Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales.
50(194):69-92, enero-marzo de 2026. doi: https://doi.org/10.18257/raccefyn.3181

**Natural Sciences**

Original article

# Main limnological patterns of the Andes and some Cis- and Trans-Andean areas of Colombia

## Principales patrones limnológicos de los Andes y algunas áreas cisandinas y transandinas de Colombia

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## Abstract

A comprehensive understanding of the structure and functioning of continental aquatic ecosystems is crucial for the effective conservation and sustainable use of water and hydrobiological resources in Colombia, a country renowned for its exceptional biodiversity and abundant water reserves. This study examines the biological arrangements and the environmental processes that structure freshwater bodies in various Colombian regions, analyzes the probable underlying causes, and suggests avenues for further research. Physicochemical variables were recorded *in situ*, and water samples were collected for nutrient analysis. Periphytic algae and aquatic macroinvertebrates were sampled from 26 lentic and 80 lotic ecosystems across different Andean, trans-Andean, and cis-Andean regions between 2005 and 2022. Data analysis involved classification (UPGMA) and ordination (PCA, UMAP, NMDS, LDA), which led to several significant findings: 1) The phycoperiphyton and macroinvertebrate assemblages showed a characteristic relationship with environmental factors, mirroring the environmental conditions of the aquatic ecosystems; 2) the physicochemical factors successfully classified different aquatic systems based on their specific geographical areas, emphasizing clear regional distinctions; 3) lentic systems exhibited more pronounced regional differences than lotic systems, implying that still-water environments may be more sensitive to local ecological effects, and 4) some physicochemical characteristics and biological composition correspondences were observed among aquatic systems in different regions, suggesting potential shared influences or similar environmental conditions affecting them. Based on these general limnological patterns, a comprehensive conceptual framework is proposed that clarifies the interactions among these factors. Potential future research topics have been identified to enhance the understanding of the structure and dynamics of these aquatic systems.

**Keywords:** Limnological regionalization; macroinvertebrates; Neotropical limnology; phycoperiphyton.

## Resumen

La comprensión de la estructura y el funcionamiento de los ecosistemas acuáticos continentales es esencial para la conservación efectiva y la utilización sostenible del agua y los recursos hidrobiológicos en Colombia, un país excepcionalmente biodiverso y rico en reservas hídricas. En este estudio se exploran los arreglos biológicos y los procesos ambientales que estructuran los cuerpos de agua dulce en varias regiones colombianas, se analizan las probables causas subyacentes y se sugieren nuevas líneas de investigación. Se registraron variables fisicoquímicas *in situ*, se recolectaron muestras de agua para el análisis de nutrientes y se muestrearon algas perifíticas y macroinvertebrados acuáticos en 26 ecosistemas lénticos y 80 ecosistemas lóticos de diferentes regiones andinas, transandinas y cisandinas entre 2005 y 2022. El análisis involucró métodos de clasificación (UPGMA) y ordenación (PCA, UMAP, NMDS, LDA), y se obtuvieron varios hallazgos significativos: 1) los ensambles de ficoperifiton y macroinvertebrados mostraron una relación característica con los factores ambientales y reflejaron las condiciones ambientales de los ecosistemas acuáticos; 2) los factores fisicoquímicos permitieron clasificar los diferentes sistemas acuáticos en función de sus áreas geográficas, revelando claras distinciones regionales; 3) los sistemas lénticos exhibieron diferencias regionales más pronunciadas que los sistemas lóticos, y 4) se notaron algunas similitudes en las características

**Citation:** Pinilla-Agudelo GA. Main limnological patterns of the Andes and some Cis- and Trans-Andean areas of Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 50(194):69-92, enero-marzo de 2026. doi: https://doi.org/10.18257/raccefyn.3181

**Editor:** Jaime Escobar

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**Received:** March 13, 2025
**Accepted:** October 14, 2025
**Published on line:** January 19, 2026

Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales.
50(194):69-92, enero-marzo de 2026. doi: https://doi.org/10.18257/raccefyn.3181

fisicoquímicas y la composición biológica entre los ecosistemas acuáticos de diferentes regiones, lo que indica posibles influencias compartidas o condiciones ambientales similares en esas áreas. Con base en estos patrones limnológicos generales se propone un marco conceptual integral que ilustra sus interacciones. Asimismo, se proponen posibles temas para futuras investigaciones que permitan profundizar en la comprensión de la estructura y dinámica de estos sistemas acuáticos.

**Palabras clave:** ficoperifiton; limnología neotropical; macroinvertebrados; regionalización limnológica.

## Introduction

The limnology of temperate zones is well understood, with its development dating back over a century. Numerous books have compiled the principles, theories, patterns, and details of the aquatic systems in these regions since the mid-twentieth century (**Welch**, 1952; **Hutchinson**, 1957; **Wetzel**, 1975; **Margalef**, 1983; **Allan & Castillo**, 2007; **Lampert & Sommer**, 2007). Although the limnological literature on the tropics is less abundant, some documents have been produced, among them those by **Payne** (1986), **Lewis** (1987), and **Dudgeon** (2008). In the specific case of the Neotropics, the works by **Esteves** (2011), **Tundisi & Matsumura-Tundisi** (2011), and **Roldán & Ramírez** (2022) stand out, providing valuable data and examples of ecosystems in the region. Despite the numerous publications on Colombia's continental aquatic ecosystems (**Roldán**, 2020), a significant gap remains in comprehensive descriptions of the broader limnological patterns that shape the structure and functioning of these ecosystems.

Understanding the organizational patterns of aquatic ecosystems, especially inland ones, is crucial for identifying mechanisms that support their long-term protection (**Gao & Qiu**, 2025). These aquatic environments provide essential services, including water, food, biodiversity conservation, and climate regulation, which directly benefit human well-being and the ecological health of the planet. However, Colombia's rivers, lakes, and wetlands are experiencing severe decline due to watershed deforestation, pollution, eutrophication, and drying up, among other stressors (**Donato-Rondón**, 2022). In this context, regional limnological classifications are helpful, despite local stressors, as they enable us to understand the general organization of water bodies, recognize large-scale pollution patterns, plan sustainable water management, and evaluate the effectiveness of local interventions within a broader framework (**Soranno *et al.***, 2010).

The initial effort to develop a comprehensive framework for understanding continental aquatic ecosystems in Colombia was undertaken by **Donato** (1998). He proposed dividing the country into four limnological provinces: tropical high mountains (páramo), Andean regions, lowlands, and coastal areas. **Naranjo *et al.*** (1999) based their definition of 27 wetland complexes in Colombia on the classification proposed by the Ramsar Convention (**Scott & Jones**, 1995). Their typology was primarily hydrological and didn't incorporate field data on the physicochemical characteristics of the water or the aquatic biological communities. Later, **Donato & Galvis** (2008) introduced a classification system for Colombian river systems based on geomorphology. They categorized rivers into two main groups: mountain (Andean) and lowland rivers, with the latter further subdivided into regions (Orinoco, jungle, inter-Andean, and Caribbean).

Additionally, the Colombian **Instituto de Hidrología, Meteorología y Estudios Ambientales** (**IDEAM**, 2013) delineated and classified five major hydrological areas: Caribbean, Magdalena-Cauca, Orinoco, Amazon, and Pacific. Each of these areas contains specific zones and subzones. The IDEAM also identified three types of hydrogeological provinces: coastal and insular, montane and intermontane, and pericratonic, coding 44 aquifer systems within these provinces.

**Ricaurte *et al.*** (2019) developed a classification system for aquatic ecosystems in Colombia using a hydrogeomorphological approach. Their classification features four hierarchical levels: system, macroregion, subsystem, and class, encompassing 89 macrohabitats across marine, coastal, continental, and artificial environments. From a continental perspective, **Prado *et al.*** (2024) proposed a classification for the lakes of the Andes Mountains, dividing them into three zones: northern, central, and southern. The northern one includes the Colombian lakes, which the authors categorize into two districts: páramo lakes (located above 3,500 m above sea level, m a.s.l.) and inter-Andean lakes (ranging from 1,000 to 3,500 m a.s.l). To establish this categorization, **Prado *et al.*** (2024) considered geographic, hydrological, and climatic factors, including elevation, residence time, air temperature, precipitation, and potential evapotranspiration.

In the Magdalena-Cauca basin, **González-Cuéllar & Obregón-Neira** (2013) used hydrological variables modeled with the Indicators of Hydrologic Alteration (IHA) program to classify the river systems within this vast area. They utilized an unsupervised neural network, specifically a Kohonen network, to validate the six river families defined using the Ecological Limit of Hydrological Alteration (ELOHA) methodology. These river families comprise the páramo, high mountain, mid-mountain, foothills, low mountain, and floodplain lotic systems. In national and regional contexts, **Plata-Días** (2016) identified four types of rivers based on their hydrological conditions and the taxonomic and functional characteristics of periphytic diatom communities, which include rivers with open vegetation and flowing water, rivers with rigid substrates and turbulent flows, rivers with considerable leaf litter and soft substrates, and rivers with riparian forests. Her study covered an altitude range of 56 to 1,815 m a.s.l., involving several hydrographic basins, including those in the Orinoquia and Amazonian foothills (Putumayo), as well as the upper, middle, and lower sections of the Magdalena River basin and the Catatumbo region. In a related report, **Mesa *et al*.** (2016) identified 28 river ecoregions in Colombia, distributed as follows: six in the Caribbean, eight in the Andes, five in the Pacific, four in the Amazon, and five in the Orinoco River basin. Their classification was based on hydrological, geographic, and ichthyological criteria, with the first aspect taken from **IDEAM** (2013); however, it excluded the low-altitude sectors (below 300 m a.s.l) of the Amazon and Orinoquia.

In another study, **Zapata *et al*.** (2021) surveyed 51 lakes in the páramo region of the Eastern Cordillera, between 3,600 and 4,400 m a.s.l. They found that the water chemistry of these lakes varied along two primary independent gradients: one related to the geology of the watershed bedrock and the other associated with the trophic state. The authors do not suggest a categorization system for these lakes. At smaller spatial scales, **Pinilla & Guillot** (1997) used the ratio of anions to cations (**Gibbs**, 1970) to regionalize a series of small rainwater reservoirs in the northern Altiplano Cundiboyacense, which averages an elevation of 2,600 m a.s.l. Their findings indicated that the ionic proportions effectively reflected the climatic variations and geological conditions of the lakes' locations, as well as the temporal changes they experienced.

Regarding the effects of human factors on the ecology of Colombian lakes and rivers, several notable studies are available. **Velez *et al.*** (2021) found that human activities, both before and after the arrival of Europeans, affected lakes, creating new conditions with different diatom species and reduced diversity. This shift indicates lakes have lost resilience. **Jiménez-Segura *et al*.** (2022) identified natural factors (landscape, rainfall, flooding, river connectivity) and human impacts (land cover change, pollution, dams, exotic species) affecting fish in the Magdalena River. **Salgado *et al.*** (2022) confirmed these impacts, citing climate change, damming, invasive species, deforestation, and pollution as threats to the river system. These human-caused modifications are essential elements to consider in the regionalization of aquatic ecosystems, as they greatly influence the natural conditions of water bodies.

A closer examination of studies on the regionalization and classification of Colombian aquatic ecosystems reveals a predominant focus on hydrological aspects, often overlooking the importance of living organisms. This paper provides basic guidelines for understanding the organization of lotic and lentic water bodies in specific areas of the country, emphasizing the interaction between key climatic, hydrological, and geological factors. It also highlights the essential physicochemical properties of water, as well as the presence

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of phycoperiphyton and macroinvertebrate assemblages in lentic and lotic freshwater ecosystems. The findings aim to enhance our comprehension of Colombia's continental aquatic environments, providing theoretical insights that will help develop effective future management strategies to promote sustainable use, conservation, and restoration of these invaluable ecosystems.

The data analyzed do not cover the entire territory of Colombia, as the Caribbean and Pacific plains were omitted, and areas like the Amazon were underrepresented. Therefore, these findings should be viewed as a preliminary understanding of the patterns that characterize Colombian limnology, particularly concerning certain mountain and lowland regions. The results focus on the Andean region's aquatic ecosystems and specific locations, both north (trans-Andean) and east of the Andes Mountains (cis-Andean). The trans-Andean area under study corresponded to the Sierra Nevada de Santa Marta (SNSM), while the cis-Andean regions analyzed included the Orinoco tropical savannas (comprising highland and flooded savannas), the Guiana Shield, and the alluvial plains of certain rivers influenced by the Amazon ecoregion. Future efforts are essential to complement and integrate the available information, providing a more comprehensive perspective, including territories not covered in the present study.

## Materials and methods

The data for this study were collected during the development of the Limnology and Continental Regional Ecology courses at the Department of Biology, Universidad Nacional de Colombia (UNC), Bogotá Campus, from 2005 to 2022. The supplementary data (**Table 1S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5279) includes details on geographic location, altitude, and physical and chemical variables. The regions visited included cis-Andean territories (east of the Andes Mountains), such as the floodplains of the Ariari, Guayavero, and Guaviare rivers with Amazonian influence, the Guiana Shield in the Vichada and Guaviare departments, the highland savannas ("altillanura") in Meta and Guaviare departments, and the flooded savannas in the Arauca and Casanare departments. The Andean areas covered the piedmont plains (Piedemonte Llanero, eastern slope of the Eastern Cordillera) in the Meta and Cundinamarca departments, the Eastern Cordillera across several departments (Boyacá, Cundinamarca, Tolima, and Caquetá), and both the Central and Western Cordilleras in Antioquia, Risaralda, Valle del Cauca, and Nariño, along with the inter-Andean lowlands of the Magdalena and Cauca rivers. The trans-Andean zone (north of the Andes) corresponds to the Sierra Nevada de Santa Marta (SNSM) in the Department of Magdalena (**Figure 1**). These areas were aligned with the geomorphological zoning proposed by **Ricaurte *et al.*** (2019). For a complete list of aquatic environments, including their respective coordinates, elevations, and physical and chemical variables, please refer to **Table 1S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5279, in the supplementary material.

Out of the 106 continental water bodies sampled, 26 were lentic ecosystems and 80 were lotic ecosystems (geographic coordinates are listed in **Table 1S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5279). In general, each ecosystem was visited once (climatic periods varied between dry and rainy seasons), and at least three replicas of the physicochemical and biological sampling were made in each water body. In most cases, and when feasible, the sampling sites were chosen in areas with minimal human disturbance, i.e., less habitat degradation and pollution from human sources, to ensure the most natural conditions possible. Geographical coordinates, elevation, water temperature, electrical conductivity, pH, dissolved oxygen, oxygen saturation percentage, and transparency were recorded *in situ*. Nutrients (phosphates, ammonium, nitrates) were analyzed in a spectrophotometer at the Laboratory of Ecology at UNC. Periphyton algae were collected by scraping known areas on rocky substrates. Macroinvertebrate collections were carried out using Surber nets (mesh size 0.5 mm) on rocky substrates, hand nets on macrophytes, and dredges and corers on sandy and muddy substrates. The recording of physical and chemical variables, as well as the collection, preservation, identification, and quantification of aquatic organisms (periphytic algae genera and freshwater invertebrates families) followed the classic methodologies outlined by **Hauer & Lamberti** (2007), **Elosegi & Sabater** (2009), **Pinilla** (2017), **IDEAM & INVEMAR** (2021), and **Roldán & Ramírez** (2022).

For the statistical analysis, the data were divided into two groups: lotic (flowing water) systems and lentic (still water) environments. Box plots were used to provide a descriptive overview of the physical and chemical variables. The abiotic and biological matrices were analyzed using statistical classification and ordination techniques after selecting the most representative taxa within each ecosystem type group based on the frequency of occurrence of the taxa and their coefficient of variation across samples. The classification analysis of

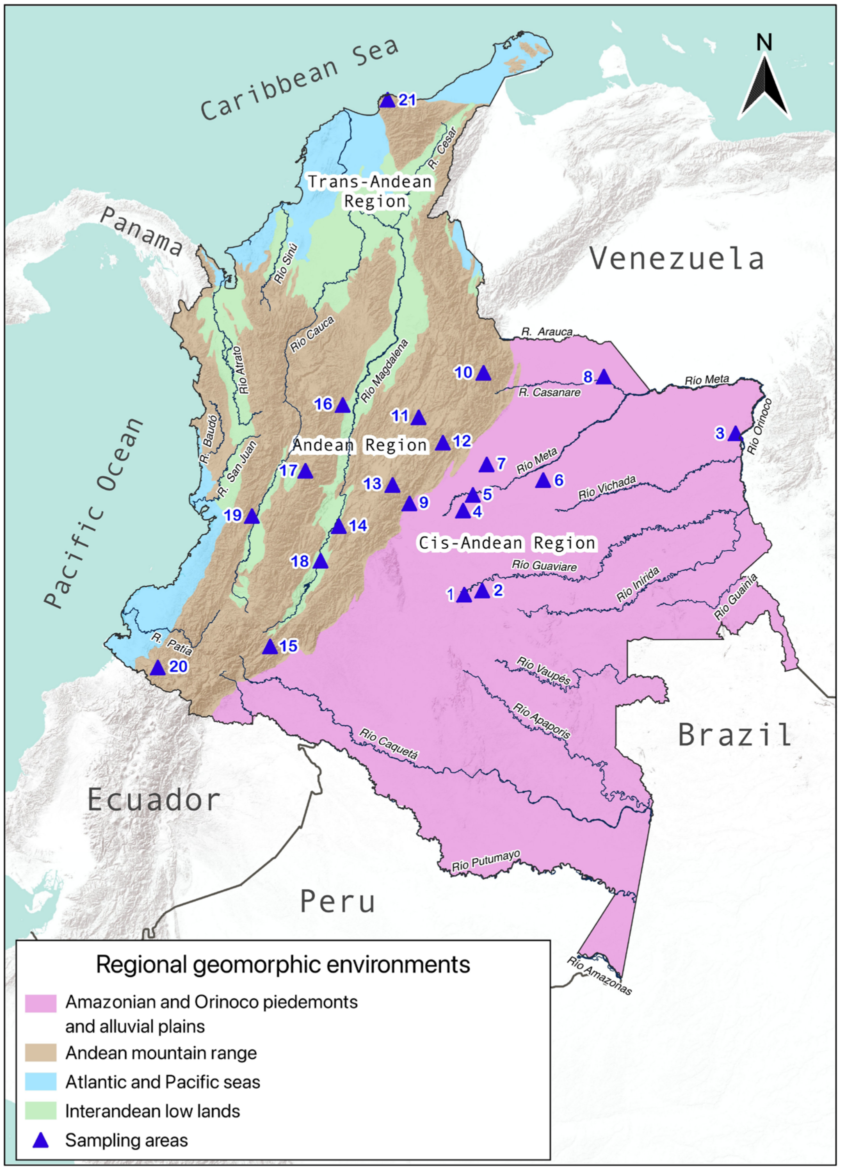


**Figure 1.** Location of the sampling areas for aquatic ecosystems in Colombia's Andean, cis-Andean, and trans-Andean regions. The 106 sampled ecosystems were distributed across the 21 sampling areas marked on the map. The location of each ecosystem in every sampling area, along with its geographical coordinates, is detailed in Table 1S. The regional geomorphic environments were obtained from **Ricaurte *et al.*** (2019).

the abiotic data was performed using the unweighted pair-group method with arithmetic averages (UPGMA). For the ordination of the environmental data, principal component analysis (PCA) and uniform manifold approximation and projection (UMAP) were employed; the latter is effective for identifying groups and gradients. The group structure of biological matrices was analyzed using linear discriminant analysis (LDA). This method effectively identifies relationships among the data groups. Non-metric multidimensional scaling (NMDS), which is suitable for data that do not satisfy the assumptions of normality or are measured on a discontinuous or arbitrary scale, was also employed to analyze the abiotic and biotic matrices simultaneously. All statistical analyses were done using PAST 4.15 software (**Hammer *et al.***, 2001), and the figures generated in PAST were edited with INKSCAPE 1.3 (**The Inkscape Project**, 2022).

## Results

***Periphytic algae distribution in the aquatic ecosystems***

Supplementary **Table 2S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5280, presents the composition of periphytic algae in all studied lentic systems. According to the UMAP analysis, the phycoperiphyton from the lakes under study was classified into three main groups (**Figure 2**). To aid in interpreting this figure and the following ones, lentic environments are indicated by a lake icon, whereas a river icon represents lotic systems. One group in the bottom right corner consisted of the lentic systems found in flooded and highland savannas. The other two groups, which included lakes from the Guiana Shield and floodplains influenced by the Amazon region, were positioned in the center of the ordination. In the Eastern Cordillera, high savanna, and inter-Andean lowlands, only one lentic system was sampled in each area, while no lakes were sampled in the Central Cordillera. Due to the much smaller sample size of lakes, the observed patterns should be interpreted with caution.

The NMDS analysis revealed associations between algal taxa and the physicochemical variables of specific lentic ecosystems (**Figure 2**). Transparency and oxygen saturation vectors primarily pointed toward lakes in the flooded savanna, where benthic microalgae genera such as *Lyngbya*, *Mougeotiopsis*, and *Planctonema* were found. The orthophosphate vector was oriented towards the inter-Andean lowland, which was associated with genera including *Navicula*, *Melosira*, *Gyrosigma*, *Fragilaria*, *Cyclotella*, *Eunotia*, *Surirella*, *Microcystis*, *Phormidium*, *Nostoc*, and *Haematococcus*, among others. The taxa *Gymnodinium*, *Xanthidium*, *Synecochococcus*, *Lepocinclis*, and *Mougeotia* were present in the lentic system of the Eastern Cordillera, characterized by higher electrical conductivity and ammonium. The remaining genera from the lentic ecosystems did not exhibit a distinct clustering pattern in relation to other specific variables or regions.

The complete composition of benthic algae in the fluvial systems analyzed is included in Supplementary **Table 3S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5281. The ordination of phycoperiphyton in the rivers (**Figure 2**) revealed notable trends in the organization of stream algal assemblages. According to the UMAP analysis, the fluvial systems across the three mountain ranges exhibited some degree of separation in their algal assemblages. The rivers of the Central Cordillera were positioned on the left side of the ordination (group A), while the ecosystems of the trans-Andean region and the Eastern and Western Cordilleras were intermixed. The lotic systems of the SNSM and the Eastern Cordillera (group B) tended to be located in the upper part of the graph. In contrast, the rivers of the Western Cordillera (group C) were arranged toward the lower region. Moreover, the cis-Andean rivers, including those from the Piedmont, Guiana Shield, flooded areas, and highland savannas, did not display a clustering pattern and were scattered throughout the ordination.

The results indicate that the river phycoperiphyton assemblages in the Andean and trans-Andean fluvial systems are likely characteristic of these regions, particularly those in the Central Cordillera. In contrast, the benthic algal assemblages in the cis-Andean regions appear to consist of widely distributed genera, including generalist and cosmopolitan taxa.

As observed in the UMAP analysis, the NMDS ordination also congregated the rivers of the Central Cordillera into one group (Group A). The SNSM and the Western and Eastern Cordilleras formed a mixed conglomerate in another group (Group B), which also included the lotic systems from the cis-Andean regions. The physicochemical variables influencing the phycoperiphyton in the Central Cordillera rivers were ammonium and pH. Additionally, electrical conductivity, which indicates the ionic richness of the water, was the key physical factor organizing the algal assemblages in many of the lotic environments of the Western and Eastern Cordilleras, as well as the SNSM.

The discriminant analysis (**Figure 2**) effectively separated the fluvial phycoperiphytic assemblages of several cis-Andean regions. This ordination created compact groups of rivers, such as the Guiana Shield, which was approached by a river from the Amazonian-influenced floodplains. The genera *Cosmarium* and *Oedogonium* were associated with these zones. The flooded savanna formed another dense conglomerate, characterized by

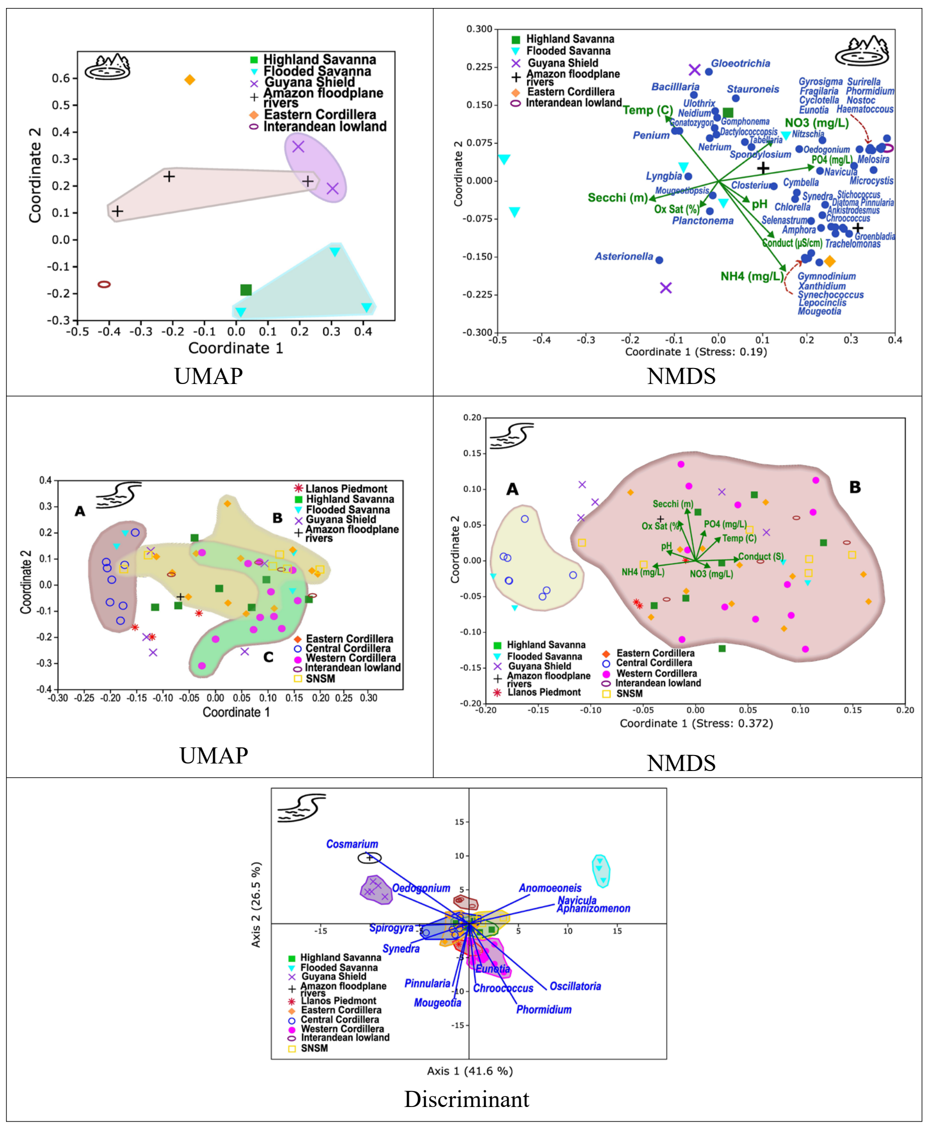


**Figure 2.** Ordination of periphytic algal assemblages in the studied lentic and lotic ecosystems. UMAP: Uniform manifold approximation and projection; NMDS: Non-metric multidimensional scaling. The icons representing lakes and rivers in each illustration were sourced from Flaticon.com.

*Anomoeoneis*, *Navicula*, and *Aphanizomenon*. In the cis-Andean regions, the highland savanna rivers overlapped with the lotic systems of other zones. The same occurred with the trans-Andean region (SNSM). In the case of the Andean river systems, only the streams of the inter-Andean lowlands formed a slightly isolated group. The other areas tended to overlap in the center of the ordination. However, the algal assemblages of the Western Cordillera rivers showed some degree of separation, with a predominance of taxa such as *Eunotia*, *Chroococcus*, *Phormidium*, and *Oscillatoria*.

### *Macroinvertebrates distribution in the aquatic ecosystems*

Supplementary **Table 4S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5282, shows the composition of aquatic invertebrates in the lentic water bodies visited. As illustrated in **Figure 3**, aquatic invertebrate assemblages in lentic environments exhibit distinct compositional patterns. The UMAP analysis showed a gradient that goes from the lakes in the Western Cordillera on the left to the water bodies in the flooded savanna and the Guiana Shield on the right. Between these two areas, the lakes affected by the Amazonian floodplains and the lentic ecosystems of the highland savanna are found.

Similarly, the NMDS ordination displayed a comparable gradient, where electric conductivity, pH, and nitrite levels primarily influenced the Andean lakes. In contrast, temperature, orthophosphates, and ammonium appeared to affect the macroinvertebrate assemblages within the flooded savanna, highland savanna, and Guiana areas. This pattern was corroborated by the discriminant analysis, which highlighted several families, including Diptera (Culicidae, Leptoceridae, and Chironomidae) and the family Corixidae (Heteroptera), that were particularly prominent in the Eastern Cordillera. Notably, the analysis did not identify determinant taxa for the cis-Andean lakes.

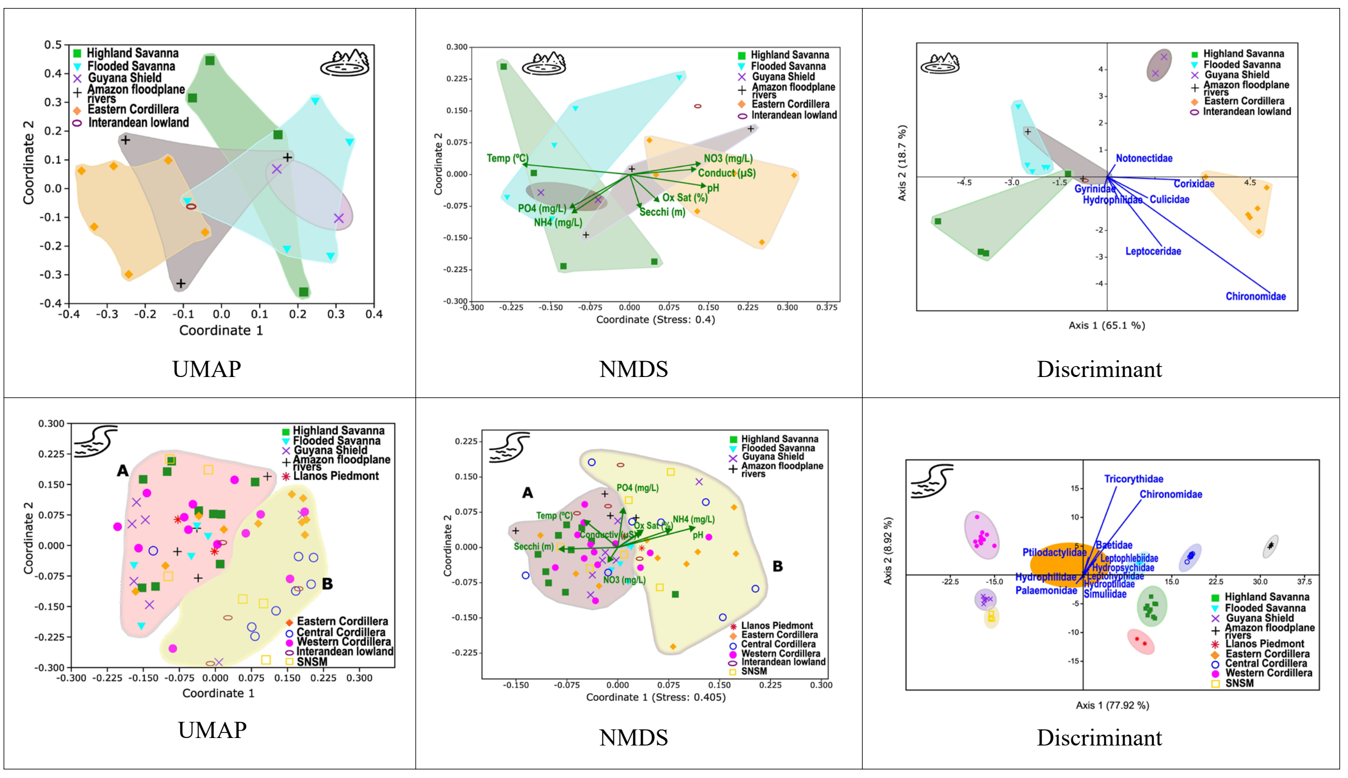


**Figure 3.** Ordination of aquatic invertebrate assemblages in the studied lentic and lotic ecosystems. UMAP: Uniform manifold approximation and projection; NMDS: Non-metric multidimensional scaling. The icons representing lakes and rivers in each illustration were obtained from Flaticon.com.

The complete list of macroinvertebrates from the studied rivers is shown in Supplementary **Table 5S,** https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5283. In the rivers, the organization patterns of macroinvertebrate assemblages were more diffuse. There was a high degree of mixing among the regions; however, the UMAP analysis revealed that the cis-Andean rivers, encompassing highland and flooded savannas, Guiana, and floodplains influenced by the Amazon region, formed a large cluster (Group A) in the upper left corner of **Figure 3**. This group also included rivers from the other areas, with most ecosystems of the Western Cordillera noticeably represented. In contrast, Group B brought together the fluvial systems of the Central Cordillera, which formed a loose conglomerate alongside several rivers from the other two mountain ranges and the SNSM.

The NMDS ordination confirmed the earlier grouping, showing that environmental factors, such as transparency and water temperature, were primarily linked to the lotic environments of the highland savanna and the Western Cordillera. The macroinvertebrate distribution and organization in the rivers of the Central Cordillera and other Andean Mountain areas appear to be related to pH and ammonium levels. Discriminant analysis clearly separated the different regions and highlighted the association of the Chironomidae (Diptera) and Tricorythidae (Ephemeroptera) families with the rivers of the three Andean Mountain ranges. Mayflies from the Baetidae family and beetles from the Ptilodactylidae family were also linked to Andean lotic systems. In contrast, Palaemonidae (Decapoda) and Hydrophilidae (Coleoptera) families tended to associate with the SNSM and the Guiana Shield rivers. A weaker association appears to exist between the families Leptophlebiidae (Ephemeroptera) and Hydropsychidae (Trichoptera) and the flooded savanna streams.

***General physical and chemical characteristics of water***

As mentioned, a total of 106 aquatic ecosystems were sampled, 26 of them being lentic systems, within an altitudinal range of 6 to 4,372 m a.s.l. Water temperature varied between 10 and 35.6ºC, while electrical conductivity ranged from 1.6 to 1,950 µS/cm. The pH levels oscillated from 3.6 to 8.8. Oxygen saturation reached a minimum of 5.6% and a maximum of 125%. Phosphates ranged from 0 (not detectable) to 2.75 mg/L, ammonium from 0 to 47.9 mg/L, and nitrates from 0 to 9 mg/L. **Table 1S** (in the supplementary material) presents the results of the physicochemical variables for water across all ecosystems visited.

The box plot analysis (**Figure 4**) reveals distinct differences among the regions. As with the biological ordination figures, a lake icon indicates lentic environments, while a river icon represents lotic systems. In the Eastern Cordillera, the water temperature in lentic environments was low, averaging 15ºC. In general, water in the Andean Cordilleras' lotic systems was typically cold, averaging 16ºC to 20ºC. The ecosystems with the highest oxygen saturation, averaging over 90%, were present in both lentic and lotic environments across all three Cordilleras. In lentic water bodies, the most mineralized systems (rich in inorganic ions) were found in the mountain ranges and inter-Andean lowlands, with an average conductivity of 75 to 80 µS/cm. Similarly, rivers in the foothills, inter-Andean lowlands, and the SNSM exhibited average conductivities ranging from 300 to 400 µS/cm.

The clearest lakes were located in the cis-Andean regions, which include the floodplains with Amazonian influence, Guiana, and highland savannas, displaying average vertical transparency (Secchi depth) ranging from 0.7 to 1 meter. The clearest rivers were found in Guiana and the Western Cordillera, with an average horizontal water transparency of about 4 meters. pH levels varied significantly across the regions; lakes in the Amazonian floodplains and highland savannas were particularly acidic, with a median pH of 5.4. In contrast, pH levels approached neutrality in Guiana and the Andean Cordilleras, while they were slightly alkaline in the inter-Andean lowlands, nearing a pH of 8. In river systems, pH levels were generally acidic in the cis-Andean regions and the Western Cordillera, averaging between 5.2 and 6.7. Conversely, rivers in other Andean areas and the trans-Andean zone had more basic pH values, ranging from 7.8 to 8.3.

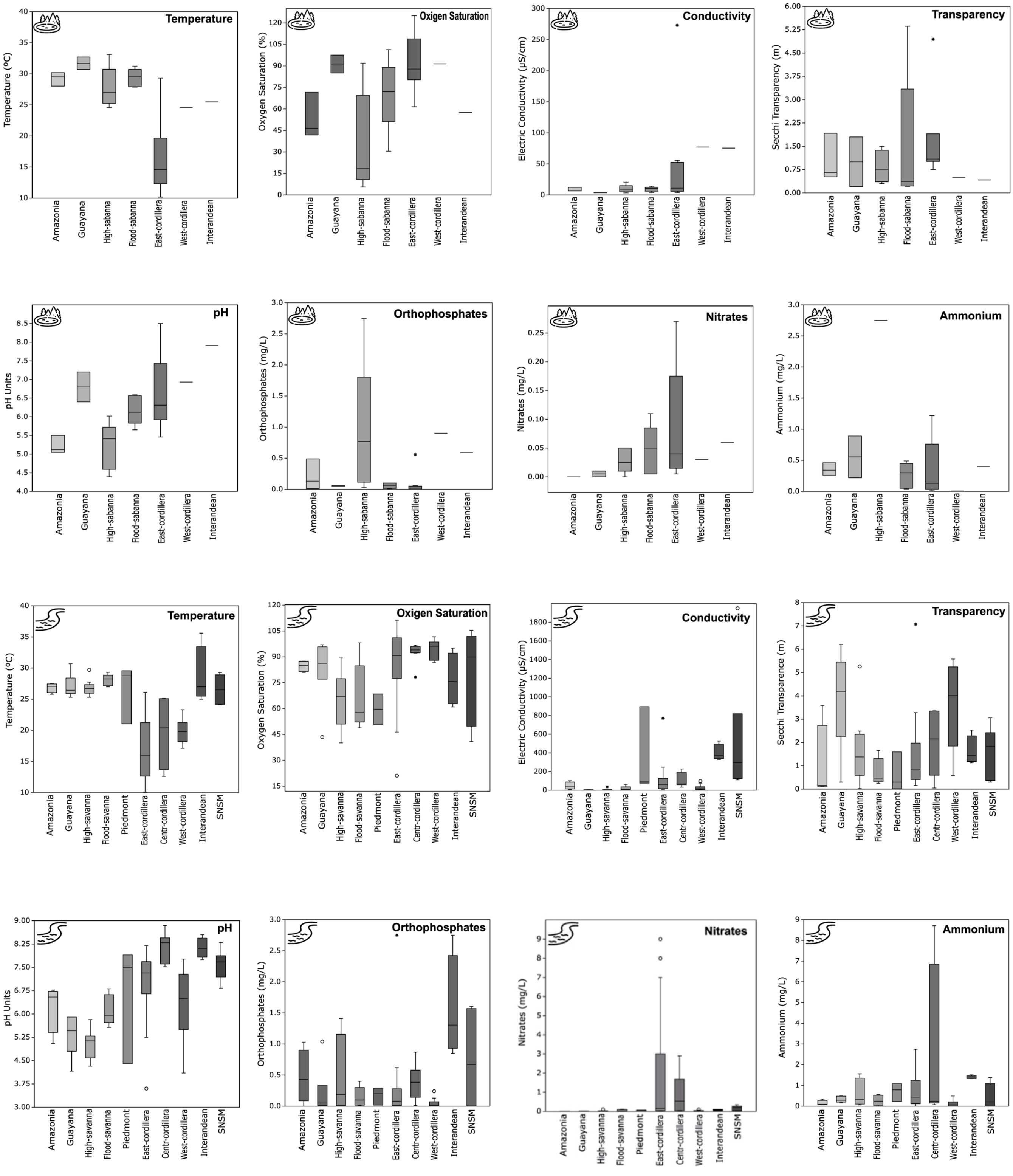


**Figure 4.** Box plots illustrating the physical and chemical variables of the lentic (lakes) and lotic (rivers) ecosystems under study. The icons representing lakes and rivers in each illustration were sourced from Flaticon.com.

The nutrient levels were highly variable, but a trend toward higher concentrations was observed in the Andean and trans-Andean fluvial systems, while the cis-Andean lentic ecosystems appear to have more ammonium (**Figure 4**).

***Aquatic ecosystems regional arrangement according to physical and chemical variables***

The results of the multivariate tests of lentic and lotic systems based on their physical and chemical water characteristics are presented in **Figure 5**. For lentic water bodies, the analyses revealed several groups linked to their geographic locations. Group A1 includes all the lakes in the Eastern Cordillera, while Group A2 contains lakes in the Amazon-influenced floodplain, those from the Guiana Shield, and lakes found in the Orinoco highlands savanna. Group B1 includes ecosystems situated in highland and flooded savannas, and, lastly, Groups B2 and B3 comprise a mix of Andean, Orinoco, and floodplain lakes influenced by the Amazonian region.

The UMAP analysis of the lentic environments revealed a clear separation by regions and confirmed some findings regarding the corresponding clusters. To the right of this ordination were the cis-Andean systems, while on the far left were the Eastern Cordillera lakes. Generally, a similar pattern appeared in the PCA ordination of these lentic systems. However, a more noticeable overlap was observed between the highland savanna lakes and those of the Amazon-influenced floodplain. Ammonium emerged as the variable determining the association of the lentic environments in these two cis-Andean zones. Other physicochemical variables contributing to the segregation of the regions included nitrites and conductivity for the Eastern Cordillera lakes, and orthophosphates for those in the Orinoco-flooded savanna. The highland savanna systems tended to be warmer, while the Andean lakes were cooler.

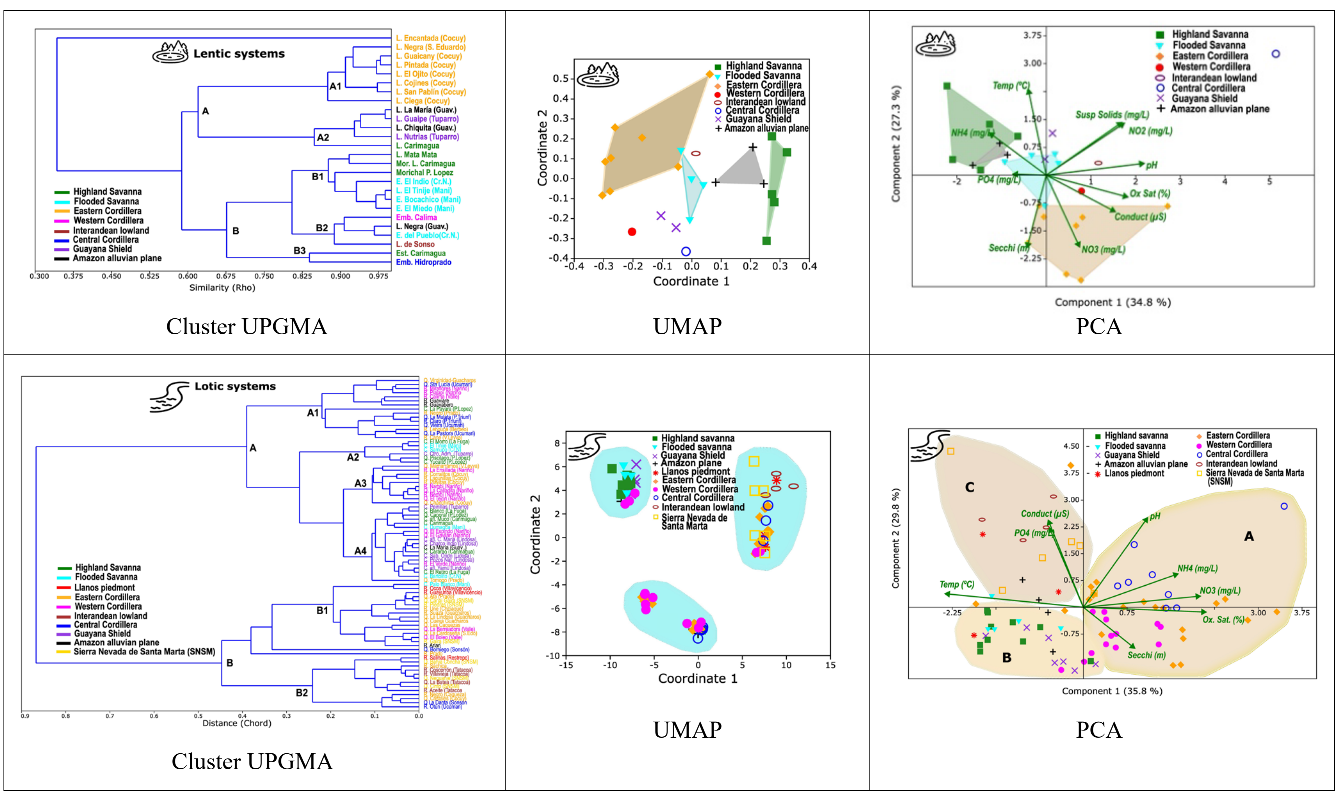


**Figure 5.** Analysis of classification and ordination of lentic and lotic ecosystems based on their physical and chemical variables. UPGMA: Unweighted pair-group average; UMAP: Uniform manifold approximation and projection; PCA: Principal component analysis. The icons representing lakes and rivers in each illustration were obtained from Flaticon.com.

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Regarding river ecosystems, the classification shown by the cluster (**Figure 5**) was less definitive. However, it is noteworthy that the composition of group B was primarily shaped by rivers from the Eastern and Central Cordilleras, the Piedmont, the SNSM, and the inter-Andean lowlands, specifically by Andean and trans-Andean streams. In contrast, group A represented a mixture of rivers from the Western Cordillera, incorporating systems from the other two mountain ranges but predominantly featuring all the lotic ecosystems of the Orinoquia (highland savanna, flooded savanna, Guiana shield) and the Amazon (river floodplains influenced by the Amazon region).

The UMAP ordination of the rivers revealed three distinct groups encompassing river ecosystems from various regions. The group in the top right included streams from the three mountain ranges, the inter-Andean lowlands, foothills, and the SNSM (Andean and trans-Andean lotic systems). The lower group exclusively comprised streams from the Andean Mountain ranges. The group in the top left represented the cis-Andean rivers, including those from highland and flooded savannas, the Guiana Shield, floodplains with Amazonian influence, and several Western Cordillera rivers. The PCA ordination confirmed the organization observed in the UMAP analysis. Group A of the fluvial PCA, consisting of rivers from three mountain ranges, showed a more basic pH, elevated nitrogen concentrations, and higher oxygen saturation levels. Group C, which comprised rivers from the Piedmont, inter-Andean lowlands, and SNSM, was associated with higher electrical conductivity and increased levels of orthophosphates. Group B included all cis-Andean environments, featuring several Andean rivers from the Western Cordillera. The river ecosystems in this group displayed a more acidic pH and lower nutrient levels, and, along with Group C, they had warmer water temperatures.

## Discussion

### *Biological arrangement*

Geology may significantly impact the composition and structure of aquatic life. **Macario-González *et al.*** (2022) demonstrated that geology has a direct influence on the limnological regionalization of Central America, as evidenced by freshwater ostracods. Similarly, **Benito *et al.*** (2018a) reported findings from a study of 195 lakes in the tropical Andes and surrounding lowlands showing a notable association between geographic clusters of lakes based on geo-climatic gradients and the diatom assemblages within those lakes. This geological influence on Colombian limnology is evident in the ordination analyses of periphytic and macroinvertebrate communities in fluvial systems, where a discernible trend was observed in the grouping of rivers across different regions resulting from these assemblages. The effect of geological factors on water chemistry, in turn, shapes the structure of aquatic communities. Specifically, the rivers of the Central Cordillera seem to be influenced by the geological features of this branch of the Andean Mountain range, affecting both periphytic algae and stream invertebrates. The volcanic rocks in this area contribute fewer ions to the streams, resulting in waters with lower mineralization levels (**Figure 4**). This condition, combined with the mountain range's intermediate geographic position, may influence the composition of aquatic organisms. Furthermore, factors such as migratory bird routes (see, for instance, **Coesel *et al.***, 1988), air mass circulation, and unintentional human transport could influence the aquatic assemblages in the Central Cordillera. These processes have not yet been extensively studied, and they constitute significant subjects for future investigation.

Interestingly, lakes appear to demonstrate regional differences more effectively than rivers. This is likely due to the stationary nature of this type of lentic system, which implies significantly increased water residence times compared to river systems. Under these conditions, the abiotic characteristics and specific traits of biological assemblages are more stable, allowing aquatic organisms to develop and thrive in a less variable environment. In this context, the arrangement of biological components in the lentic ecosystems of the Western and Eastern Cordilleras, particularly the phycoperiphyton, exhibits a high degree of similarity. As discussed, the geological composition of these two mountain ranges differs, as do their periods of formation, despite both having emerged after the Central Cordillera. It is essential to examine the underlying reasons behind the apparent similarity in the biotic composition of the aquatic systems in these two Andean branches. As mentioned, it would be interesting to determine whether macroclimatic events, such as the confluence of trade winds, or biogeographical events, such as bird migration routes, account for these limnological patterns. A similar phenomenon occurs with the limnological responses of the trans-Andean SNSM region, which seem to align more closely with those of the Andean Mountain ranges, likely because these regions share a similar mountainous environment.

***Abiotic setting***

The physical and chemical characteristics of water in continental aquatic ecosystems are substantially related to the region's geology (**Macario-González *et al.***, 2022) and climatology (**Galloway & Cowling**, 1978). The results of the present study indicate that rivers and lakes in the Andean Mountain ranges and those in the SNSM trans-Andean region generally exhibit a higher degree of water mineralization, as indicated by their higher electrical conductivity and nutrient concentrations. This increased ionic richness of water bodies in Colombia's mountainous areas is attributed to the erosion of the rocks that constitute the mountain range systems (**Restrepo & Kjerfve**, 2004). However, it is essential to consider that the geological composition of the three Colombian Andean branches varies. Thus, the ion contributions to the rivers are greater in the Eastern Cordillera, which is predominantly composed of sedimentary rocks.

In contrast, the ion input is lower in the Central Cordillera, mainly characterized by volcanic and metamorphic rocks (**Donato & Galvis**, 2008). The Western Cordillera consists of both sedimentary rocks and volcanic minerals of gabbroic and basaltic types. The SNSM essentially comprises plutonic rocks with sedimentary substrates and high-grade metamorphic rocks (**Gómez-Tapias *et al.***, 2020).

The aquatic environments of the cis-Andean regions (Orinoquia, Amazonia) rest on very old and demineralized geological substrates, such as the Precambrian granitic and metamorphic rocks of the Guiana Shield and Pleistocene sedimentary deposits characterized by a predominance of terraces and alluvium that cover a large area of these regions (**Gómez *et al.***, 2007). The soils derived from these geological substrates in the Orinoco plains of Colombia are primarily dystrophic, meaning they are very acidic, with low cation exchange, reduced carbon content, few ions (calcium, magnesium, potassium), high phosphorus fixation capacity, and high concentrations of aluminum (**Celis *et al.***, 2019). Under these conditions, the aquatic ecosystems of the Orinoco savannas, particularly those with running waters, exhibit lower pH and low amounts of dissolved inorganic elements (**Figure 4**). The rocks of the shield have undergone intense weathering processes, for which their contribution to the rivers is mainly limited to silica (**Edmond *et al.***, 1996). Additionally, the increased acidity of the cis-Andean surface waters is linked to the minimal contribution of carbonates, which reduces their neutralization capacity, as well as to the influx of humic acids resulting from the leaching of organic matter accumulated on the slopes of the rivers and within the substrate of aquatic environments (**Mora-Polanco *et al.***, 2008).

In terms of nutrients such as nitrogen and phosphorus, their levels are generally higher in the rivers of the Andean Mountain ranges and the inter-Andean valleys, where human activity is particularly intense, as more than 56% of the country's population resides in these areas (**Baena-Salazar *et al.***, 2020). The increased ammonium concentration in the lentic environments of the Orinoquia and the floodplains influenced by the Amazon may result from the mineralization of organic nitrogen accumulating in their soils and sediments, as has been suggested for the "morichales" (swamps of the palm *Mauritia flexuosa*) in the Orinoquia (**Chacón *et al.***, 2017). In this context, the lentic ecosystems in this region accumulate organic matter, which can decrease dissolved oxygen; however, the elevated water temperature may also speed up its biological breakdown.

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The geological characteristics of various regions, along with the organization of the physical and chemical variables identified through multivariate analysis, indicate that geology has played a crucial role in shaping the water geochemistry of Colombia's continental aquatic ecosystems. This conclusion aligns with findings from the examination of 51 páramo lakes in the Eastern Cordillera, where a significant environmental gradient affecting water chemistry was the bedrock geology of the watersheds (**Zapata *et al.***, 2021). The rivers, lakes, and other wetlands of the country can be classified, from a hydrochemical perspective, into mountain limnological systems (Andean and SNSM) and Orinoquia and Amazonia (cis-Andean) water bodies, consistent with the proposal by **Donato & Galvis** (2008) for river systems. However, classification and ordination analyses revealed that the rivers and lakes of the Western Cordillera were chemically more similar to cis-Andean aquatic environments than to those of the other two mountain range branches. This is likely due in part to the igneous and sedimentary nature of the Western Cordillera, which somewhat resembles the geological conditions of the Orinoquia. A detailed study of the mineralogy of the aquatic systems in both regions will be necessary to better understand this similarity.

Remarkably, altitude does not seem to significantly influence the regional grouping of Colombian aquatic ecosystems based on water quality parameters. While it is true that freshwater ecosystems at higher elevations are colder and likely contain fewer ions and nutrients due to their smaller basins, the differences noted here were eclipsed by more dominant factors, such as geology and precipitation.

Although this research may not have captured the full range of abiotic and biotic patterns due to incomplete spatial coverage and limited taxonomic detail, it nonetheless successfully identified several key patterns that provide a basic framework for understanding the factors influencing the limnological characteristics of Colombia's continental aquatic ecosystems. The primary findings can be summarized as follows:

1) The assemblages of phycoperiphyton and macroinvertebrates demonstrated a robust correlation with environmental variables, reflecting the ecological conditions of the aquatic ecosystems.

2) The analysis of physicochemical variables effectively categorized various aquatic systems according to their specific regions, highlighting distinct regional differences.

3) Lentic systems displayed more significant regional differentiation than lotic systems, suggesting that standing water environments might react more to regional ecological influences.

4) Interestingly, several similarities in physicochemical parameters and biological composition were observed among the Eastern and Western Cordilleras rivers and between the fluvial systems of the Western Cordillera and the cis-Andean regions. This suggests that there may be shared influences or environmental conditions affecting these diverse regions, although the causes of their similarity remain unclear.

These findings enhance our understanding of Colombia's continental aquatic environments and establish a basis for future research exploring these important ecological patterns.

***Synthesis: the underlying causes of limnological patterns in Colombia***

I will conclude this analysis with a summary, synthesis, and speculation about the underlying environmental drivers that ultimately shape the limnological patterns in Colombia. To achieve this, I will examine geological, climatic, and anthropogenic aspects to establish a framework of key state factors that define the characteristics of the country's freshwater ecosystems. This approach resembles the state factors established by **Chapin *et al.*** (2011) as controls governing the structuring of terrestrial ecosystems, which include climate, parent material (rocks that originate the soils), topography, potential biota, and human activities. In the case of Colombian freshwater ecosystems, these state factors have been expanded and categorized into first, second, and third-order factors, establishing a sequence of importance based on the magnitude and scalar influence of these external factors that modify the internal processes of aquatic environments.

**Primary factors. Lewis**'s article (1987) emphasizes that the equatorial location of countries like Colombia, with high annual solar irradiance, low temporal variability, and generally low wind speeds due to a weak Coriolis force, significantly influences the temperature and productivity of tropical lakes, resulting in warmer, more stable waters compared to temperate or subtropical regions. This planetary framework is relevant to Colombian freshwater ecosystems, and it is also essential to consider local geological and climatic factors. A study by **Benito *et al.*** (2018b) demonstrates that diatom assemblages in the Andean Cordillera are modeled by regional geoclimatic factors, contributing to homogenization within ecoregions. The geological and climate characteristics of the Colombian regions I examined are described below.

*Geology.* The geological features of the Andes branches in Colombia significantly influence the hydrochemistry of their aquatic systems. The Central, Western, and Eastern Cordilleras have distinct geological origins and rock types, which influence ion contributions to freshwater ecosystems. The Western Cordillera is primarily composed of sedimentary and igneous rocks; the Central Cordillera is characterized by low-grade metamorphic rocks intruded by plutons, and the Eastern Cordillera features high-grade metamorphic rocks and sedimentary sequences (**Irving**, 1975). The Eastern Cordillera contributes the most particles to water bodies, while the Central Cordillera's volcanic rocks are less affected by rainfall leaching. The Sierra Nevada de Santa Marta (SNSM) has limited sedimentary areas and consists of Jurassic plutons and metamorphic rocks (**Colmenares *et al.***, 2018), resulting in a negligible influence on river hydrochemistry. The basement of Orinoquia and Amazonia comprises various metamorphic rocks, along with granitic intrusions and sedimentary layers, spanning from the Neoproterozoic to the Cenozoic eras (**Dueñas-Jiménez & Montalvo-Jónsson**, 2020). High rainfall in the Guiana Shield erodes the strata, leading to poorer rock outcrops. Additionally, rivers from the Andes are richer in ions and sediments compared to the less mineralized streams of the Amazonian region (**Sioli**, 1984).

*Rainfall*. Colombia experiences two main types of precipitation distribution: unimodal and bimodal (**Jaramillo-Robledo & Chaves-Córdoba**, 2000). The trans-Andean and cis-Andean regions, alongside the Llanos Piedmont, exhibit unimodal rainfall from April to November, followed by a dry season. Conversely, bimodal patterns occur in the Andean mountains, resulting from the movement of the Intertropical Convergence Zone (ITCZ). Precipitation levels vary significantly across regions, with the trans-Andean region receiving about 500 mm annually, while the Llanos Piedmont sees over 5000 mm, and cis-Andean areas receive between 3000 and 4000 mm (**Jaramillo-Robledo & Chaves-Córdoba**, 2000). In the Andean mountains, rainfall decreases from north to south and increases with elevation up to 1300-1500 m a.s.l. Precipitation and evapotranspiration are generally balanced in the Andean regions (**IDEAM**, 2023), which affects local water chemistry. In these mountainous areas, where rainfall and evaporation are in equilibrium, ions mainly come from rock weathering (**Gibbs**, 1970).

**Secondary factors.** Other local factors influence the structure and function of water bodies at a secondary level. These factors are delineated in broad terms below.

*Geomorphology.* Colombia's relief is shaped by geological structures, impacting continental aquatic ecosystems (**Ricaurte *et al.***, 2019). The main geomorphological environments are: a) the Andes Mountains; b) the inter-Andean lowlands and the Depresion Momposina; c) the Amazonian-Llanos foothills, and d) the coastal and marine regions. Flat terrains support lentic systems, such as lakes and wetlands, while mountainous areas promote dynamic lotic systems. Elevation gradients influence temperature, dissolved oxygen levels, and the distribution of riparian vegetation.

*Hydrology.* Surface water availability in Colombia varies significantly due to precipitation and geomorphology. The Orinoquia region has the highest runoff (19,230 m³/s, 27% of the national total), while the Caribbean region contributes only 4,881 m³/s (8%) and the Andean region 9,500 m³/s (13%) (**Sánchez *et al.***, 2010). Hydrological connectivity plays a central role in structuring communities and varies significantly at headwaters compared

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to main channels (**Brown *et al.***, 2011). Current speed (**Choy *et al.***, 2023) and water level changes (**Evtimova & Donohue**, 2016) not only affect habitat conditions but also impact the composition and function of aquatic organisms. Increased runoff affects water chemistry, leading to greater dilution, soil leaching, and ecological disturbances. Aquatic communities adapt their life cycles and structures to these changes.

*Soils*. Edaphic factors driven by geomorphology and climate shape vegetation types in a region. In mountainous areas like the Andes, andisols thrive in humid climates, supporting a diverse range of vegetation (**Malagón-Castro,** 2003). Oxisols dominate highland savannas, while entisols and inceptisols sustain biomass in flooded savannas. The Guiana Shield is primarily characterized by oxisols and ultisols, which significantly influence the types of vegetation that grow in this region. Soil composition influences riparian vegetation and, indirectly, the allochthonous inputs that reach aquatic ecosystems.

*Riparian vegetation.* The impact of riparian vegetation on aquatic ecosystems is underexplored. Some studies (**Chará *et al.*,** 2007; **Lozano-Peña *et al.*,** 2019; **Salazar-Castellanos *et al.*,** 2020) suggest that forested areas contribute organic matter, which reduces oxygen levels and supports detritivorous macroinvertebrates. Forests limit the infiltration of light, thereby influencing the density of periphytic algae, whereas open areas substantially modify the habitat conditions for aquatic communities. These modifications are further regulated by factors such as elevation, human activity, and climate change.

**Tertiary factors.** A third category of factors influences the primary and secondary determinants mentioned above, altering the limnology of freshwater ecosystems locally. These drivers are briefly outlined below.

*Human activities.* **Donato-Rondón** (2022) highlights deforestation, chemical contamination, eutrophication, pesticide accumulation, and overfishing as key threats to Colombian freshwater ecosystems. Deforestation, primarily concentrated in the Andean regions (**Calderón & Benavidez**, 2022), disrupts hydrological patterns, increases extreme flows, and leads to biodiversity loss. Agrochemical pollution, particularly in the Llanos foothills and Orinoquia savannas, leads to pesticide accumulation, fish mortality, and eutrophication. Other activities, such as gold mining, hydrocarbon extraction, and wetland desiccation, also harm freshwater systems (**Donato-Rondón**, 2022).

*Regional determinants.* Local factors and features influence the structure and function of the aquatic environment, leading to varying biological diversity and endemism in different areas (**González-Orozco**, 2021). Historical and evolutionary processes influence metacommunities, resulting in diverse organizational patterns among aquatic organisms across ecoregions (**González-Trujillo *et al.***, 2019). Additionally, local climate variations and disturbance regimes shape specific limnological conditions in the freshwater ecosystems.

### *A general framework for limnological patterns in Colombia*

Considering the descriptions of the environmental features outlined above, **Figure 6** presents a model of the first, second, and third-order factors that influence Colombia's continental aquatic ecosystems. The model serves as a general framework to be tailored to each region's specific geological, climatic, and human activity characteristics. For example, in the Eastern Mountain range, aquatic ecosystems may exhibit moderate to high mineralization due to the presence of sedimentary rocks, with precipitation balancing evapotranspiration, thereby preventing excessive leaching. These areas are likely nutrient-rich due to significant human settlement and experience fluctuations in flow from bimodal rainfall, which maintains medium to low temperatures due to elevation and limited riparian vegetation resulting from agricultural activities. Given the physical and chemical conditions described, it can be expected that the water bodies of the Eastern Cordillera exhibit moderate to high primary productivity, that the lakes mix at least once during one of the periods of highest precipitation, and that both the lentic and lotic systems progress toward a state of increased eutrophication. Concerning benthic algae, the establishment of diverse assemblages is anticipated, with representatives

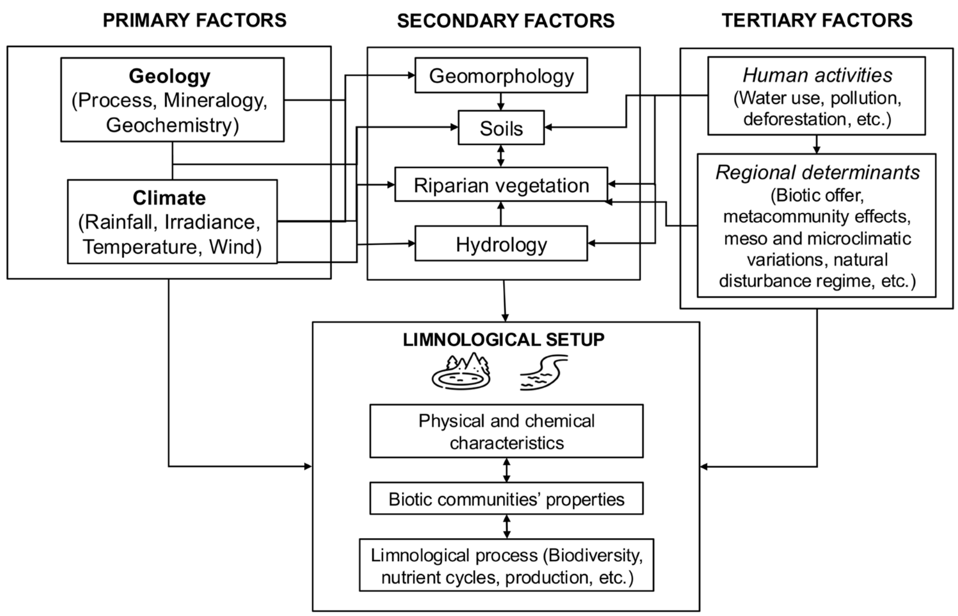


**Figure 6.** A framework illustrating the first, second, and third-order factors influencing the limnological features of Colombia's continental aquatic ecosystems.

from classes such as Dinophyceae, Xanthophyceae, Euglenophyceae, Zygnemataceae, Bacillariophyceae, and Cyanobacteria. Some macroinvertebrates likely to inhabit the aquatic systems of the Eastern Cordillera include Coleopterans (Dytiscidae, Gyrinidae, Scirtidae, Hydrophilidae), Diptera (Culicidae, Leptoceridae, Chironomidae), and Heteropterans (Corixidae, Naucoridae).

Within the scope of the various methodologies proposed for the classification of Colombian aquatic systems, **Table 1** offers a comprehensive summary of the different classifications suggested by authors such as **Donato** (1998), **Naranjo *et al.*** (1999), **Donato & Gálvis** (2008), **IDEAM** (2013), **Ricaurte *et al.*** (2019), **González-Cuéllar & Obregón-Neira** (2013), **Plata-Días** (2016), **Mesa *et al.*** (2016), and **Zapata *et al.*** (2021). Each classification provides a unique approach to addressing this challenge, yet none is entirely exhaustive or inclusive. Some models strive for greater comprehensiveness but do not encompass the entire Colombian territory, as is the case with the model presented herein. Nevertheless, the significance of the scheme introduced here lies in its attempt to integrate the individual factors considered by the aforementioned authors, namely hydrology, geology, geomorphology, and biological communities, into a multivariate framework that elucidates the interactions and combinations of diverse physical, chemical, biological, and anthropogenic elements to generate a basic general model. Undoubtedly, this constitutes an initial approximation using an integrative approach, which will necessitate further research and data collection to enhance prediction accuracy at more localized spatial scales. Consequently, this paper aims to complement the previously proposed limnological classifications for Colombia, addressing this objective more comprehensively while explicitly acknowledging the aforementioned limitations.

### *Future perspectives*

The general framework and regional limnological patterns presented here are limited both spatially and taxonomically. For greater generalizability and robustness, it is necessary to include lesser-known limnological regions (i.e., Amazon piedmont, Amazonian plain, biogeographical Chocó, Caribbean plain, Pacific plain) and a larger number of biological groups. Conducting analyses with a broad taxonomic scope, including amphibians, reptiles,

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**Table 1.** Comparison of Colombia's different classification and regionalization systems for its aquatic ecosystems.

| Authors by year of publication | Type of water bodies included | Main factors of the classification | Secondary factors of the classification | Geographical scope | Integrity* |
|---|---|---|---|---|---|
| **Donato** (1998) | All freshwater environments | Altitudinal position | Climate, human activity | All the country | Low |
| **Naranjo *et al.*** (1999) | All freshwater and marine environments | Hydrology | Geomorphological, physicochemical, and biological variables | All the country | Medium |
| **Donato & Gálvis** (2008) | Rivers | Altitudinal position | Physicochemical variables, benthic microalgae | All the country | Medium |
| **IDEAM** (2013) | Hydrographic basins | Regional macro-basins | Subdivisions of watersheds, hydrogeological provinces | All the country | Low |
| **Ricaurte *et al.*** (2019) | All freshwater and marine environments | Geomorphology | Climate, hydrology | All the country | Low |
| **González-Cuéllar & Obregón-Neira** (2013) | Rivers | Hydrological variables | Altitudinal position | Magdalena-Cauca macro-basin | Low |
| **Plata-Días** (2016) | Rivers | Hydrogeomorphic variables | Physicochemical variables, benthic diatoms | Orinoquia, Caguán, Magdalena, and Catatumbo basins | High |
| **Mesa *et al.*** (2016) | Rivers | IDEAM's hydrographic zoning (2013) | Fish distribution and composition | Trans-Andean region and part of the Orinoquia and Amazon basins | Medium |
| **Zapata *et al.*** (2021) | Páramo lakes | Altitude | Morphometrical and physicochemical variables | Central Eastern Cordillera | Low |
| This work | Rivers and lakes | Geology, climate | Geomorphology, hydrology physicochemical variables, benthic algae and macroinvertebrate assembles | Andes and part of cis- and trans-Andean regions | High |

*Integrity, understood as the degree of interconnectedness among abiotic and biotic elements of the classification, considering their multiple interactions.

birds, mammals, and macrophytes, will help delineate larger patterns and improve our understanding of general limnological configurations (**Mueller *et al.***, 2013). Additionally, higher-resolution analyses at the species level and advances in environmental DNA identification methods (**Chen *et al.***, 2025) can help clarify the distribution and organization of taxa in Colombian aquatic ecosystems, making them suitable as indicator organisms.

It is hypothesized that aquatic beetles could serve as essential indicators in Colombian Andean lentic ecosystems, similar to findings by **Martínez-Román *et al.*** (2023) in the Argentine Andes; therefore, further analysis might clarify their role in freshwater ecosystems. Additionally, the similarities observed between phycoperiphyton and macroinvertebrate assemblages across cis-Andean rivers and the Western Cordillera present opportunities for further investigation. Paleolimnological studies (**Cuenca-Cambronero *et al.***, 2022), bird migration route research (**Viana *et al.***, 2016), biogeographical processes integrating historical, geological, and ecological factors (**Leroy *et al.***, 2018), regional metacommunity structure analysis (**He *et al.***, 2023), and phylogeographic techniques revealing historical influences like sea-level changes and geological events, all of which have shaped current genetic and biogeographic patterns (**Kochanova *et al.***, 2021), can aid in understanding these limnological aspects. These diverse approaches could also help identify cryptic diversity, define species complexes, and highlight patterns of potential conservation hotspots.

From other perspectives, examining the influence of wind speed and direction on the dispersal of aquatic organisms (**Horváth *et al.***, 2016) and analyzing the structural and functional connectivity among aquatic habitats (**Mushet *et al.***, 2019) may enhance understanding of the specific distribution patterns of aquatic biota. This approach can elucidate how organisms migrate between interconnected environments, thereby affecting their capacity to locate resources, reproduce, evade stressors, and influence community dynamics. In the future, it would be beneficial to develop maps showing the main groups of organisms by limnological region, which would help to understand the distribution patterns of aquatic biota more easily. Nutrient concentrations measured in continental freshwater ecosystems were either outside detection limits or very high, highlighting the need for greater sensitivity and consistency in nutrient analysis in Colombian water analysis laboratories, which requires further investigation to improve their sensitivity and standardization, similar to the approach proposed for sub-Saharan Africa by **Peletz *et al.*** (2018).

Ultimately, it would be necessary and advantageous to implement a predictive classification modeling system grounded in landscape limnology principles, which is fundamental for defining a limited set of ecosystem classes (**Soranno *et al.***, 2010). This could enable effective customization of management actions. Such categorization system is basic for the adaptive management of complex freshwater ecosystems and for balancing the various demands of ecosystem services under shifting environmental conditions.

## Ethics statement

The author declares that he agrees with this publication and has made conceptual, methodological, and analytical contributions that justify his authorship; that there is no conflict of interest of any kind, and that he has complied with all relevant ethical and legal requirements and procedures.

## Acknowledgments

I extend my heartfelt gratitude to all the students in the Limnology and Continental Regional Ecology courses at the Department of Biology of the National University of Colombia from 2005 to 2022. I am also sincerely grateful for the support and collaboration of my esteemed colleagues in the Department of Biology. I would also like to acknowledge the National University of Colombia for creating an environment that enabled me to pursue my academic and research endeavors.  I want to thank the anonymous reviewers for their significant contributions, which greatly enhanced the final version of this work.

## Supplementary material

Table 1S: https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5279

Table 2S : https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5280

Table 3S : https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5281

Table 4S : https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5282

Table 5S : https://www.raccefyn.co/index.php/raccefyn/article/view/3181/5283

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