Parasiewicz 2007). In relation to the types of microhabitats, the proportion of organic and inorganic substrate was estimated according to the following categories: boulders (diameter >300mm), cobble (diameter 60-300mm), pebble (diameter 20-60mm), gravel (diameter 0.2 - 20mm), sand (diameter 0.006-0.2mm), silt (diameter < 0.006 mm), leaf litter, branches and trunks. Finally, the Andean riparian vegetation quality index (QBR-And) was estimated according to Acosta et al. (2009) (Appendix 1). With the exception of the QBR-And, at each site the measurements were taken in triplicate and then the average was calculated for use in subsequent analyses.

(2) Landscape-scale variables. As landscape-scale descriptors, the proportion of the classes of land use and the geomorphology were obtained for the catchment area defined from each sampling site. As land use classes, the proportions of reservoir, cattle production, potato farming, other agricultural uses, urban, mining, other anthropic uses, other water bodies, forest cover, grasslands and shrubs, and degraded areas were considered (See Appendix 2 for a detailed description). As geomorphological classes, the proportions of trough floor, trough slopes,

summits and slopes, structural slope, erosional slope, scarp, structural plain, glacia plain, terrace plain and floodplain were considered (See Appendix 2 for a detailed description). The classes of land use, geomorphological descriptors and limits of the hydrographic basin were obtained from the GRB development and management plan (POMCARG; CORPOCHIVOR 2018) in shapefile format, a geospatial vector data format, by consulting this entity's geographic data portal (<https://datosgeo.graficos.car.gov.co>). The definition of the catchment area for each site and the subsequent estimation of the proportion of each class of land use was carried out in QGIS software, version 3.4.11 (See Appendix 2 for a detailed description).

2.2.2 Alpha and beta diversity

The richness of genera by sampling site was considered as a proxy for the alpha diversity component of the aquatic macroinvertebrate community. For the beta diversity component, the multiple beta diversity was obtained based on Anderson et al. (2011). This method describes the dissimilarity of the entire system and is interpreted by at least three values: global beta diversity, and turnover and nestedness phenomena (Baselga 2010; Anderson et al. 2011). To estimate beta diversity, the betapart package was used with the functions "beta.pair.abund" and "beta.multi.abund" in the RStudio v3.4.2 software. To determine the reliability of the sampling, the non-parametric estimators Chao 2, Jackknife 1, Jackknife 2 and Bootstrap were used and the genera accumulation curves were plotted (Gotelli and Chao 2013).

2.3 Data analysis

2.3.1 Environmental gradients

To recognize the main environmental gradients of the area under study, the following sequence of analysis was considered. First, to reduce the number of environmental variables and examine the multicollinearity between them, an exploratory data analysis was performed for each set of variables (local and landscape) using the Spearman correlation, in which the relationship was examined in pairs and those close to or higher than a correlation ($\rho \geq |0.7|$) were filtered (Dormann et al. 2013). Second, a principal component analysis (PCA) was carried out, which allowed the exploration of the ordination and

clustering between sites along axes defined by combinations of environmental parameters (Legendre and Legendre 2012). The variables were previously standardized to zero mean and unit standard deviation (Legendre and Legendre 2012). PCA was processed with FactoMineR library and Factoextra package; the correlation biplot of the two first PCs was drawn using the `fviz_pca_biplot` function.

2.3.2 Relationship between alpha diversity and multiscale variables

To establish the relationship between local and landscape variables with alpha diversity (i.e., genera richness), we performed a hierarchical generalized additive mixed model (GAMM), using the `gamm` function from the `mgcv` package (Wood and Wood 2015). The GAMM results were adjusted with landscape variables nested within sites as random effects to account for the spatial structure in the data (Dormann et al. 2007). The above was done in this way, as the sites belong to the same hydrographic basin and when delimiting the watershed of each sampling site, the landscape variables of some of the watersheds were nested. Although this does not fulfill the assumption of independence, a network sampling approach is commonly used when studying diversity patterns in lotic systems (Clarke et al. 2008). Furthermore, other studies use GAMM to assess the influence of nested environmental factors on macroinvertebrate diversity (Mouton et al. 2020; Mouton et al. 2022). Prior to the analyses, all predictor variables were Box-Cox transformed and later standardized to their mean and 1 unit variance.

2.3.3 Relationship between beta diversity and multiscale variables

In order to estimate the relationship between local and landscape variables with global beta diversity, a redundancy analysis (RDA) and partial redundancy analysis (pRDA) were carried out (Anderson et al. 2011). The RDA is an ordination method that combines the regression and principal component analysis, determining the effect of explanatory variables (local and landscape) on response variables (aquatic macroinvertebrate composition) (Borcard et al. 2018). The pRDA allowed the recognition of the independent effects of local and landscape variables, through the variance partition that includes the total contribution, and shared and exclusive explanation (Borcard et al. 2011). The `ordistep` function was used to perform a selection

of the models forward, backward and step by step through permutation tests. Two stopping criteria were applied: (1) an alpha significance level in which the null hypothesis is rejected and (2) the adjusted R^2 (R^2_{adj}) applying all the explanatory variables (Blanchet et al. 2008). This method allowed the selection of local and landscape variables that significantly influence the structure of the aquatic macroinvertebrate community (Blanchet et al. 2008). Likewise, the variance inflation factor (VIF) was verified. All the variables selected in the model presented a $VIF < 10$. Finally, to check the significance of RDA and pRDA, a permutation test was executed (10,000 permutations). All the functions were performed with the `vegan` package in RStudio (Oksanen et al. 2020). Likewise, a Hellinger transformation was carried out previously for the community abundance data (Legendre and Gallagher 2001) and a square root for the local and landscape variables, these in turn were standardized to zero mean and unit standard deviation to be dimensionally heterogeneous variables (Legendre and Legendre 2012).

Finally, to establish the relationship between local and landscape variables with beta diversity phenomena, a multiple regression on distance matrices (MRM) was performed using the `ecodist` package (Goslee and Urban 2007). The MRM analysis is similar to a multiple regression, in this case using the distance or dissimilarity matrices as predictors and the importance of the coefficient is calculated using permutation tests (1,000 permutations) (Gutiérrez-Cánovas et al. 2013).

3 Results

3.1 Environmental gradients

The PCA for local variables accumulated 45% of the environmental variation in the first two axes (Fig. 2a) and that of the landscape variables 60% (Fig. 2b). Regarding the local variables, the first axis explained 24.5% of the total variation. This axis differentiated sites with high temperatures, sand and silt-clay substrate, and rooted floating vegetation at sites with low current velocity, whereas the PC2 (19.84%) distinguished sites with a higher proportion of the glide mesohabitat, dissolved oxygen and conductivity (Fig. 2a). In relation to the landscape variables, PC1

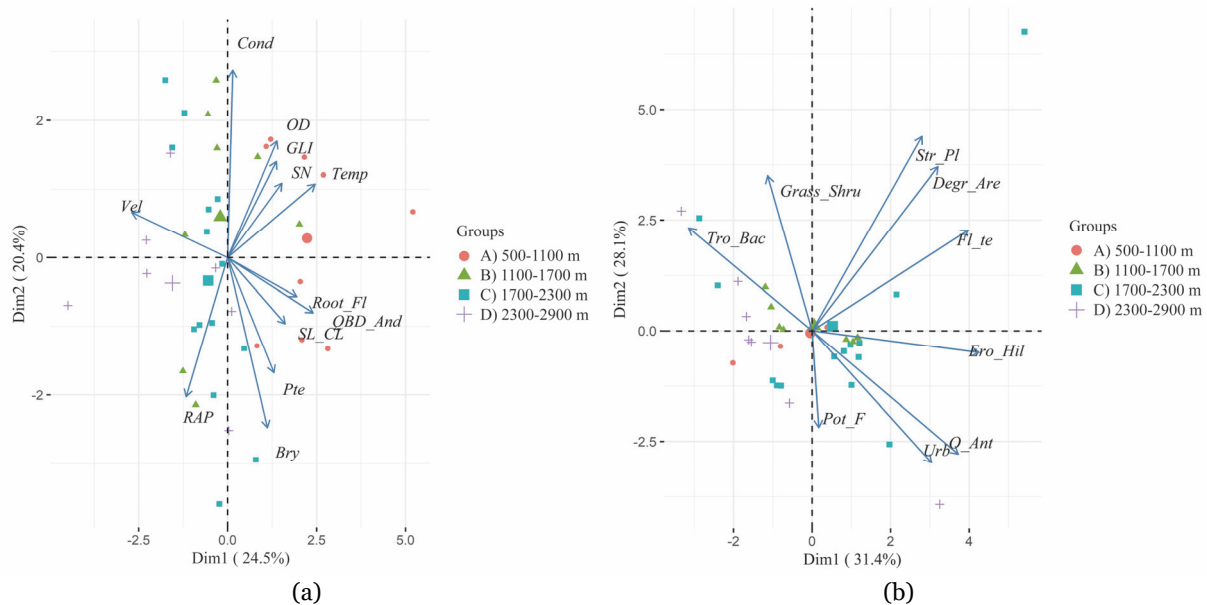


Fig. 2 Principal component analysis biplot representing (a) the local environmental gradients and (b) the landscape environmental gradients in the Garagoa river basin, upper Orinoco river basin, Colombia. For variable codes, see [Appendix 1](#). Environmental variables in blue, symbols and colors of the sites represent the altitude ranges.

(31.4%) represented a gradient of systems with a higher proportion of erosional slope and terrace plain geomorphologies and other anthropic uses (rural dwelling, industrial zones and road network); while PC2 (28.1%) differentiated sites with a structural plain geomorphology and higher proportions of degraded areas (rock outcrops, bare and degraded lands, natural sandy areas and burned areas) and grasslands-shrubs (shrubland, grassland and secondary vegetation) from sites with a greater proportion of urban and other anthropic uses ([Fig. 2b](#)).

3.2 Alpha diversity and multiscale variables

A total of 13,621 specimens belonging to 16 orders, 41 families and 58 genera were recorded ([Appendix 3](#)). The order Diptera had the highest number of specimens (9,598), with the families Chironomidae represented by the genera *Cardiocladius* sp., *Cricotopus* sp., and *Parachironomus* sp., and Simuliidae with *Simulium* sp., being the families with the greatest abundance. Other taxa with significant numbers were *Hyaella* sp., *Americabaetis* sp., *Physa* sp., *Culoptila* sp., *Leptonema* sp. and *Heterelmis* sp. The accumulation curves and non-parametric estimators indicated that between 66% and 81% of the genera from the study area were collected ([Appendix 4](#)).

Both local and landscape variables influenced the alpha diversity of macroinvertebrate communities (hierarchical GAMM R^2 adj. = 0.579). Ten local variables were related to genera richness, silt-clay microhabitats, bryophytes, dissolved oxygen, conductivity, Andean riparian vegetation quality index (QBR-And), pteridophytes, rooted floating vegetation, as well as rapid, glide and mean water velocity ([Table 1](#)). Four landscape variables were significant in predicting alpha diversity, terrace plain, degraded areas, trough floor, grasslands-shrubs, potato farming and other anthropic uses ([Table 1](#)).

3.3 Beta diversity and multiscale variables

Global beta diversity of the benthic macroinvertebrate community was also explained by the combined effect of local and landscape variables (R^2 adj. = 0.19; p = 0.003). The significant local variables were current velocity, conductivity, rooted floating vegetation and silt-clay microhabitats and the significant landscape variables were structural plain, terrace plain and potato farming ([Fig. 3a](#)). The first RDA axis showed a gradient related to the structural plain variables associated with *Limonia* sp., silt-clay with *Leptohyphes* sp. and *Leptonema* sp., the rooted floating vegetation showed affinity with *Baetodes* sp. and *Belostoma* sp., and potato farming with *Cardiocladius* sp. ([Fig. 3a](#)). The second axis related

Table 1 Results from the hierarchal generalized additive mixed model (GAMM) relating alpha diversity (genera richness) to local and landscape environmental variables. Landscape variables were nested within sites as a random effect to account for spatial structure. DF (Estimated degrees of freedom), F (F value), p (P value).

Spatial scale (R^2 adj. =0.579)	Variable	DF	F	p
Local	Silt Clay	2.788	11.658	<0.001
	Bryophytes	1.000	10.005	0.007
	Conductivity	1.000	8.466	0.011
	Rooted floating vegetation	1.000	6.944	0.019
	Andean riparian vegetation quality index (QBR-And)	1.000	6.673	0.021
	Pteridophytes	1.000	5.817	0.030
	Rapid	1.000	5.713	0.031
	Dissolved oxygen	1.000	5.653	0.032
	Mean water velocity	1.000	4.734	0.047
	Glide	1.000	5.120	0.040
	Sand	1.000	2.645	0.126
	Temperature	1.000	1.073	0.317
	Terrace plain	1.000	25.796	<0.001
Landscape	Degraded areas	1.000	18.316	<0.001
	Trough floor	1.000	17.189	<0.001
	Grasslands and shrubs	1.000	9.143	0.009
	Potato farming	1.000	7.196	0.017
	Other anthropic uses	1.000	7.003	0.019
	Structural plane	1.000	4.247	0.057
	Erosional slope	1.000	2.086	0.170
	Urban	1.000	0.444	0.516

the variables of terrace plain and current velocity with *Parachironomus* sp., *Cricotopus* sp., *Culoptila* sp., *Hyalella* sp. and *Simulium* sp. respectively (Fig. 3a).

The pRDA indicated a large proportion of the variation in global beta diversity of macroinvertebrates driven by landscape variables (R^2 adj. = 0.09; p < 0.001) with potato farming being positively associated with *Parachironomus* sp., *Simulium* sp. and *Cardiocladius* sp. and having a negative relationship with *Belostoma* sp., and *Leptohyphes* sp.; terrace plains were associated with *Culoptila* sp. and *Heterelmis* sp., and the structural plain with *Americabaetis* sp. (Fig. 3b). On the other hand, the local variables contributed to a lesser degree (R^2 adj. = 0.06; p = 0.003 **), with rooted floating vegetation being associated with *Simulium* sp., conductivity with *Belostoma* sp. and *Leptonema* sp. and the silt-clay variables mainly with

Macrobrachium sp (Fig. 3c).

The turnover phenomenon was predominant in the beta diversity of macroinvertebrates (0.802), while nestedness (0.154) had a lower contribution. Different relationships of the local and landscape variables with the turnover and nestedness phenomena were observed (Table 2). For instance, bryophyte vegetation, rooted floating vegetation and trough floor geomorphology had a positive association with turnover, as opposed to dissolved oxygen which had a negative association (R^2 = 0.17, p = 0.013, F = 6.644). Regarding nestedness, dissolved oxygen was positively related to this phenomenon, while bryophytes were negatively related (R^2 = 0.191, p < 0.001, F = 7.656).

4 Discussion

The Garagoa river basin exhibits high environmental heterogeneity that could be related with the wide altitudinal gradient studied, which ranged from 500 to 2900 m.a.s.l. Shrubs, grassland and secondary vegetation was recognized in this gradient, which is consistent with the classification of other Andean systems (Villamarín et al. 2014). In addition, the various morphological typologies (e.g., trough floor, terrace plain) determined by the slope and soil categories also prevail, which influence the increase in erosion, runoff and the loss of organic matter (Acosta et al. 2009; Sun et al. 2015). In the area under study, extensive transformation of the landscape associated with anthropic activities was observed, such as livestock, agriculture (mainly potato farming), mining, constructions near rivers, and domestic and industrial effluent. This transformation of the landscape has repercussions in areas with bare and degraded soils and in the alteration of habitat quality due to a decrease in the availability of allochthonous material and the type of substrate, which directly and indirectly leads to changes in the diversity of the macroinvertebrate community (Galeano-Rendón and Mancera-Rodríguez 2018; Giraldo et al. 2020). These anthropic activities are also reflected in the expression of local physical and chemical variables. For instance, water conductivity was not correlated with the altitudinal gradient, therefore it is not solely related to the geochemical nature of the watershed, but it is attributed more to the anthropic activities described above, which tend towards mineralization (Rivera Usme et al. 2013).

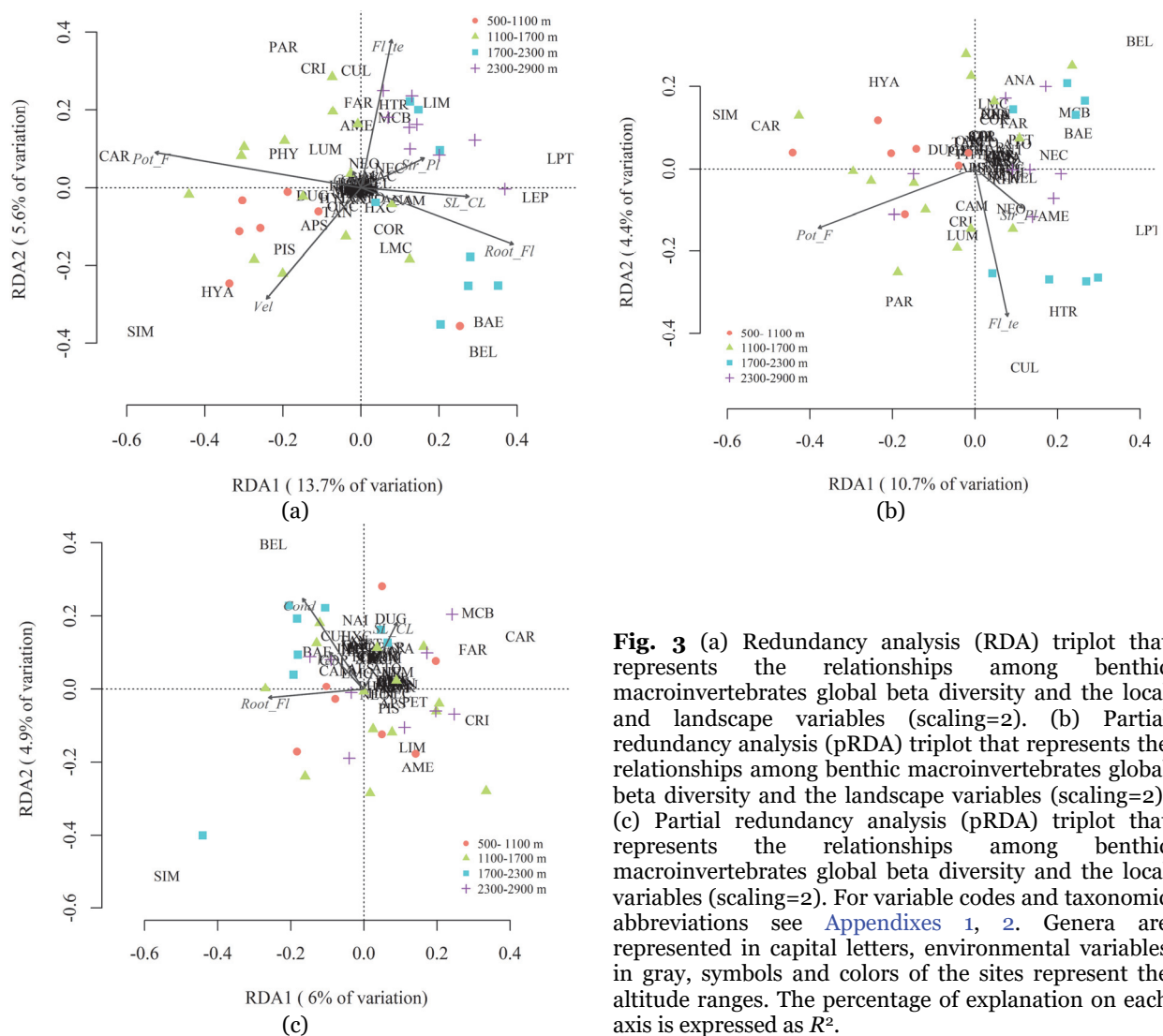


Fig. 3 (a) Redundancy analysis (RDA) triplot that represents the relationships among benthic macroinvertebrates global beta diversity and the local and landscape variables (scaling=2). (b) Partial redundancy analysis (pRDA) triplot that represents the relationships among benthic macroinvertebrates global beta diversity and the landscape variables (scaling=2). (c) Partial redundancy analysis (pRDA) triplot that represents the relationships among benthic macroinvertebrates global beta diversity and the local variables (scaling=2). For variable codes and taxonomic abbreviations see [Appendixes 1, 2](#). Genera are represented in capital letters, environmental variables in gray, symbols and colors of the sites represent the altitude ranges. The percentage of explanation on each axis is expressed as R^2 .

Table 2 Results for multiple regression on distance matrices (MRM) relating beta diversity phenomena (turnover and nestedness) with landscape and local variables. -- means no data.

Variable	Turnover ($R^2 = 0.170$, $p = 0.013$, $F = 6.644$)		Nestedness ($R^2 = 0.191$, $p = 0.0004$, $F = 7.656$)	
	Beta coefficients	p	Beta coefficients	p
Intercept	0.470	0.938	0.240	0.726
Dissolved oxygen	-0.036	0.027	0.059	0.0003
Bryophytes	0.030	0.036	-0.034	0.0090
Rooted floating vegetation	0.037	0.034	--	--
Trough floor	0.037	0.078	--	--

Other local variables showed the typical characteristics of rivers in the Andean region such as temperature, which is inversely related to altitude and dissolved oxygen concentration, hydromorphological conditions (e.g., rapids and pools) related to different current velocities, and the combination of bryophyte and pteridophyte vegetation which provides refuge availability and food for different biological

communities (Jacobsen 2004; Ríos-Touma et al. 2011; Walteros-Rodríguez and Castaño-Rojas 2020).

4.1 Relationship between alpha diversity and local and landscape variables

Our results revealed that the variation in genera richness was influenced by both local and landscape

variables with an apparent emphasis on the latter, which somewhat controverts our original hypothesis that local variables would be better predictors than landscape variables (Hill et al. 2017). Regarding local variables, a heterogeneous set of factors influenced alpha diversity. For instance, a silt-clay microhabitat is characterized by a very fine substrate with low stability and organic matter, which limits the availability of refuges for the settlement of aquatic organisms that do not have morphological and behavioral characteristics to resist events such as changes in the speed of flow (Baptista et al. 2001; Vimos-Lojano et al. 2018). On the other hand, rapid and glide mesohabitats favor the establishment of some taxa with morphological adaptations to higher water flow (e.g., *Nanomis* sp. and *Leptohyphes* sp. which have denticles in their claws); however, other organisms, despite not having these traits, have the ability to locate themselves beneath large substrates using their portable homes (e.g., *Helicopsyche* sp., *Nectopsyche* sp.) (Forero-Céspedes et al. 2016; Ríos-Pulgarín et al. 2016; Motta-Díaz and Vimos-Lojano 2020). Therefore, it is evident that the type of substrate was decisive for alpha diversity, as it affected habitat availability. In addition, the hyporheic exchange process occurs when the flow is laminar and due to irregular pressure, it probably allows water to enter and leave the channel (Mugnai et al. 2015). This process is also related to the predominance of fine sediments in the hyporheic substrate, which generally results in a reduction in diversity (Allan and Castillo 2007; Nogaro et al. 2010; Ballesteros-Navia et al. 2022). However, this conclusion is not perceived in our findings, probably because the taxa that were recorded present adaptive characteristics to counteract the effects of suspension and deposition. This is consistent with the Chironomidae organisms found in these substrates (Olsen and Townsend 2003; Lin et al. 2020).

The association of macroinvertebrates with conductivity could indicate a dependence on the input of external energy from the aquatic system that generally comes from the native riparian vegetation (Peeters et al. 2004; Heino et al. 2015; Godoy et al. 2017), but at the same time, it may be related to the constant disturbance and re-suspension of river banks and substrate, typical in lotic systems immersed in an agricultural matrix (Molina et al. 2017), like those evaluated in this study. We also observed a clear dominance of genera from Diptera,

Ephemeroptera and Trichoptera, taxa that are associated with riverbank vegetation which is composed of bryophytes, pteridophytes and rooted floating vegetation, this being characteristic of Andean rivers (Ríos-Touma et al. 2011; Walteros-Rodríguez and Castaño-Rojas 2020). This is similar to other studies in which these orders are related to heterogeneous environments with coarse allochthonous organic matter deposited on rocks (leaf litter and periphyton), which affects the supply of food and shelter (Vásquez-Ramos and Reinoso 2012; Villada-Bedoya et al. 2017; Walteros-Rodríguez and Castaño-Rojas 2020).

In the same vein, dissolved oxygen was related to temperature and altitude and it is well known that at lower altitudes the temperature increases and the oxygen absorption capacity decreases; however, some authors have found contrasting effects between these variables (Mantyka-Pringle et al. 2014; Croijmans et al. 2021). For instance, our results show that the sites that presented the highest (up to 23°C) and the lowest (11°C) temperatures were associated with a low richness of macroinvertebrates, while sites located at intermediate altitudes (1100-2300 m.a.s.l.) showed an increase. These increases in richness at intermediate elevations can be explained by a combination of factors such as area, channel morphology and anthropic activities, which would create more appropriate habitats for the persistence and diversification of the macroinvertebrate community. For these reasons, it can be considered as a transition zone between sectors of contrasting features (e.g., high mountains and lowlands) (Villamarín et al. 2014; Meza-Salazar et al. 2020). This suggests a modal pattern with a peak at intermediate elevations, as has already been documented for other groups (liverworts, amphibians, rodents and others) (Lomolino 2001; Ferro and Barquez 2014; Feuillet-Hutado and Torres 2016; Armesto and Señaris 2017). However, it is also possible that this result is related to the predominance of rainfall in the sampling period, a factor that leads to community drift processes (Ramírez and Pringle 2001; Vimos-Lojano et al. 2017; Villamarín et al. 2020).

Our findings indicate that landscape variables that describe geomorphology were important factors that predict changes in alpha diversity, suggesting that this characteristic shapes the set of genera in a local community. The terrace plain, degraded areas, and trough floor are factors that reflect the processes

of erosion, transportation and sedimentation of the watershed, generating a greater heterogeneity of habitats and resources which is reflected in the community structure (Smits et al. 2015; Galeano-Rendón and Mancera-Rodríguez 2018). Likewise, landscape variables that reflect anthropogenic disturbance (i.e., potato farming, grasslands-shrubs and other anthropic uses) were also determinants of alpha diversity. Overall, the substitution of the riparian forest by these types of landcover would have an impact, decreasing the buffering capacity of the system and influencing the stability of the watershed, which would contribute to a change in alpha diversity (Gualdoni et al. 2011). However, in the area under study there is a variety of substrates, sediments and litter supply, fundamental characteristics for the colonization and distribution of the macroinvertebrate community (Giraldo et al. 2014; Galeano-Rendón and Mancera-Rodríguez 2018), which may be mitigating the effects of the loss of riparian vegetation. All these findings are consistent with research in which landscape factors are important for aquatic macroinvertebrates, and are even more relevant than local factors (Cortes et al. 2011; Castro et al. 2017).

4.2 Relationship between beta diversity and local and landscape variables

Local and landscape variables were suitable predictors of beta diversity and its phenomena, in particular, beta diversity was mainly driven by the phenomenon of turnover, while nestedness was negligible. These results agree with previous studies that indicate that turnover is up to five times more influential than nestedness, suggesting that the difference in richness is less predominant in beta diversity patterns (Soininen et al. 2017). The predominance of the turnover phenomenon has been observed in different regions and groups of organisms (Florencio et al. 2016; Branco et al. 2020). Turnover predicts that a species found at a given site is relatively exclusive compared to other sites in the system, suggesting environmental heterogeneity (Langer et al. 2016; Hill et al. 2017; Castro et al. 2019; Keke et al. 2020; Bispo et al. 2021). In this regard, bryophyte vegetation and rooted floating vegetation were positively related with the turnover phenomenon. Bryophytes and aquatic plants provide shelter against currents and play a role as a food

source, which allows for the accumulation of debris and a heterogeneity of resources that increases the complexity of the system (Meza-Salazar et al. 2020). In contrast, the negative relationship of turnover with dissolved oxygen could be related to an increase in organic matter, possibly associated with the modification of riparian vegetation and changes in vegetation cover in areas surrounding the system, which affect the reduction of oxygen and this is limiting for some taxa (Jacobsen 2008; Molina et al. 2017; Croijmans et al. 2021). Based on the positive relationship between nestedness and dissolved oxygen, and the negative association with bryophytes, it is evident that these factors favor the loss of specialized taxa, leading to a consequent process of extinction-colonization (Si et al. 2016; Soininen et al. 2017). These findings are consistent with research indicating that disturbance factors can impact the loss of specialist taxa and cause nestedness phenomena, contrary to what happens with generalist taxa (e.g., Chironomidae) which have adaptations that allow them to occupy a large proportion of habitats or sites (Gutiérrez-Cánovas et al. 2013; Hawkins et al. 2015; Liu et al. 2021).

Furthermore, the positive relationship of *Baetodes* sp. and *Belostoma* sp. with rooted floating vegetation and the rapid flow of the current could be explained by their physiological and morphological adaptations (cylindrical, flattened bodies and claw-like grip structures) to habitats with these features (Galeano-Rendón and Mancera-Rodríguez 2018; Galetti et al. 2020; Quesada-Alvarado et al. 2020). *Cardiocladius* sp. (Diptera) was positively associated with potato farming, and changes in the substrate and the vegetation cover observed in the evaluated sites, indicating a link with conditions of anthropic disturbance (Rojas-Sandino et al. 2018; Rodríguez-Rodríguez et al. 2021). This finding agrees with other studies in which this taxon is recorded in areas of fast flow, pebble and rock substrate, the presence of detritus and rooted floating vegetation, this being mediated by its biological traits (small size and cylindrical body shape) (Oviedo-Machado and Reinoso-Flórez 2018; Rojas-Sandino et al. 2018).

Regarding the relationships between landscape variables and global beta diversity, it should be noted that the landscape could indirectly influence the characteristics at a local scale, regulating the hydraulic flow, the input of allochthonous material, aquatic vegetation, bryophytes, the size and

compaction of the substrate, among others (Molina et al. 2017; Jacobsen et al. 2020). Consequently, the landscape variables could be affecting the community structure indirectly and this is supported by studies in which the percentage of natural cover and the hydromorphology determine the biological characteristics or traits of the community (Milesi et al. 2016; Castro et al. 2017; Callisto et al. 2021) or when the variation in soil cover promotes erosion and sedimentation at a local scale and therefore, contributes to changes in macroinvertebrate beta diversity (Cortes et al. 2011; Giraldo et al. 2014). This can be observed in the patterns of occurrence of some taxa and their relationship with landscape variables in the GRB. For example, *Culoptila* sp. has the characteristics of being small in size, with a flattened shape and integumentary respiration and it tends to be found in areas with a lithology characteristic of alluvial deposits, that is, areas in which the current is reduced and deposition and sedimentation increase (Dávila-Recinos et al. 2019). In the case of conductivity, which is a variable associated with the effects of erosion, sediment drag and runoff, it showed an affinity with *Leptonema* sp., this being a taxon that is generalist in habitat selection, due to its ability to build shelters with stones, leaves and trunks (Serna et al. 2015; Quesada-Alvarado et al. 2020).

An interesting result was that not all taxa respond in the same way to local and landscape variables, but rather, on the contrary, they can be affected in a different way or to a different degree. For instance, genera such as *Hyalella* sp. and *Simulium* sp. are associated with high current velocities and stable substrates, possibly due to *Hyalella* sp. exhibiting larger morphological characteristics, breathing through gills and integuments and that the simuliids have suckers to cling to the substrate and avoid being dragged by the current (Ríos-Touma et al. 2011; Espinosa et al. 2020; Motta-Díaz and Vimos-Lojano 2020). However, *Hyalella* sp. seems to be more affected by landscape-scale variables, in particular, by flat terraces and potato farming. The same applies for *Limonia* sp., a taxon related with the structural plain geomorphology, a type of relief that includes deposition zones and moderate slopes, high current velocity and allochthonous plant material, typical of non-degraded streams (Mesa 2010; Nautiyal and Mishra 2022).

5 Conclusion

Our results indicate that the alpha and beta diversities of benthic macroinvertebrates were driven by the combination of landscape and local environmental factors in the GRB. This concurs with the view of an environmental and spatial hierarchy within the river ecosystem, where the community structure is determined by a nested spatial hierarchy and that some of the environmental variables exhibit an important variation as a result of natural and anthropic factors. These factors operate at multiple spatial scales, acting as filters and enabling different niches for the community (Hynes 1975; Frissell 1986; Allan 2004). The above suggests that for the environmental management and conservation purposes of Andean streams and rivers, both local and landscape scales must necessarily be considered, since the ecological integrity of these ecosystems results from their interaction. Additionally, since alpha and beta diversity components provide complementary information on the structure of the communities, the importance should be noted of simultaneously evaluating both, and not exclusively alpha diversity as is traditionally done. For future studies, the evaluation of complementary facets of diversity (e.g., functional) is suggested, which are determinant for the conservation and management of ecosystems in disturbance scenarios of anthropic origin and link biodiversity with ecosystem processes, which is fundamental in a biodiversity hotspot such as the tropical Andes region.

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Author Contribution

Roa-Fuentes conceptualized and obtained the funds for the research; Pedroza-Ramos, Barrera-Herrera and Diaz-Rojas carried out the collection and taxonomic identification of specimens. All the authors

participated equally in the data validation, formal analysis, editing, and writing of the manuscript.

Ethics Declaration

Data Availability: The data that support the findings of this study are available from the author, CARF, upon reasonable request.

Conflict of Interest: The authors declare that they all agree with this publication and that they have made contributions that justify their authorship; that there is no conflict of interest of any kind; and that they have complied with all relevant ethical and legal requirements and procedures.

Electronic supplementary material:

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