

Fish diversity of post-conflict Colombian Andes-Amazon streams as a reference for conservation before increased land use

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Abstract

Reference conditions are difficult to find in the Anthropocene but essential for effective conservation of biodiversity. Aquatic ecosystems in the Andes-Amazon transition zone of Colombia are now at high risk due to expanded human activities after peace agreements in 2016 ended armed conflict. Expanding human land use may reduce fish diversity across the altitudinal gradient but especially in premontane streams (i.e., <500 m a.s.l.) because lands are more amenable to human use than at greater altitudes. We evaluated natural fish diversity in twelve sites over eight years bracketing the end of armed conflict. Strong differences in community structure (measured as species richness, total abundance, and effective species number, and multivariate analyses) occurred as a function of altitude, as measured by. Our results provide a baseline to identify short-term and long-term changes due to impending human land use at a critical moment for the conservation of tropical fish diversity.

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Abstract

Reference conditions are difficult to find in the Anthropocene but essential for effective conservation of biodiversity. Aquatic ecosystems in the Andes-Amazon transition zone of Colombia are now at high risk due to expanded human activities after peace agreements in 2016 ended armed conflict. Expanding human land use may reduce fish diversity across the altitudinal gradient but especially in premontane streams (i.e., <500 m a.s.l.) because lands are more amenable to human use than at greater altitudes. We evaluated natural fish diversity in twelve sites over eight years bracketing the end of armed conflict. Strong differences in community structure (measured as species richness, total abundance, and effective species number, and multivariate analyses) occurred as a function of altitude, as measured by. Our results provide a baseline to identify short-term and long-term changes due to impending human land use at a critical moment for the conservation of tropical fish diversity.

Key words: Amazon piedmont, land use, altitudinal gradient, species richness, effective diversity, abundance, multivariate analysis, regressions

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Introduction

Increased human activities have already transformed and degraded many ecosystems worldwide due to urbanization, agriculture, and extraction of natural resources (IPBES, 2019; Achiso, 2020; Feng *et al.*, 2022). As a result, diversity is often reduced, measured as a decrease in both species richness and relative abundance (Newbold *et al.*, 2015) and it is difficult to understand reference conditions before human impacts occurred. However, some areas are more affected by humans than others, where differences may be related to human access and landscape suitability for human uses (e.g., agriculture, urban expansion). Among regions undergoing anthropogenic land use change, the Amazon is known for its remarkable biodiversity and endemics (Mittermeier *et al.*, 2003). Amazonian lowlands contain the largest biodiversity in the world (Gentry, 1988; Wilson, 1992), including both terrestrial and aquatic faunas (Myers *et al.*, 2000; Reis, Kullander and Ferraris, 2003). Amazonia hosts about 17% and 10% of all known vascular plants and vertebrate species, respectively (Lundberg *et al.*, 2000; Myers *et al.*, 2000). Freshwater aquatic ecosystems of the Amazon Basin are megadiverse (Myers *et al.*, 2000) and host the most diverse ichthyofauna in the world (Lundberg, 2001; Reis, Kullander and Ferraris, 2003). In highly diverse systems such as the Amazon Basin, many species are relatively rare and occupy specific niches accordingly to their morphological and physiological traits (Hercos *et al.*, 2013). In addition, most species are not evenly distributed, whether measured in presence/absence or in abundance (Magurran and Henderson, 2003; Magurran, 2004; Bell, 2005).

High freshwater diversity of the Amazon provides crucial ecosystem services, and in many cases represents the sole financial income for human communities in the region (Agudelo, Alonso and Moya, 2006; Agudelo Córdoba *et al.*, 2011). Within Colombia, Amazonian aquatic ecosystems are now at high risk due to expanded human activities, especially expanding agriculture after the establishment of the peace agreements to end armed conflict in 2016 (Tellez, 2019). This scenario sets up a critical moment for the establishment of management and conservation policies (Clerici *et al.*, 2019; Agudelo Hz, Barrera and Uriel, 2023) to avoid negative conservation outcomes (Feng *et al.*, 2022).

Much of the Amazonian basin is lowland, but not everywhere. For example, the Colombian Amazon includes the Andean-Amazon transition, where natural ecosystems of basimontane altitudes (i.e., 500 - 1700 m a.s.l.) are less affected by human activities than those in the premontane zone (i.e., < 500 m a.s.l.) because the steep basimontane landscape complicates human activities whereas flat and smooth premontane terrain enables most human activities, despite infertile soils (Galvis *et al.*, 2007). Altitudinal gradients in diversity are well-recognized worldwide, where diversity is generally expected to decrease with altitude because more stringent environmental conditions occur at greater altitude (Figure 1; Heegaard and Vandvik 2009, Lomolino *et al.* 2010, De La Barra *et al.* 2016). In addition, different selective conditions across the altitudinal gradient provide different selective conditions, leading to different diversities. For example, basimontane fishes more often have morphological adaptations for attachment to surfaces and behaviors and morphologies to reduce flow forces acting on the fish body (Maldonado-Ocampo *et al.*, 2005). In comparison, lowland species are more often adapted for less flow forces and instead develop physiological adaptations for warmer temperatures, lower dissolved oxygen, and different pH and conductivity (Saint-Paul *et al.*, 2000; Bogotá-Gregory *et al.*, 2020).

Thus, the Andes-Amazon transition zone provides a double opportunity to evaluate natural diversity patterns across a strong altitudinal gradient and to evaluate reference conditions for differential and impending anthropogenic effects. The natural altitudinal diversity gradient should interact with spatially-biased anthropogenic effects of land use to further modify diversity patterns (Figure 1), where diversity reduction may not be uniform across altitudes (Penjor, Jamtsho and Sherub, 2022). Anthropogenic effects may be local and point-source (e.g., mining; Rehmana *et al.* 2024), but more generally extensive, nonpoint-source anthropogenic effects occur, related to land use (e.g., agriculture, urban systems). Land use change is often greatest and earliest in lowlands due to simple economics of access and labor (Shively, 2001). Well-known effects include habitat loss and fragmentation on lands (Plieninger, 2006; Adhikari and Hansen, 2018) and non-point source pollution (e.g., sediment loading, nutrient runoff) in streams and rivers (Martinelli *et al.*, 1989; Ikeda, Osawa and Akamatsu, 2009). This bias of human activities among terrains seems general, given

it is repeated in other landscapes (e.g., Mclain et al. 2013, Bürgi et al. 2017).

Expanding human land use in the Colombian Andes-Amazon transition zone may reduce diversity but is unlikely to cause biological homogenization between altitudinal levels because the altitudinal gradient is selective (e.g., fishes adapted to low-slope streams may not move into high-slope conditions). Instead, premontane streams should become more similar to each other in species richness and abundance, though with different suites of species in lowlands than in uplands (Figure 1). For practical reasons, premontane land use may also be expected to precede that in basimontane regions, with matching timing for diversity effects.

Here we evaluate fish diversity patterns in basimontane and premontane streams of the Caquetá River basin in the Colombian Andes-Amazon transition zone, using data from samples collected between 2013 and 2022 in 12 localities. We expected greater fish diversity in premontane streams than in basimontane streams, corresponding to an altitudinal gradient. We also expected no great change pre- and post-2016 in patterns because land use had not yet accelerated. Data represent barely-impacted conditions soon after the conflict ended and before development of formerly avoided lands (Calle-Rendón, Moreno and Hilário, 2018), especially given the COVID-19 pandemic. Results are especially relevant considering the importance of Andean-Amazonian connectivity (Melack and Fosberg, 2001; Anderson *et al.*, 2018; Clerici *et al.*, 2019) and the high rates of endemism that characterizes the area (Tognelli *et al.*, 2016). Our study sets a baseline for evaluating future changes in Andean-Amazonian biodiversity.

Methods

Study Area

The Caquetá River basin is a western Amazonian affluent of Andean origin, formed at 3,850 m above sea level (a.s.l.) by the confluence of three different minor tributaries in the Peñas Blancas Páramo, located in the East Mountain Chain in the Southeast Region in Colombia (IGAC, 1996). It runs over 1,200 km in a southeast direction before it merges to the main channel of the Amazon River, crossing the Caquetá, Putumayo, and Amazonas departments in Colombia, until it's named the Rio Japura at the Colombian-Brazilian border (IGAC, 1996, 1999).

The upper section of the Caquetá River drains most of the western uplift of the Guyana Shield, a formation from the Miocene characterized by a crystalline basement. Shields are very evolved soils with low nutrient and organic contents. Above 500 m a.s.l. (Figure 2a), the aquatic systems of the Caquetá basin are typically Andean ecosystems with dominant rocky substrates, abrupt slopes, and high flow (Figure 2b). Below the 500 m a.s.l., denoted as Amazonian Piedmont, aquatic ecosystems are characterized by basement alluvial fans (Figure 2b) of volcanic origin with elements from the Andes Mountain chain (Hoorn, 1994; Galvis *et al.*, 2007).

Data collection in situ

Sample sites were selected based on location (basimontane and premontane levels) and access. All sample sites are located in the Caquetá Department in the municipalities of Belén de los Andaquíes, Florencia, and Morelia, between 200 and 1500 m a.s.l. (Figure 2, Table 1). Twelve sites (four sites at the basimontane level and eight at the premontane level) were sampled during the falling water season in each of eight years (2013, 2015-2019, 2021, and 2022). However, three sites were not sampled in 2019 due to access restriction because of weather conditions. In total, data represent 91 sample events.

Fish were sampled using SAMUS725M electrofishing equipment, along a 100 m stretch in each of the sample sites. This sampling methodology follows the standardized sampling technique of Maldonado-Ocampo *et al.* (2005) for subsequent data comparisons. Fish were euthanized with clove oil and fixed in a 10% formaldehyde solution. Prior to species taxonomic identifications, specimen vouchers were transferred for preservation in a 75% ethanol solution. All the fish specimens were deposited in the Ichthyological Collection of the Colombian Amazon (CIACOL) at the Amazonian Scientific Research Institute (SINCHI) in Leticia, Amazonas, Colombia (<https://sinchi.org.co/ciacol>).

Data analysis

We evaluated the efficiency of our overall sampling effort for basimontane and premontane levels using rarefaction curves and the Chao1 species estimator for data pooled across sample years (Chao, 1984). Extrapolating a species accumulation curve to its asymptote and estimating species richness via rarefaction and the Chao 1, respectively, both provide an estimate of the performance of the proposed sampling method (Magurran, 2004; Chao *et al.*, 2009)

We evaluated diversity components using both univariate and multivariate analyses. We used generalized linear mixed effects models to evaluate the effect of altitude on species richness, total abundance, and effective diversity (i.e., $e^{H'}$, where H' is the Shannon diversity index; Jost 2006). Sampling year was a random effect because we used a repeated measures sampling design. Sample sites were also included as a random effect to address unmeasured differences in sites. As a result of this analytical model, results are general for altitudinal effects on fish diversity in the Caquetá River through years, including pre and post conflict time-periods, and among sites. Alternative models were compared using the corrected Akaike's Information Criterion (AICc) with the `bbmle` package (Bolker, Team and Giné-Vázquez, 2022), where we emphasized AICc weights to identify the most plausible model after discounting for model complexity (Burnham and Anderson, 2002). Different alternative residual distributions (e.g., Gaussian, Gamma, negative binomial) in generalized linear models were iteratively evaluated and compared to log-transforms of response variables to best meet model assumptions (using `check_model` in the `performance` package; Lüdecke 2023). Given a chosen distribution, alternative models were then compared by AICc, where compared models included a null, random effects only, potential fixed effects (i.e., a dummy variable representing pre- and post-cease-fire conditions and altitude effects), and combinations of fixed and random effects. Finally, we used nonmetric multidimensional scaling (NMDS) with PERMANOVA to confirm differences in community structure between basimontane and premontane sites.

Data management and statistical analyses were performed in R (R Core Team, 2021) using functions from the `glmmTMB` (Magnusson *et al.*, 2020), `vegan` (Oksanen *et al.*, 2020), `devtools` (Hadley, Hester and Chang, 2022), `iNEXT` (Hsieh, Ma and Chao, 2016), `ggplot2` (Kassambara, 2018), `MASS` (Ripley *et al.*, 2019), `multcompView` (Graves and Piepho, 2022), and `performance` (Lüdecke, 2023) packages.

Results

Samples included 4216 fish, belonging to 100 species, 58 genera, 24 families, and six orders (Supplementary file F1). Rarefaction curves reached asymptotes for both basimontane and premontane levels (Figure 3a). Premontane sites had >3 times more fish and >5 times more species than those recorded in basimontane sites (Figure 3b). In addition, basimontane sites had a different taxonomic composition than premontane sites. Basimontane sites had similar numbers of Characiformes and Siluriformes and some (<10%) of the Blenniiformes (mainly in the Cichlidae family; Figure 3c). In contrast, the premontane level was clearly dominated (>75%) by the Characiformes fishes which comprised a higher diversity at the order level (Figure 3c). Fish community structure disparities between altitudinal levels are confirmed by the PERMANOVA ($F = 3.04$, $R = 0.23$, $P < 0.05$), and the NMDS in which two clear groups, corresponding to the basimontane and premontane sites, are depicted in the multidimensional space representing the analysis (Figure 3d).

Species richness was most efficiently modeled as a power law (i.e., log-log) function of altitude and the random effects of year and site (supplementary Table S1; Table 2). Although altitude alone has a good predictive power ($R^2 = 0.42$) predictions improve with the random effects ($R^2 = 0.62$), as confirmed by the model performance procedure (supplementary Figure S1). The model output suggests a significant mean decrease by 0.98 log(species richness) per unit of log-altitude (Table 2; see Figure 4a for regression line).

As for species richness, a power law model for total abundance using altitude as a fixed effect and the random effects was most predictive compared to other models (Supplementary Table S2; Table 3). Altitude alone represented 42% of variation in species richness, but model predictions improve with random effects ($R^2 = 0.62$; supplementary Figure S2). The model output suggests a 0.72 significant decrease in log(fish abundance) per unit of log-altitude (Table 3; see Figure 4b for regression line).

Effective diversity was also most plausibly modeled as a power law (Supplementary Table S3; Table 4). Altitude alone has substantial predictive power (R-squared = 0.433), but adding year as a random effect slightly improved fit (R-squared = 0.456; Supplementary Figure S3). The model output suggests a significant 0.834 mean significant decrease in $\log(\text{effective diversity})$ per unit of $\log(\text{altitude})$ (Table 4; see Figure 4c for regression line).

Overall, for all of the diversity components evaluated herein, using altitudinal level as fixed and site and year as mixed effects was rather predictive, and no pre- and post-conflict difference was apparent in results (i.e., results here represent conditions before further human land use effects). Fish diversity predictably decreased with altitude as a power law function.

Discussion

Our study is the first of its kind to evaluate fish community structure in the Colombian Andes-Amazon transition zone. Results here provide a baseline for conservation of regional streams across premontane and basimontane zones because data represent the period when armed conflict ended but before potential development of formerly avoided lands (Calle-Rendón, Moreno and Hilário, 2018).

Our results confirmed that altitudinal gradients in fish community assembly are important (van der Hammen and dos Santos 1995) and that fish diversity is greater at lower altitudes, no matter how we estimated diversity (e.g., Jaramillo-Villa *et al.* 2010, Lomolino *et al.* 2010, Lujan *et al.* 2013). Considering that effective mitigation of anthropogenic pressures on streams and fish assemblages should account for site-specific conditions and at different scales (Poiani *et al.*, 2000; Newbold *et al.*, 2015), altitudinal gradients in the study area may be predictive for conservation and management. We note that the basimontane streams are important to conserve despite their relatively low diversity because fishes there are notably different from those downstream.

Changes in community composition through time are typically complex and depend on spatial and land use contexts (Allen *et al.*, 2019; Hillel *et al.*, 2021). We expect that fish diversity might be most heavily affected at the premontane level over time due to human activities that will be stronger and earlier at lower altitudes. Conservation practices (e.g., riparian buffer zones, runoff settling ponds) to maintain stream conditions can be implemented early in regional land changes to best conserve diversity.

Given species extinction rates due to habitat degeneration in ecosystems similar to those sampled here (Manjarrés-hernández *et al.*, 2021), this study is valuable as a baseline of barely-impacted conditions soon after the conflict ended in Colombia and before encroaching development of formerly avoided lands (Calle-Rendón, Moreno and Hilário, 2018). We expect future sampling will compare results to those reported here to document changes in fish assemblages due to land use changes. We also expect land use to be most changed at lower altitudes, where soils and slopes are more amenable to agriculture, roads, and housing. If so, then it is possible that fish assemblages will be degraded by increased land use to become simpler and later affected by upstream effects (Figure 1). If ongoing deforestation and encroaching anthropogenic land use in the hyper-diverse Amazon basin is to be managed to minimize species losses, then some lands and streams must be preserved (McKinney and Lockwood, 1999; Granada-Lorencio, Cerviá and Lima, 2007; Rull, 2007). Results here suggest that land surrounding premontane streams should take priority to conserve the most species in areas that are most vulnerable. Upstream catchments in basimontane areas can also be preserved to maintain water quality flowing into premontane streams and conserve unique fishes in those upstream reaches (Booth and Jackson 1997, Klauda *et al.* 1998, Araújo and Tejerina-Garro 2009, de Melo *et al.* 2009). Future work in the study area should evaluate relative effects of changing land use in upper and lower catchments on fish diversity in the lower reaches.

So far, most emphasis on ecological studies on understanding diversity has been on spatial patterns of biological diversity rather than analyzing temporal patterns. Understanding temporal changes is essential to predict possible scenarios of the most diverse world's biota in natural ecosystems of the Amazon. Fish assemblages are affected by processes occurring at multiple scales, including those covered in our analyses (Livingstone, Rowland and Bailey, 1982; Jackson, Peres-Neto and Olden, 2001; Tedesco *et al.*, 2005; Oberdorff

et al., 2011). Future surveys could integrate data at scales obtained here with even greater spatial and temporal extents. We regard results here as a potential baseline for future work in the same drainages, where future work may reveal effects of coming anthropogenic land use in the Amazon basin.

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Tables

Table 1. Sample sites localities, geographical coordinates and altitude (m a.s.l.)

<i>Sites</i>	<i>Locality</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Altitude</i>
S1	La Portada Stream	1.8139	-75.6591	1253
S2	Sucre River	1.7953	-75.6465	1013
S3	Paraíso River	1.7472	-75.6283	676
S4	Las Doradas Stream	1.7289	-75.6464	530

<i>Sites</i>	<i>Locality</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Altitude</i>
S5	La Sardina Stream	1.6797	-75.6225	386
S6	La Carbona Stream	1.7064	-75.6253	439
S7	La Yuca Stream	1.6078	-75.6383	277
S8	La Mochilero Stream	1.5508	-75.6756	285
S9	Aguas Calientes Stream	1.4758	-75.7694	286
S10	La Chocho Stream	1.4472	-75.8117	316
S11	La Arenosa Stream	1.4644	-75.8633	360
S12	Bodoquerito River	1.4971	-75.8741	382

Table 2. Details for the most efficient model to predict species richness, total abundance, and effective diversity (${}^1D = \exp(\text{Shannon entropy})$) of fishes in the Caquetá River, Colombia, based on 91 samples among 12 sites collected in 8 years during the 2013-2022 interval.

	<i>Model distribution</i>	<i>Fixed Effects R²</i>	<i>Fixed + Random R²</i>	<i>Random Effects</i>	<i>Std. Deviation</i>	<i>Fixed</i>
Species richness	Gaussian	0.42	0.62	Year Sites	0.1950 0.2612	Inte log(
Total abundance	Gamma (log link)	0.13	0.48	Year Sites	0.359 0.437	Inte log(
Effective diversity	Gamma (log link)	0.43	0.57	Year Sites	0.146 0.170	Inte log(

Figure legends

Figure 1: Hypothetical effects of potential land use on fish local (alpha) diversity across elevation gradients. The solid curve represents a decay of diversity with altitude. The lower dashed curve represents potential diversity after natural lands are converted to agriculture and other human uses, where greatest diversity loss (arrows) occurs at lower altitude.

Figure 2: a) Geographical location of the sample sites. b) Examples of the aquatic ecosystems within the altitudinal levels, which are the ones recognized by van der Hammen and dos Santos (1995).

Figure 3. Comparisons of premontane and basimontane fish communities. a) Rarefaction curves approach asymptotes, indicating representative sampling. Premontane sites were inhabited by more species, as supported by evidence in b) for total abundance, richness, and effective diversity. c) Taxonomic composition differed between premontane and basimontane sites, where Siluriformes were more prominent in basimontane sites than in premontane sites. Characiformes were dominant in both site types, but in different proportions. d) NMDS of fish communities from the sampled sites. Dots represent pooled temporal data (2013-2022) for sites. Polygons represent fish communities based on altitudinal levels recognized by van der Hammen and dos Santos (1995).

Figure 4. Regression lines for species richness (a), total abundance (b), and effective diversity (c) ~ altitude, where regression lines represent GLMM predicted values and error bars. Note log axes; regressions represent power law functions.

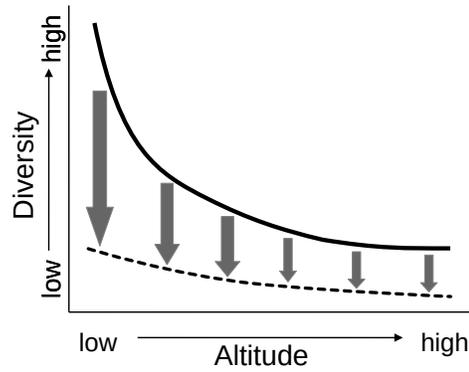
Data accessibility: Supporting data are available at <https://doi.org/10.5281/zenodo.10424407>

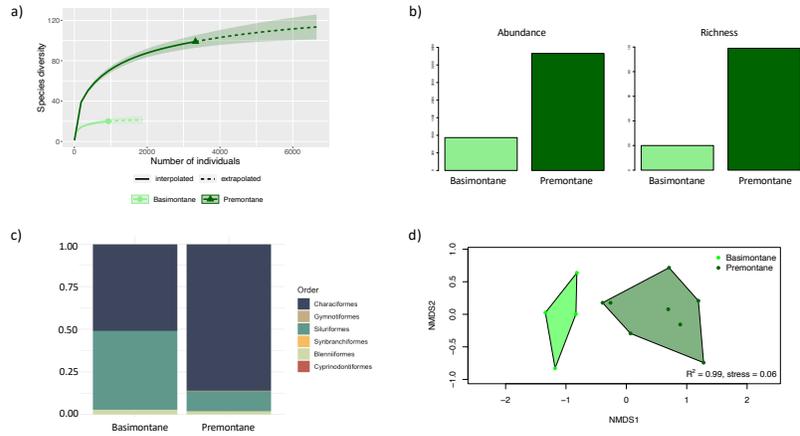
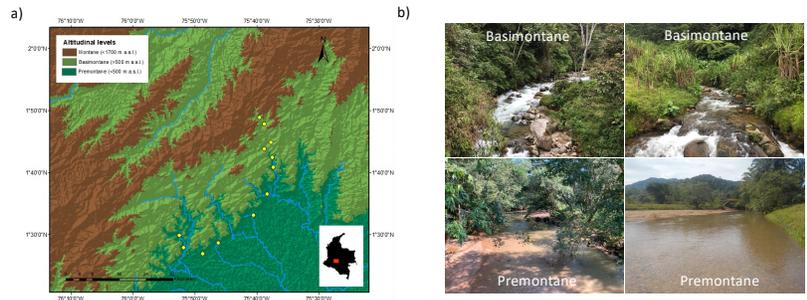
Competing Interests Statement: All authors declare that there are no competing interests.

Author contributions:

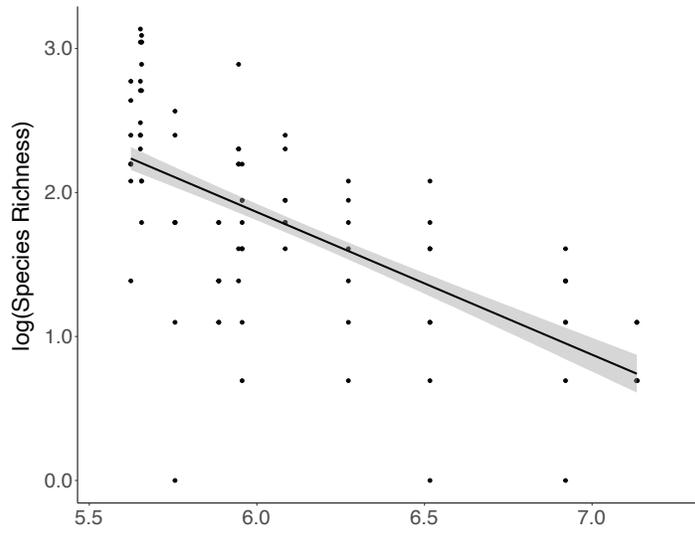
Juan David Bogotá Gregory: Conceptualization (Lead); Data curation (Lead); Formal analysis (Lead); Investigation (Lead); Methodology (Lead); Project Administration (Lead); Resources (Lead); Writing - original

draft (Lead). *David G. Jenkins*: Conceptualization (Lead); Formal analysis (Lead); Methodology (Lead); Writing – review & editing (Lead). *Astrid Acosta-Santos*: Data curation (Equal). *Edwin Agudelo*: Resources (Supporting).

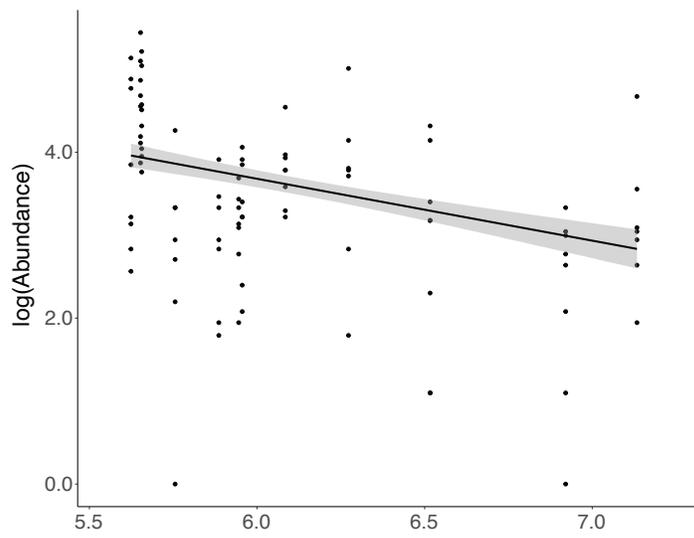




a)



b)



c)

