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Taxonomic diversity and conservation priorities of amphibians in Northeastern Colombia: Insights from the Pamplonita River Basin and its five biomes

Diversidad taxonómica y prioridades de conservación de los anfibios en el nororiente de Colombia: hallazgos desde la cuenca del río Pamplonita y sus cinco biomas

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ABSTRACT

Colombia, one of the most biodiverse countries and the second richest in amphibian species worldwide, requires comprehensive assessments to improve the understanding and conservation of its amphibian fauna. This need is especially urgent in potentially species-rich regions facing increasing anthropogenic threats. In this context, we evaluated the diversity and conservation status of amphibians in the Pamplonita river basin, which encompasses five biomes: dry forest, sub-Andean forest, Andean forest, high-Andean forest, and páramo. Over twelve weeks of active sampling (more than 35 days in the field), we recorded 591 individuals belonging to 33 species, fourteen genera, and seven families. Diversity estimates were based on Hill numbers and Bray–Curtis dissimilarities. Our results show a clear altitudinal pattern, with species richness decreasing at higher elevations (dry forest = 14 spp.; sub-Andean = 16 spp.; Andean = 10 spp.; high-Andean = 4 spp.; páramo = 5 spp.), along with significant species turnover between biomes. Among the recorded species, two are classified as Vulnerable and two as Endangered, and are primarily threatened by cattle ranching, agriculture, mining, forest loss, and feral or domestic animals. This study presents the first systematic assessment of amphibian diversity along the entire altitudinal gradient of the Pamplonita river basin, revealing previously undocumented ecological patterns. Taken together, our findings underscore the strategic importance of this basin for amphibian conservation in northeastern Colombia and the need to implement tailored conservation actions.

Keywords: Amphibian assemblages, conservation priorities, Hill numbers, species turnover, altitudinal gradient.

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RESUMEN

Colombia, uno de los países más biodiversos del mundo y el segundo con mayor riqueza de especies de anfibios, requiere evaluaciones integrales que permitan mejorar el conocimiento y la conservación de su herpetofauna. Esta necesidad es especialmente urgente en regiones potencialmente ricas en especies que enfrentan amenazas antrópicas crecientes. En este contexto, evaluamos la diversidad y el estado de conservación de los anfibios en la cuenca del río Pamplonita, la cual abarca cinco biomas: bosque seco, bosque subandino, bosque andino, bosque altoandino y páramo. A lo largo de doce semanas de muestreo activo (más de 35 días en campo), registramos 591 individuos pertenecientes a 33 especies, catorce géneros y siete familias. Las estimaciones de diversidad se basaron en los números de Hill y en análisis de disimilitud de Bray–Curtis. Nuestros resultados muestran un claro patrón altitudinal, con una disminución en la riqueza de especies a mayor elevación (bosque seco = 14 spp.; bosque subandino = 16 spp.; bosque andino = 10 spp.; bosque altoandino = 4 spp.; páramo = 5 spp.), así como una marcada rotación de especies entre biomas. Entre las especies registradas, dos se encuentran clasificadas como Vulnerables y dos como En Peligro, amenazadas principalmente por la ganadería, la agricultura, la minería, la pérdida de cobertura boscosa y la presencia de animales ferales o domésticos. Este estudio constituye la primera evaluación sistemática de la diversidad de anfibios a lo largo de todo el gradiente altitudinal de la cuenca del río Pamplonita, revelando patrones ecológicos previamente no documentados. En conjunto, nuestros resultados destacan el valor estratégico de esta cuenca para la conservación de los anfibios en el nororiente de Colombia y la necesidad de implementar acciones de conservación diferenciadas.

Palabras claves: Ensamblajes de anfibios, prioridades de conservación, gradiente altitudinal, números de Hill, recambio de especies.

INTRODUCTION

Amphibians are the most threatened group of vertebrates globally and are in a critical state of conservation due to the negative impact of anthropogenic activities on their populations (IUCN SSC, 2024). Climate change, emerging infectious diseases, the introduction of exotic species, habitat fragmentation caused by agriculture and inadequate biodiversity and wildlife management are among the main factors affecting amphibians (IUCN SSC, 2024). Among these, habitat fragmentation is particularly concerning due to its strong association with livestock farming, agriculture, logging, and infrastructure development, all of which are expanding at an alarming rate (Urbina-Cardona *et al.*, 2006). This fragmentation restricts amphibian mobility, and when combined with their permeable skin, makes them highly sensitive to environmental changes and the emergence of new physiological challenges that not all species can withstand (Santos-Barrera & Urbina-Cardona, 2011).

These threats drive population modifications and hinder species stability over time, leading to variations in abundance and distribution (Nowakowski *et al.*, 2017). However, these changes are also influenced by precipitation,

elevation gradients, and habitat structure (Cortés-Gómez *et al.*, 2013; Navas, 2006). High precipitation levels, lower elevations, and increased habitat heterogeneity favor species presence and abundance, thereby leading to higher diversity values (Cortés-Gómez *et al.*, 2013; Navas, 2006). Accurately estimating amphibian populations and diversity remains a significant challenge today (Urbina-Cardona *et al.*, 2023).

Colombia harbors the second highest amphibian diversity in the world, with approximately 910 species; however, it also has the highest number of threatened species, with 365 currently at risk (Acosta-Galvis, 2026; IUCN, 2026). Amphibians in Colombia inhabit both dry and humid biomes, ranging from sea level to páramo ecosystems above 3600 m (Navas, 2006). While such a wide altitudinal range is common when assessing large areas (>5000 km²), it is uncommon in smaller regions (Galeano, 2016). An exception is the Pamplonita river basin, which spans only 1345 km² yet encompasses this full elevation range, including dry forest, sub-Andean, Andean, high-Andean, and páramo biomes (POMCA, 2014). This watershed is of particular interest due to its territorial significance, as it supplies water to 65 % of the population of Norte de

Santander, a department with nearly 60 species of amphibians (Acevedo *et al.*, 2016; Acevedo *et al.*, 2018). In this basin, species under anthropogenic pressure and environmental disturbance have been documented (Arrieta-García *et al.*, 2025; Díaz *et al.*, 2025).

These Andean ecosystems bordering the Pamplonita river basin offer ideal humidity and temperature conditions for amphibians. Nonetheless, their populations remain poorly documented, and the patterns of species richness and abundance across these continuous yet threatened elevation gradients are still largely unknown (Díaz *et al.*, 2025). Although previous studies have highlighted the presence of threatened species and localized disturbances, no comprehensive evaluation has examined how diversity patterns vary across the full altitudinal sequence of biomes in this basin. This gap limits our understanding of how regional threats interact with environmental gradients to shape amphibian assemblages. In this context, our study aims to assess the taxonomic diversity of amphibians across the five biomes surrounding the Pamplonita river basin in northeastern Colombia and to document key conservation aspects of these species along an elevational gradient ranging from 400 to over 3600 m.

MATERIALS AND METHODS

Study area

This study was conducted in the Pamplonita river basin in Norte de Santander, which ranges from 51–3640 m above sea level and exhibits a bimodal precipitation regime (900–2700 mm/year) with rainy seasons in April–May and October–November. Mean annual temperature ranges from 10 to 29 °C, conditions that favor amphibian presence and activity in the basin (Díaz *et al.*, 2026). The basin includes 26 micro-watersheds and spans multiple thermal zones, where elevation and rainfall variability support agriculture, livestock, forestry, and mining activities (POMCA, 2014). These activities are concentrated in localities such as California, El Naranjal, San Antonio, Alto Grande, and Tierra Negra, where this study was conducted. These localities contain five distinct biome types (dry forest, sub-Andean forest, Andean forest, high-Andean forest, and páramo), each with differentiated ecological characteristics (Arrieta-García *et al.*, 2025; Díaz *et al.*, 2026; POMCA, 2014). To ensure a comprehensive and representative sample, field surveys were conducted across these five biomes, covering an altitudinal gradient from 400–3600 m (Fig. 1).

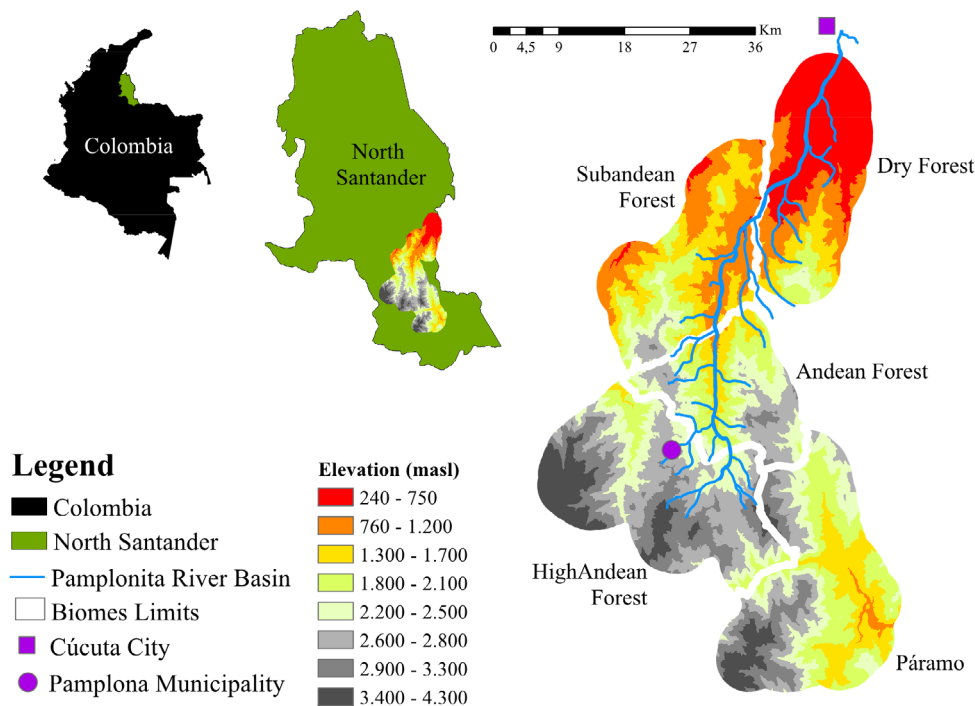


Figure 1. Map of the Pamplonita river basin and study area included in this research. It shows the elevation gradients and biomes from dry forest to páramo.

Data collection

This study was conducted between August 2023 and March 2024, with two sampling sessions per locality. A maximum interval of 20 days was maintained between sampling sessions (logistical constraints), with the first session lasting five consecutive days and the second lasting three consecutive days. The exception was San Antonio, where the second session lasted five consecutive days to ensure adequate completeness. Nocturnal surveys were carried out by three observers between 17:00 and 24:00 using visual and acoustic encounter surveys combined with opportunistic searches. Searches were conducted on and beneath leaf litter, rocks, and fallen logs, as well as in forest habitats, streams, and open areas (Angulo *et al.*, 2006).

To avoid resampling the same area within a locality, independent survey sites were selected for each visit. Additionally, individuals collected during consecutive surveys were stored separately in plastic bags to ensure sample independence and prevent pseudo-replication (Angulo *et al.*, 2006). Sampling efforts at each locality were randomly distributed within the study period, depending on community availability and site accessibility. However, efforts were balanced to include both rainy and dry seasons.

Habitat type, substrate (leaf, leaf litter, water, stem, trunk), and geographic coordinates (Garmin eTrex 22x GPS) were recorded. Up to four individuals per species were collected for tissue sampling and swabbing following Angulo *et al.* (2006). Specimens were identified to species or morphotypes using reference material from national collections and specialized literature and were deposited in the Museo de Historia Natural Luis Gonzalo Andrade (UPTC-MHN-1651-1732). This research was conducted under the general scientific permit granted by the Corporación Autónoma Regional de la Frontera Nororiental (Corporon), under reference number 200 of 2015.

Analysis

Given the sampling design, nonparametric analysis methods were applied, as they have been shown to provide robust estimates of species richness, particularly in faunal datasets (Gotelli & Chao, 2013; Reese *et al.*, 2014). Specifically, richness estimates based on abundance data were used, as they offer equally efficient calculations (Chao *et al.*, 2017).

Upon completion of the planned sampling, an estimation of sampling completeness was performed by calculating the percentage of detected species relative to the estimated total number of species (Pineda-López, 2019). A low proportion of rare or uncommon species was assumed to indicate adequate sampling, whereas increased sampling effort was expected to reduce the number of rare species (López *et al.*, 2012). Species richness was estimated by considering the presence of singletons (species with only one record) and doubletons (species with two records), applying the Chao1 index (Chao *et al.*, 2017; Pineda-López, 2019). Sampling completeness was then calculated using a proportional rule, assuming that the estimated species richness represents 100 % of the community's species (Chao *et al.*, 2017; Pineda-López, 2019).

All calculations were performed separately for each sampled biome using R version 4.3.1 (R Core Team, 2025). Species richness estimation was conducted using the “ChaoSpecies” function in the SpadeR package, with values exceeding 80 % considered indicative of high sampling completeness (Chao & Chiu, 2012; Chao *et al.*, 2016). Visualization was performed via species accumulation curves, generated using the “specaccum” function in the Vegan package and plotted with the “ggplot” function from the ggplot2 package (Oksanen *et al.*, 2007; Wickham, 2016).

Alpha diversity (α) was estimated using Hill numbers, also known as true diversity indices (Hill, 1973; Jost, 2006), following an interpolation-extrapolation approach based on sampling coverage (Chao & Jost, 2012). The results were expressed in terms of the effective number of species, a standardized unit for any qD value (Jost, 2006). Since diversity cannot be adequately represented by a single measure, qD was calculated at three levels (q_0 , q_1 and q_2) to capture different aspects of species diversity (Chao & Jost, 2012; Jost, 2006). The calculations were performed for each biome using R version 4.3.1 (R Core Team, 2025), employing the “iNEXT” function from the iNEXT package based on species abundances (Hsieh *et al.*, 2016). Results were visualized using diversity profiles generated with the “HillNumbersProfile” function, facilitating biome comparisons (Hsieh *et al.*, 2016).

Beta diversity (β), defined as variation in species composition among biomes, was evaluated using two

complementary approaches. First, compositional differences were partitioned into total dissimilarity (β_{cc}), species turnover (β_3), and richness differences (β_{rich}) following Schmera and Podani (2011). Second, abundance-based compositional dissimilarity among biomes was assessed using the Bray-Curtis index (Carvalho et al., 2013). This approach provides a robust assessment of abundance gradients, capturing the inverse relationship between species abundance decreases and concurrent increases in other species (Baselga, 2013). Significant differences in species composition were tested with an Analysis of Similarities (ANOSIM) (Calderón-Patrón et al., 2012), and patterns of compositional variation were visualized using a Principal Coordinates Analysis (PCoA), both based on the Bray-Curtis dissimilarity matrix. All analyses were performed in R version 4.3.1 (R Core Team, 2025). Beta diversity partitioning was conducted using the “betadivers” function in the Vegan package, whereas Bray-Curtis dissimilarity and ANOSIM were calculated with the “vegdist” and “anosim” functions, respectively (Oksanen et al., 2007).

RESULTS

Following a sampling effort of approximately 70 person-hours per biome, sampling completeness was high across all biomes. Sampling completeness reached 100 % in the dry forest (DF), where 14 species were recorded; 99.3 % in the sub-Andean forest (SaF), where 16 species were recorded; 100 % in the Andean forest (AF), where 10 species were recorded; 98.7 % in the high-Andean forest (HaF), where 4 species were recorded; and 100 % in the páramo (Pa), where 5 species were recorded (Fig. 2). These values indicate that twelve weeks of active sampling, distributed over more than 35 effective field days, were sufficient to provide a representative inventory for each biome.

Across the five biomes of the Pamplonita river basin, a total of 591 individuals were recorded, distributed across seven families, fourteen genera, and 33 species (Table 1). The most representative families in the basin were Strabomantidae, with thirteen species, and Hylidae, with nine species. The most abundant genera were

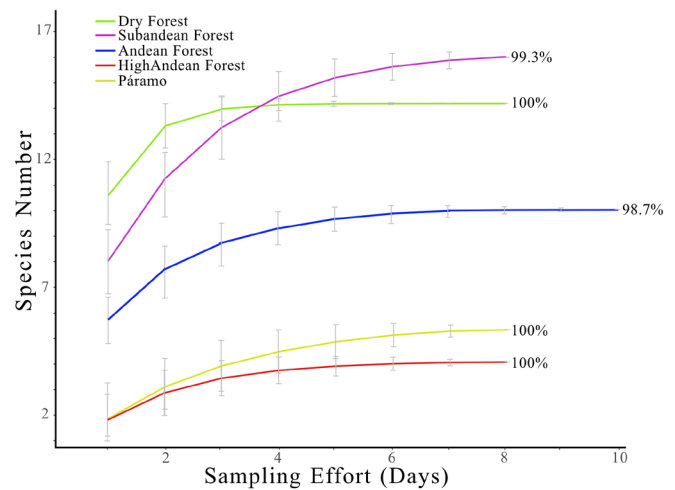


Figure 2. Species accumulation curve for five biomes of the Pamplonita river basin, where the X axis represents the sampling effort in days and the Y axis represents the number of new species added to the sample.

Pristimantis Jiménez de la Espada, 1870 (166 individuals, 28 %), followed by *Leptodactylus* Fitzinger, 1826 (81 individuals, 14 %) and *Dendropsophus* Fitzinger, 1843 (72 individuals, 12 %). Conversely, the least abundant genera were *Centrolene* Jiménez de la Espada, 1872 (nine individuals, 1.5 %), followed by *Lithobates* Fitzinger, 1843 and *Lithodytes* Fitzinger, 1843, each with thirteen individuals (2.2 %). *Pristimantis* was the most diverse genus, with eleven species, whereas the least diverse genera (*Aromobates* Myers, Paolillo-O. & Daly, 1991, *Boana* Gray, 1825, *Centrolene*, *Engystomops* Jiménez de la Espada, 1872, *Hyloscirtus* Peters, 1882, *Lithobates*, *Lithodytes*, and *Phyllomedusa* Wagler, 1830) each contained only one species (Fig. 3a). In the dry forest (DF), ten genera were recorded, with *Leptodactylus* and *Rhinella* Fitzinger, 1826 being the most representative (spp. = 2, abundance = 22, proportion = 14 %) and *Phyllomedusa* the least representative (sp. = 1, abundance = 7, proportion = 4 %) (Fig. 3b). In the sub-Andean forest (SaF), eleven genera were recorded; *Rhinella* had the highest abundance (spp. = 2, abundance = 32, proportion = 23 %), while *Leptodactylus* was the most diverse (spp. = 3, abundance = 11, proportion = 8 %). The least representative genera were *Lithodytes* and *Lithobates* (sp. = 1, abundance = 2, proportion = 2 %) (Fig. 3c).

Table 1. Amphibian species recorded in the Pamplonita River Basin and the main ecological and conservation information compiled in this study

Cd	Species	Bio	Hab	Sust	n	IUCN	TR	Geo Coord
1	<i>Aromobates cf. saltuensis</i> Rivero, 1980	SaF	F	Rt, LF, W, Ro and St	19	EN	C, FA and Cr	7.675315°N 72.616774°W
2	<i>Boana platanera</i> La Marca et al., 2021	DF and SaF	F, P, NL, AL and B	T, St and W	38	LC	C, FA and Cr	7.694553°N 72.567532°W
3	<i>Centrolene daidalea</i> Ruiz-Carranza & Lynch, 1991	AF	R	S and St	9	LC	TF and M	7.461486°N 72.612850°W
4	<i>Dendropsophus microcephalus</i> Cope, 1886	DF and SaF	P, NL and AL	S, Rt, W, and St	22	LC	C, Cr, and FA	7.693925°N 72.570024°W
5	<i>Dendropsophus minutus</i> Peters, 1872	DF and SaF	P, NL and AL	S, Rt, W, and St	9	LC	C, Cr, and FA	7.693260°N 72. 570137°W
6	<i>Dendropsophus molitor</i> Schmidt, 1857	AF, HaF and Pa	P, NL, AL and B	S, Rt, W, T, St and Ro	41	LC	C, Cr, and FA	7.353483°N 72.621445°W
7	<i>Engystomops pustulosus</i> Cope, 1864	DF and SaF	P, NL, AL and B	LF and W	23	LC	C, Cr, and FA	7.683706°N 72.577409°W
8	<i>Hyloscirtus platydactylus</i> Boulenger, 1905	AF	R	S, St and Ro	28	VU	C, TF, M, Cr and FA	7.461343°N 72. 613525°W
9	<i>Leptodactylus colombiensis</i> Heyer, 1994	DF, SaF and AF	P, NL, AL and B	LF and W	65	LC	C, Cr, and FA	7.681200°N 72.577409°W
10	<i>Leptodactylus poecilochilus</i> Cope, 1862	DF and SaF	P, NL, AL and B	LF and W	16	LC	C, Cr, and FA	7.690706°N 72.617591°W
11	<i>Leptodactylus</i> sp.1 Fitzenger, 1826	AF	P, NL, AL and B	LF and W	2	NE	C, M, Cr, and FA	7.676471°N 72.616732°W
12	<i>Lithobates palmipes</i> Spix, 1824	DF and SaF	NL and AL	W	13	LC	C, Cr, and FA	7.674025°N 72.617013°W
13	<i>Lithodytes lineatus</i> Schneider, 1799	DF and SaF	F and B	T, St and Ro	13	LC	C, TF, Cr, and FA	7.679173°N 72.617999°W
14	<i>Phyllomedusa venusta</i> Duellman & Trueb, 1967	DF and SaF	NL, AL and B	S, Rt, T, and St	19	LC	TF, Cr, and FA	7.695641°N 72.578400°W
15	<i>Pristimantis cf. anolirex</i> Lynch, 1983	Pa	B	S, Rt, T, and St	39	VU	C, TF, Cr and FA	7.323972°N 72...569528°W
16	<i>Pristimantis</i> sp.1 Jiménez de la Espada, 1870	AF	F	S, LF, T, and St	7	NE	C, TF, M and Cr	7.461229°N 72..616991°W
17	<i>Pristimantis</i> sp.2 Jiménez de la Espada, 1870	AF	F	S, LF, T, and St	9	NE	C, TF, M and Cr	7.461405°N 72. 618580°W
18	<i>Pristimantis</i> sp.3 Jiménez de la Espada, 1870	AF	F	S, LF, T, and St	2	NE	C, TF, M and Cr	7.461054°N 72.612420°W
19	<i>Pristimantis</i> sp.4 Jiménez de la Espada, 1870	AF	F and R	S, LF, T, and St	4	NE	C, TF, M and Cr	7.462221°N 72.616912°W
20	<i>Pristimantis</i> sp.5 Jiménez de la Espada, 1870	HaF	F	S, LF, T, and St	24	NE	C, TF, Cr and FA	7.346424°N 72.683352°W
21	<i>Pristimantis</i> sp.6 Jiménez de la Espada, 1870	HaF	F	S, LF, T, and St	17	NE	C, TF, Cr and FA	7.345359°N 72.683352°W

Cd	Species	Bio	Hab	Sust	n	IUCN	TR	Geo Coord
22	<i>Pristimantis</i> sp.7 Jiménez de la Espada, 1870	SaF	F	S, LF, T, and St	4	NE	C, TF, Cr and FA	7.675458°N 72.683820°W
23	<i>Pristimantis</i> sp.8 Jiménez de la Espada, 1870	Pa	F	S, LF, T, and St	13	NE	C, TF, Cr and FA	7.342696°N 72.595780°W
24	<i>Pristimantis</i> sp.9 Jiménez de la Espada, 1870	Pa	F	S, LF, T, and St	17	NE	C, TF, Cr and FA	7.342054°N 72.599344°W
25	<i>Pristimantis taeniatus</i> Boulenger, 1912	DF and SaF	F and R	S, LF, T, and St	30	LC	C, TF, Cr and FA	7.684876°N 72.574960°W
26	<i>Rhinella horribilis</i> Wiegmann, 1833	DF and SaF	P and B	W	26	LC	C, Cr and FA	7.680955°N 72.615416°W
27	<i>Rhinella humboldti</i> Gallardo, 1965	DF	NL and AL	W	9	LC	C, Cr and FA	7.690212°N 72.571449°W
28	<i>Rhinella margaritifera</i> Laurenti, 1768	SaF	P, NL and AL	W	19	LC	C, Cr and FA	7.683840°N 72.617147°W
29	<i>Scinax manriquei</i> Barrio-Amorós, 2004	AF	P, NL, AL and B	S, Rt, W, and St	2	NT	C, TF, M and Cr	7.467585°N 72.626544°W
30	<i>Scinax rostratus</i> Peters, 1863	DF and SaF	P, NL and AL	S, Rt, W, and St	14	LC	C, Cr, and FA	7.674178°N 72.617059°W
31	<i>Scinax x-signatus</i> Spix, 1824	DF	P, NL and AL	S, Rt, W, and St	8	LC	C, Cr, and FA	7.683630°N 72.570176°W
32	<i>Tachiramantis lentiginosus</i> Rivero, 1984	AF	F	S, LF, T, and St	25	EN	C, TF, M and Cr	7.465477°N 72.614701°W
33	<i>Tachiramantis prolixodiscus</i> Lynch, 1978	HaF and Pa	F	S, LF, T, and St	5	LC	C, TF, M, Cr and FA	7.346997°N 72.608685°W

Abbreviations: Code (Cd); biomes (Bio): dry forest (DF), sub-Andean forest (SaF), Andean forest (AF), high-Andean forest (HaF), and páramo (Pa). Habitats (Hab): forest (F), pasture (P), ravine (R), natural lagoon (NL), artificial lagoon (AL), and bushland (B). Substrates (Sust): sheet (S), root (Rt), leaf litter (LF), water (W), trunk (T), stem (St), and rock (Ro). IUCN threat categories: Not Evaluated (NE), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), and Endangered (EN). The threats recorded for each species (TR) correspond to cattle ranching (Cr), mining (M), logging (TF), planting (C), and feral animals (FA). Geographic Coordinates (Geo Coord, WGS84, Decimal format).

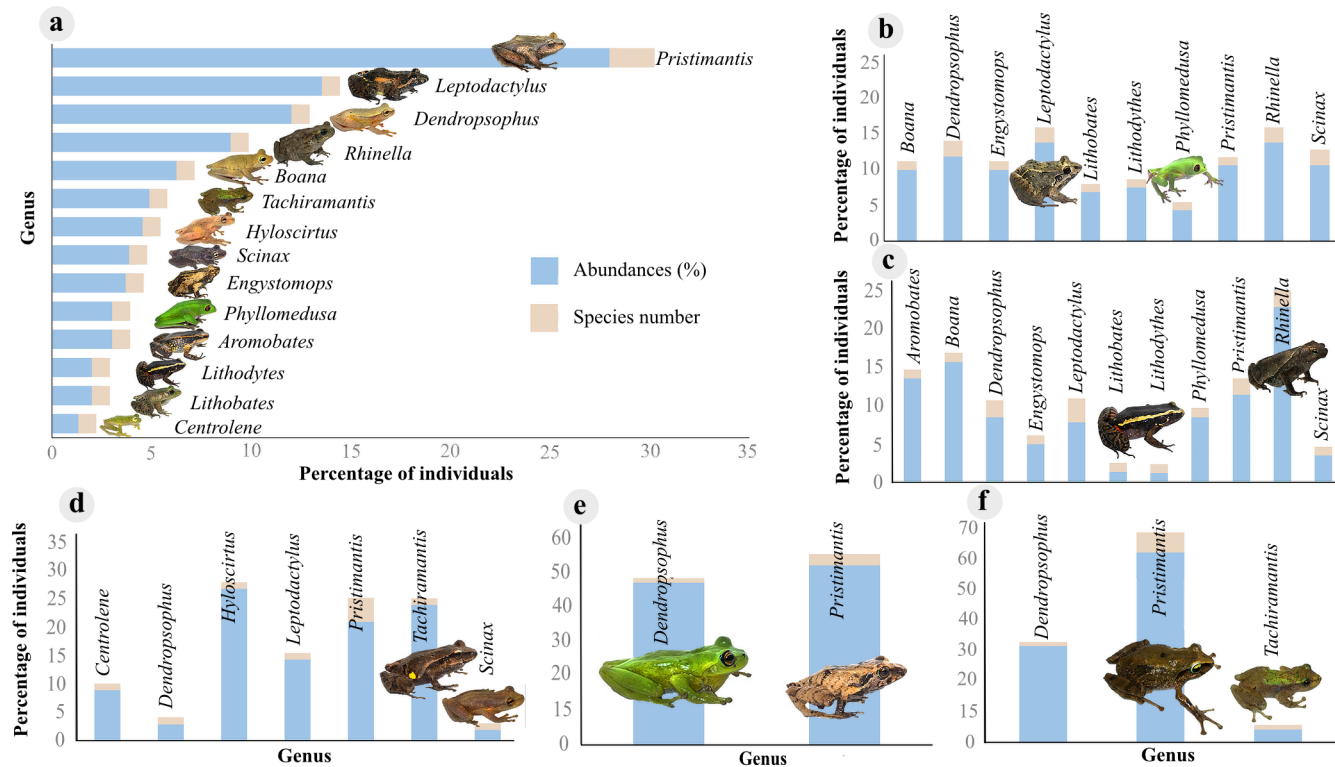


Figure 3. Percentage representativeness of anuran genera recorded in the Pamplonita river basin and across its five biomes. **a**) Overall percentage of individuals per genus (blue bars) and number of species per genus (beige bars) across the entire basin. **b-f**) Percentage of individuals by genus in each biome: **b**) Dry forest (DF), **c**) Sub-Andean forest (SaF), **d**) Andean forest (AF), **e**) High-Andean forest (HaF), and **f**) Páramo (Pa). Percentages were calculated based on the total number of individuals recorded in each biome. Representative species images are included for each genus.

In the Andean forest (AF), seven genera were reported. The most representative were *Hyloscirtus* (sp. = 1, abundance = 28, proportion = 25 %), *Tachiramantis* Heinicke, Barrio-Amorós & Hedges, 2015 (sp. = 1, abundance = 25, proportion = 24 %), and *Pristimantis* (spp. = 4, abundance = 22, proportion = 21 %), whereas *Scinax* Wagler, 1830 (sp. = 1, abundance = 2, proportion = 2 %) was the least representative (Fig. 3d). In the high-Andean forest (HaF), only two genera were recorded with relatively similar representation: *Pristimantis* (spp. = 4, abundance = 42, proportion = 53 %) and *Dendropsophus* (sp. = 1, abundance = 38, proportion = 47 %, Fig. 3e). In the páramo (Pa), three genera were recorded, with *Pristimantis* being the most representative (spp. = 3, abundance = 69, proportion = 63 %) and *Tachiramantis* the least representative (sp. = 1, abundance = 5, proportion = 5 %, Fig. 3f).

Alpha (α) and beta (β) taxonomic diversity

The rank-abundance curves (Fig. 4) indicate that species abundance distribution varies across biomes. In the

dry forest (DF), species had relatively similar abundances, suggesting diffuse dominance and rarity, with species such as *Pristimantis taeniatatus* (Boulenger, 1912) (n = 17), *Boana platanera* (La Marca, Escalona, Castellanos, Rojas-Runjaic, Crawford, Señaris, Fouquet, Giaretta et al., 2021) (n = 16), and *Engystomops pustulosus* (Cope, 1864) (n = 16) exhibiting comparable abundance levels. In the sub-Andean forest (SaF) and Andean forest (AF), abundance was more variable, with a marked dominance of *B. platanera* (n = 22) in the SaF and *Hyloscirtus platydactylus* (Boulenger, 1905) (n = 28) in the AF; rare species in these biomes included *Lithodytes lineatus* (Schneider, 1799) (n = 2) and *Scinax manriquei* Barrio-Amorós, Orellana & Chacón-Ortiz, 2004 (n = 2), respectively. In the high-Andean forest (HaF) and páramo (Pa), most species exhibited high abundance, while a few had low abundance. The dominant species were *Dendropsophus moliator* (Schmidt, 1857) (n = 35) in the HaF and *Pristimantis* cf. *anolirex* (n = 39) in the Pa. Among the rarest species, *Pristimantis* sp.7 (n = 1) was notable in the HaF.

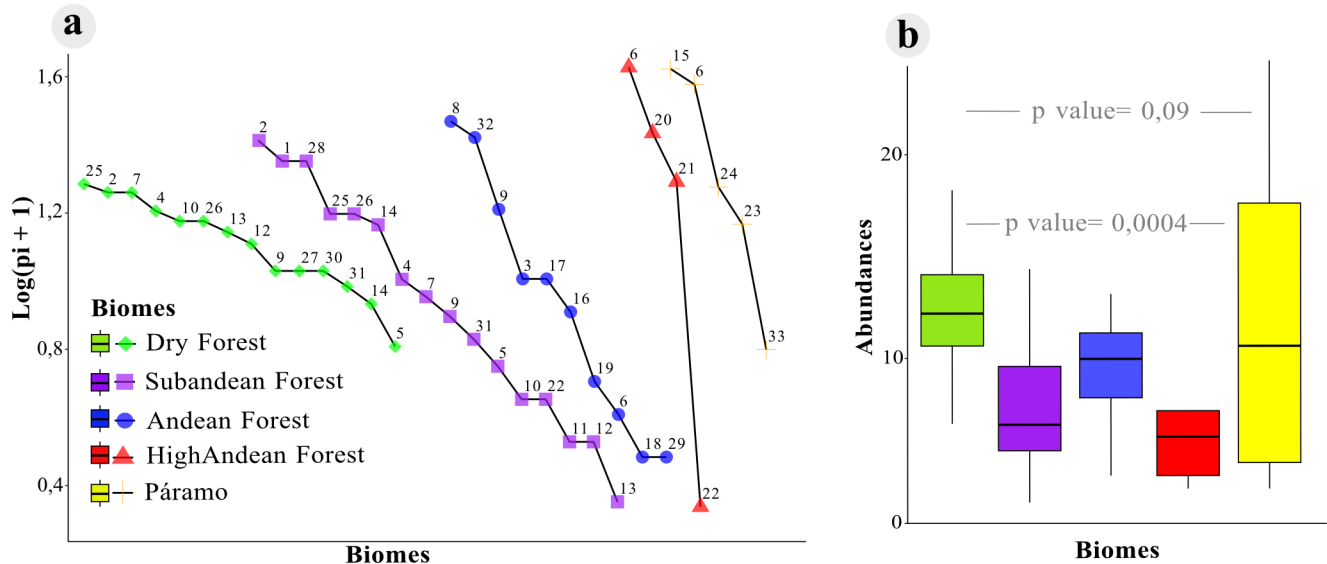


Figure 4. Abundance comparison of the five biomes of the Pamplonita river basin. **a.** Rank-abundance curve, where each trend line corresponds to the behavior of abundances per species in each biome. The codes corresponding to each species are described in Table 1. Abundance values were transformed into equivalences when subjected to the form $\text{Log}_{10}(\pi + 1)$. **b.** Comparative box-and-whisker plot between the abundances of the five biomes of the Pamplonita river basin, under the Kruskal-Wallis test comparison criterion.

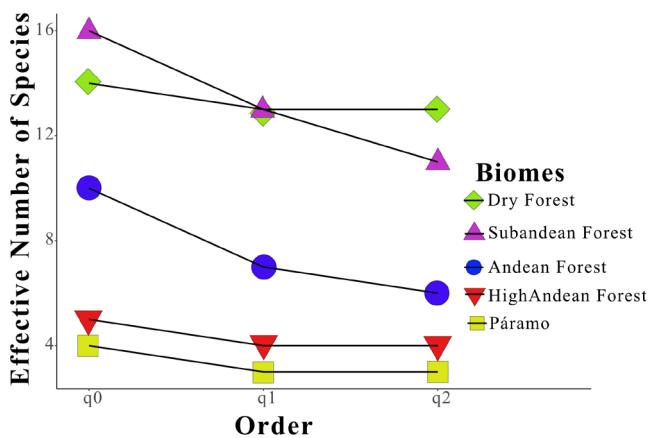


Figure 5. Alpha diversity profiles of the five biomes of the Pamplonita river basin, where the number of effective species is represented in the order q0 (richness), q1 (common species), q2 (dominance).

Estimates of Hill numbers in terms of the effective number of species for each biome indicated an inventory completeness greater than 95 % for all diversity profile values (q0, q1 and q2). It was observed that the biome with the highest species richness (q0) was SaF (16 spp.), followed by DF (14 spp.), AF (10 spp.), Pa (5 spp.), and HaF (4 spp.) (Fig. 5). On the other hand, when considering common species (q1) as an explanation for the homogeneity of spe-

cies within biomes, we found that DF had 13.88 equally common species, compared with 12.72 in the SaF, 7.43 in the AF, 3.06 in the HaF, and 4.20 in the Pa (Fig. 5, Table 2). These values suggest that DF is 1.09 times more diverse than SaF, with SaF being 1.71 times more diverse than AF, and AF 2.43 times more diverse than HaF, and HaF slightly less diverse than Pa (Fig. 5, Table 2). Likewise, the effective number of dominant species (q2) was 13.79 in the DF, 10.86 in the SaF, 6.04 in the AF, 2.83 in the HaF, and 3.77 in the Pa (Fig. 5, Table 2).

Table 2. Diversity values of the five biomes of the Pamplonita river basin. The Shannon index and species diversity are presented in terms of the actual number of observed and expected species.

Biome	Shannon index	Observed diversity			Expected diversity		
		q0	q1	q2	q0	q1	q2
Dry forest	1.09	14	13.31	12.76	14	13.88	13.79
Sub-Andean forest	1.71	16	12.01	10.14	16.25	12.72	10.86
Andean forest	2.43	10	7.1	5.76	10	7.43	6.04
High-Andean forest	0.73	4	3	2.77	4	3.06	2.83
Páramo	1.37	5	4.13	3.68	5	4.2	3.77

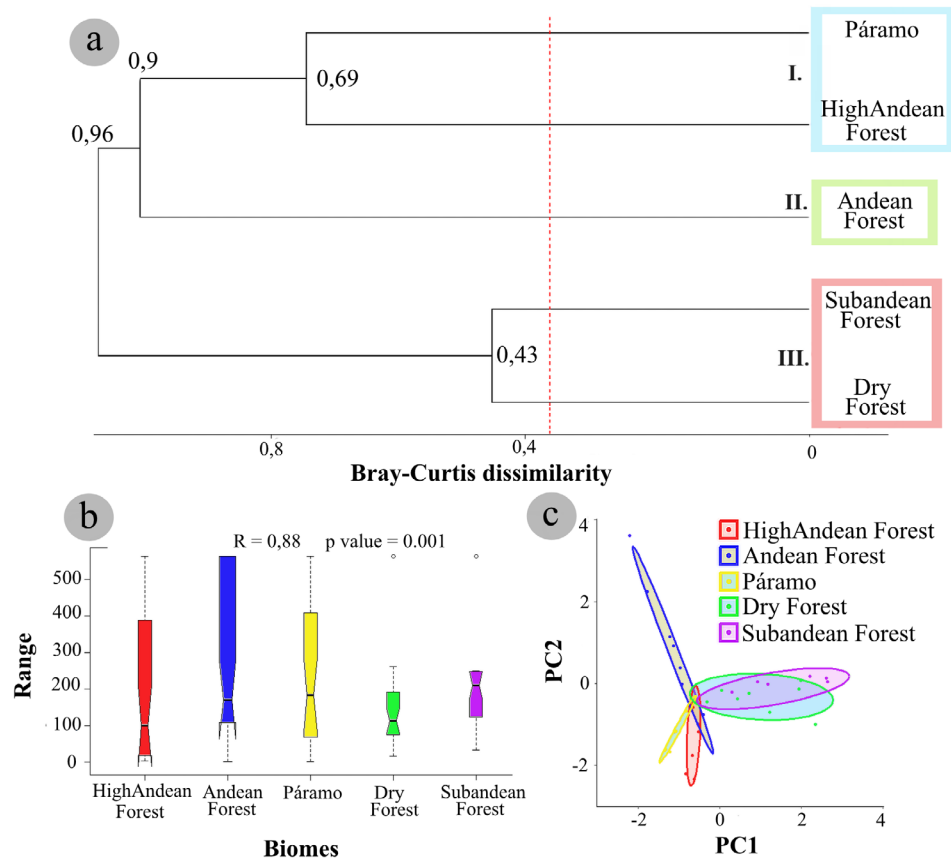


Figure 6. Dissimilarity analysis of the five biomes of the Pamplonita river basin, which is composed of **a.** Cluster Dendrogram based on Bray-Curtis dissimilarity, **b.** ANOSIM of the dissimilarities and **c.** Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity.

The Bray-Curtis dissimilarity analysis ($p = 0.001$) revealed three compositional patterns among biomes. Dry forest (DF) and sub-Andean forest (SaF) were the most similar pair (dissimilarity = 0.43), high-Andean forest (HaF) and páramo (Pa) showed intermediate similarity (dissimilarity = 0.69), and Andean forest (AF) was the most distinct biome, with high dissimilarity relative to the others (dissimilarity = 0.90) (Figs. 6a-b).

When beta diversity was partitioned into turnover, nestedness, and total dissimilarity (Table 3), the DF-SaF pair showed the strongest species replacement, sharing taxa such as *P. taeniatus* and *B. platanera*, whereas *Rhinella humboldti* (Gallardo, 1965) was exclusive to DF and *Rhinella margaritifera* (Laurenti, 1768) to SaF (Figs. 6c-7). The HaF-Pa pair also showed species turnover, sharing *D. molitor*, whereas *Pristimantis* sp.5 was exclusive to HaF and *P. cf. anolirex* to Pa (Figs. 6c-7). In contrast, AF differed strongly from the other biomes and shared only a few taxa, including *Leptodactylus colombiensis* (Heyer, 1994) with SaF and *D. molitor* with HaF. Nestedness remained

low (<6 %), suggesting largely independent assemblages among biomes (Figs. 6c-7).

Conservation aspects

Of the 33 amphibian species recorded in the Pamplonita river basin, species were distributed across five IUCN categories: Not Evaluated (NE), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), and Endangered (EN) (Fig. 8, Table 1). We identified three biomes in the Pamplonita river basin as conservation priorities, namely the sub-Andean forest, Andean forest, and páramo, because they harbor the species of greatest conservation concern according to IUCN criteria (Fig. 8, Table 1). These species include *Aromobates* cf. *saltuensis*, categorized as Endangered, in the sub-Andean forest; *Tachiramantis lentiginosus* (Rivero, 1984), categorized as Endangered, and *H. platydactylus*, categorized as Vulnerable, in the Andean forest; and *P. cf. anolirex*, categorized as Vulnerable, in the páramo (Fig. 8, Table 1). Species were recorded in both conserved forests and stream habitats (48 %), while others exhibited broader habitat distributions and substrate pref-

Table 3. Beta diversity values, estimated from the Bray-Curtis dissimilarity using decomposition total dissimilarity (β_{cc}), species turnover ($\beta-3$), and nestedness-driven richness differences (β_{rich}). Biomes (Bio) are dry forest (DF), sub-Andean forest (SaF), Andean forest (AF), high-Andean forest (HaF), páramo (Pa).

Bio	β_{cc}					$\beta-3$					β_{rich}				
	DF	SaF	AF	HaF	Pa	DF	SaF	AF	HaF	Pa	DF	SaF	AF	HaF	Pa
DF	—	0. 43	0. 9	0. 96	0. 96	—	0. 45	0. 9	—	—	—	0. 04	0 .06	—	—
SaF	0. 43	—	0. 9	0. 96	0. 96	0. 45	—	0. 9	—	—	0. 04	—	0. 06	—	—
AF	0. 9	0. 9	—	0. 9	0. 9	0. 9	0. 9	—	0. 9	0 .9	0. 06	0,06	—	0. 06	0. 06
HaF	0. 96	0. 96	0. 9	—	0. 69	—	—	0. 9	—	0. 3	—	—	0. 06	—	0. 05
Pa	0. 96	0 .96	0. 9	0. 69	—	—	—	0. 9	0. 3	—	—	—	0. 06	0. 05	—

Biomes (Bio) are dry forest (DF), sub-Andean forest (SaF), Andean forest (AF), high-Andean forest (HaF), páramo (Pa).

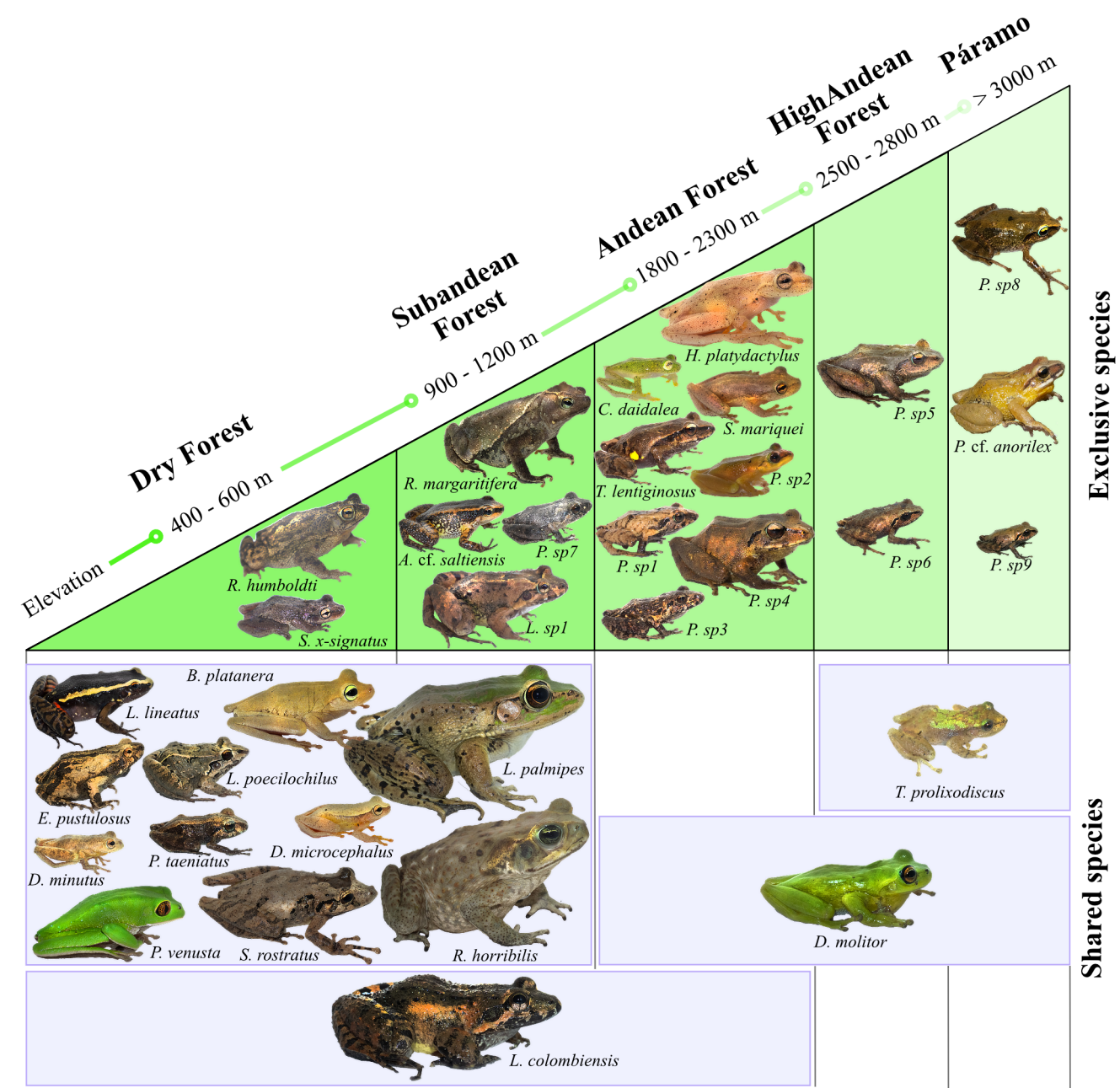


Figure 7. Amphibian species recorded in the five biomes of the Pamplonita river basin. Exclusive species and shared species are represented in an altitudinal gradient from 400 to just over 3000 m.

erences (52 %, Table 1). The main threats associated with species occurrence across the basin were cattle ranching, agriculture, mining, forest loss, and feral or domestic animals (Table 1).

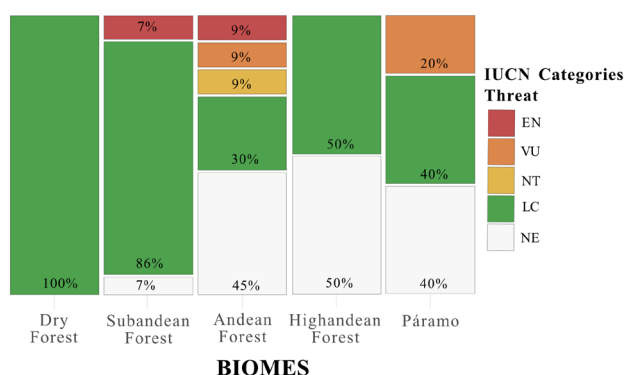


Figure 8. Mosaic graph showing the proportion of threatened species in each biome of the Pamplonita river basin, classified according to IUCN criteria. Threat categories include: Not Evaluated (NE), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), and Endangered (EN).

DISCUSSION

Colombia hosts a remarkable diversity of amphibian species, with significant aspects of their natural history, geographic distribution, systematics, and taxonomy extensively studied and published (Urbina-Cardona *et al.*, 2023). However, major knowledge gaps remain, highlighting the need for long-term monitoring studies that cover broad spatial gradients and provide robust species inventories, both of which are addressed in this study (Urbina-Cardona *et al.*, 2023). Despite the growing interest in amphibian research in Colombia, no extensive studies, apart from the present work, have monitored this taxonomic group along a broad altitudinal gradient, where dry forest, sub-Andean, Andean, high-Andean, and páramo biomes are integrated within the same slope (Rojas-Morales & González-Carvajal, 2024; Urbina-Cardona *et al.*, 2023). This context highlights the novelty of our research objective and the relevance of evaluating amphibian diversity in a basin that uniquely concentrates multiple biomes across a narrow spatial scale (Urbina-Cardona *et al.*, 2023).

This research revealed that *Pristimantis* is the most abundant and species-rich genus at high altitudes in the Andean forests, likely due to its direct development strategy and unique thermoregulatory adaptations, which enable its persistence under strict habitat conditions (Meza-Joya

& Torres, 2016; Pintanel *et al.*, 2019). Meanwhile, in low-land areas, abundance and species richness are distributed among multiple genera, including *Leptodactylus*, *Dendropsophus*, and *Rhinella*, which exhibit fixed breeding modes and periods in response to relatively stable environmental conditions (Fig. 3, Vargas-Salinas *et al.*, 2019). These differences reflect how reproductive strategies and thermoregulatory constraints interact with elevation—one of the central mechanisms we sought to evaluate (Tobar-Suárez *et al.*, 2022).

Consistent with previous studies on the site and taxonomic group, the rank-abundance curves indicate that along the altitudinal gradient of the five biomes in the Pamplonita river basin, abundance structure follows a pattern characterized by the presence of dominant and rare species in varying proportions across biomes (Fig. 4, Rojas-Morales & González-Carvajal, 2024). Dominant species tend to be favored by habitat characteristics, benefiting from consecutive reproductive cycles and high clutch numbers (Rojas-Morales & González-Carvajal, 2024). In contrast, rare species require specific habitat features to maintain their populations and exhibit infrequent breeding events with smaller clutch sizes, limiting their ability to persist (Rojas-Morales & González-Carvajal, 2024). This pattern suggests that environmental filtering intensifies with elevation, favoring species capable of tolerating colder conditions, narrower thermal windows, and more restrictive habitat conditions (Rojas-Morales & González-Carvajal, 2024).

Regarding the effective number of species, diversity of order q_0 (Fig. 5) aligns with previous records from nearby altitudinal gradients. In the dry forest, amphibian richness is well-documented, with fourteen species reported in this study, which is consistent with previous findings (Armesto *et al.*, 2009; Vargas-Salinas *et al.*, 2019). In the sub-Andean forest, previous reports indicate the presence of up to 21 species, while this study recorded 16 species, also consistent with available literature (Armesto *et al.*, 2009). The Andean forest has documented diversities of up to fifteen effective species; in this study, ten species were observed, which aligns with previous studies in the region (Gutiérrez-Lamus *et al.*, 2021). The high-Andean forest and páramo biomes typically host four to six effective species. In this study, four species were recorded in the high-Andean forest and five in the páramo, results that are congruent with prior studies (Acevedo *et al.*, 2016; Acevedo *et al.*, 2018).

When analyzing diversity using q_1 and q_2 (Fig. 5), a reduction in effective common and dominant species is observed compared to q_0 . This trend occurs because species abundances are not evenly distributed; some species are significantly more frequent than others (Fedor & Zvaríková, 2019). However, the diversity values of common species (q_1) and dominant species (q_2) are similar, suggesting that within the amphibian communities of the five biomes, species are primarily distributed as either common or dominant, with rare species being less frequently recorded (Avolio et al., 2019; Fedor & Zvaríková, 2019).

The results also reveal a variation in diversity along the altitudinal gradient, supporting the hypothesis that species richness tends to decrease as elevation increases (Figs. 5-7, Saboyá & Urbina-Cardona, 2023). Unlike high-altitude biomes, the dry forest and Andean forest exhibit a more complex vegetation structure and landscape matrix, providing a variety of ecological niches that support a greater number of species (Díaz-Pérez et al., 2019). However, when comparing the high-Andean forest/páramo, diversity values do not fully conform to this hypothesis (Fig. 5). This may be attributed to the close and continuous altitudinal gradient between these biomes (Acevedo et al., 2018; Saboyá & Urbina-Cardona, 2023).

Further supporting this pattern of altitudinal continuity, the Bray-Curtis dissimilarity analysis separated the biomes into three compositional units: dry forest-sub-Andean forest, Andean forest, and high-Andean forest-páramo (Figs. 6a-7, Acevedo et al., 2018; Saboyá & Urbina-Cardona, 2023). This pattern is explained by the considerable species turnover (57 %) between dry forest and sub-Andean forest, as these biomes share a significant number of species, such as *B. platanera*, which exhibits an altitudinal range up to 2400 m (Fig. 7, Urbina-Cardona et al., 2023). In contrast, turnover between high-Andean forest and páramo is lower (31 %), with one or two species shared between these closely related biomes, such as *D. molitor*, which occurs up to 4200 m (Fig. 7, Saboyá & Urbina-Cardona, 2023; Urbina-Cardona et al., 2023).

Finally, from a conservation perspective, a considerable proportion of species in the Pamplonita river basin face significant threats. These threats have been previously documented and quantified in the region, particularly for *T. lentiginosus*, where important population modifications

have been reported (Díaz et al., 2025). Our results reinforce that anthropogenic pressures (particularly land-use change, agriculture, livestock expansion, and pollution) interact with elevation-driven environmental constraints to shape local assemblages. This highlights the need for management plans tailored to each biome, especially for species with restricted distributions or sensitivity to environmental disturbance. Given the basin's importance for regional water supply and its concentration of endangered species, our findings directly support the objective of guiding conservation strategies along the altitudinal gradient, emphasizing priority areas where habitat protection and restoration efforts would have the greatest impact.

CONCLUSIONS

This study shows that amphibian diversity in the Pamplonita river basin is structured by elevation: (1) species richness is higher at lower elevations, while higher zones host fewer but more specialized species; (2) species turnover is greatest between adjacent biomes due to shared taxa across elevation bands; and (3) nestedness patterns decline when broader altitudinal gradients are considered, likely due to greater ecological heterogeneity. These patterns highlight the ecological significance of the basin for amphibian conservation in northeastern Colombia.

The presence of threatened species marked habitat specificity, and the increasing influence of agriculture, mining, and deforestation highlight the need for urgent and biome-specific conservation actions. Based on our findings along the altitudinal gradient, conservation strategies should prioritize the protection of dry and sub-Andean forests, where richness and species turnover are highest, and should also strengthen habitat connectivity between Andean and high-Andean ecosystems, which harbor cold-adapted and range-restricted taxa. Future efforts should focus on long-term monitoring of at-risk species, restoring degraded habitats, and mitigating human impacts through improved land-use planning. Equally important is engaging local communities in participatory conservation and promoting sustainable practices that reduce pressure on the watershed. These actions will be essential to safeguard amphibian populations and maintain ecosystem integrity in the Pamplonita river basin.

AUTHOR CONTRIBUTION

GDP, AAA conceived the study, developed the sampling design, performed the data analysis, and wrote the initial draft. Data collection was performed by AAA, GDP, DAG and LJO. Audiovisual resources such as photographs were provided by GDP. All authors contributed to the writing of the manuscript and participated in its revision and editing.

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