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Challenges ahead for freshwater ecosystems in the Colombian Guiana Shield

Jhon Donato-Rondón[1]*, Juan David González-Trujillo[1], and Sergi Sabater[2,3]

[1] Universidad Nacional de Colombia, Sede Bogotá, Facultad de Ciencias, Departamento de Biología, Av (Cra) 30 No.45-03, Bogotá, 111321, Colombia.
[2] Catalan Institute for Water Research (ICRA-CERCA) Girona, Spain.
[3] Institut d'Ecologia Aquàtica (IEA), Universitat de Girona, Girona, Spain.

* Corresponding author: jcdonator@unal.edu.co

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ABSTRACT

Challenges ahead for freshwater ecosystems in the Colombian Guiana Shield.

The Guiana Shield contains multiple freshwater ecosystems that support high species diversity. This ecoregion represents a stable landscape resulting from infrequent large-scale natural disturbances (i.e., Andean orogeny, marine incursions), favoring biological adaptations and endemisms (e.g., loricariids). However, disturbing human activities in nearby areas is a warning for the future of the Colombian Guiana Shield, and this requires assembling evidence that might contribute to the conservation of the region's biodiversity. We summarize information already available for the region and use field observations and laboratory studies to characterize the region's environmental variables and freshwater biodiversity. The Colombian part of the Guiana Shield is one of the best preserved because of low human density and reduced impacts. Although still relatively pristine, this region is already experiencing high growth in farming, contributing to forest loss. Other threats include infrastructure development, small-scale mining, livestock and water contamination. We developed a typology of river systems in the Colombian Guaina Shield that might be useful for conservation. There is ample evidence of the uniqueness of freshwater biodiversity and the threats affecting its conservation in the region. We present a conceptual relationship between the drivers, pressures and impacts currently existing in the Colombian Guiana Shield. Growing environmental impacts and future transformations require preserving these systems as a necessary step to expand our knowledge of their diversity and functions. To minimize current or future impacts requires involving local communities as well as the implementation of more strict policies, leading to a respectful development. Our recommendations could be useful for other areas in the Guiana Shield.

KEY WORDS: freshwater, Guiana, local development, typology, Colombia

RESUMEN

Desafíos futuros para los ecosistemas de agua dulce en el Escudo Guayanés Colombiano.

El Escudo Guayanés contiene múltiples ecosistemas de agua dulce que sustentan una alta diversidad de especies. Esta ecorregión presenta un paisaje estable gracias a perturbaciones naturales poco frecuentes a gran escala (p. ej., orogenia andina e incursiones marinas), lo que ha favorecido adaptaciones biológicas y endemismos (p. ej., loricáridos). Sin embargo, la existencia de actividades antagónicas en áreas cercanas constituye una advertencia para el futuro del Escudo Guayanés Colombiano, lo que requiere recopilar evidencias que puedan contribuir a la conservación de la biodiversidad de la región. Resumimos la información ya disponible para la región y utilizamos observaciones de campo *y estudios de laboratorio para caracterizar las variables ambientales y la biodiversidad de agua dulce de la región. La parte colombiana del Escudo Guayanés es una de las mejor conservadas de esta ecorregión, debido a la baja densidad humana y a los reducidos impactos. Aunque aún se encuentra relativamente prístina, esta región ya experimenta un alto crecimiento de la agricultura, lo que contribuye a la pérdida de bosques. Otras amenazas incluyen el desarrollo de infraestructura, la minería a pequeña escala, la ganadería y la contaminación del agua. Desarrollamos una tipología de los sistemas fluviales en el Escudo Guayanés Colombiano que podría ser útil para la conservación. Existe amplia evidencia de la singularidad de la biodiversidad de agua dulce y las amenazas que afectan su conservación en la región. Presentamos una relación conceptual entre los factores, las presiones y los impactos actuales en el Escudo Guayanés Colombiano. Los crecientes impactos ambientales y las transformaciones futuras exigen la preservación de estos sistemas como paso necesario para ampliar nuestro conocimiento sobre su diversidad y funciones. Minimizar el impacto actual o futuro requiere necesariamente la participación de las comunidades locales, así como la implementación de políticas más estrictas que conduzcan a un desarrollo respetuoso. Nuestras recomendaciones podrían ser aplicables a otras áreas del Escudo Guayanés.*

PALABRAS CLAVE: *agua dulce, Guayana, desarrollo local, tipología, Colombia.*

INTRODUCTION

The Guiana Shield contains between 10% - 15% of the world's freshwater resources, and it is the largest expanse of tropical vegetation for pre-Cambrian areas (34%; Bovolo, 2018; de Souza, 2020). The region includes diverse ecosystems, such as savannas and lowland and mountain forests, that host thousands of tributaries flowing into the Orinoco and Amazon basins that give rise to a multitude of freshwater habitats. The freshwater ecosystems of the Guiana Shield sustain extensive biodiversity because of their unique geological, climatic, and ecological history (Ribas & Aleixo, 2019). In particular, changes in river courses and forest fragmentation led to prolonged periods of isolation (e.g., "ancestral islands" Gibbs & Barron, 1993; Rocha & Kaefer, 2019) triggering high species diversification and endemism (Huber, 1994; Mayr & Phelps, 1967; Naka, 2011; Buainain et al., 2020).

Colombia holds some of the best-preserved aquatic and terrestrial ecosystems of the South American Guiana Shield. However, as much as in regions elsewhere, the Colombian Guiana Shield is undergoing accelerated transformation associated with human activities. Logging (Ahmed & Ewers, 2012; Bovolo et al., 2018), mining (Hammond et al., 2007), infrastructure development (Armenteras et al., 2009), and water contamination (Suarez et al., 2020) are some of the drivers of ecosystem loss and degradation. Still, amidst these human interventions, the Colombian part of the Guiana Shield stands out as one of the best-preserved areas, thanks to the low intensity of human occupation and the minimal presence of anthropogenic disturbance. The historically light human occupation of the area, as in other parts of the Guiana Shield, is linked to poor soil fertility—among the lowest in the tropics (Hammond, 2005b)—and to the challenges of fluvial transport posed by natural obstacles such as rapids and waterfalls scattered throughout many river systems (Hammond, 2005a). While the Colombian part may be the best preserved, it also has ongoing problems that threaten its current state of conservation. For example, the rugged terrain and remote location have facilitated the proliferation of illegal coca plantations that once were at the center of the region's economy and perpetuated a cycle of violence (Unigarro-C, 2020). Further, extensive areas of gallery forests and "canaguchales" (swampy forested areas dominated by the canaguche palm *Mauritia flexuosa*) mostly located at the occidental part of the craton, have been transformed to oil palm tree plantations (Romero-Ruiz et al., 2012) and livestock (Rondón- Villabona, 2023), irreversibly transforming some of the most valuable wetlands.

Overall, current human activities are expanding and intensifying in the Guiana Massif wedge on the Colombian side of the Shield, and these activities threaten the conservation and functions of freshwater aquatic ecosystems. Here we describe the values of biodiversity associated with the freshwater ecosystems in the Colombian

Guiana Shield; and we propose a typification according to their hydrological and biogeochemical characteristics that could be a basis for freshwater ecosystem conservation. Finally, we discuss the predictable threats that could jeopardize the conservation status of the Guiana Shield, based on those already affecting large areas of the Shield. We provide recommendations that might preserve the freshwater ecosystems while supporting local communities in the area.

WORLD DISTRIBUTION AND DIVERSITY OF THE CRATONS AND THE GUIANA SHIELD SYSTEM

The Guiana Shield is a craton located in northern South America. Cratons are thick, ancient, and tectonically stable sections of the Earth's crust and upper mantle. These areas have usually survived continental collisions, mountain-building events, and rifting for over a billion years and correspond to extensive areas of the continental lithosphere that once were the first solid massif, and which remained consistent since the Precambrian. Owing to their beauty and singularity, these systems have attracted the attention of writers, geologists, biologists, biogeographers, and ecologists. These formations are scattered throughout several regions of our planet (Kroonenberg & de Roever, 2010). They occur on all continents. Some of the largest cratons are these: the Australian, Indian, Angaran, Baltic, Arabia-Nubian, Antarctic, North Chinese, West African and Kalaharian. The Canadian (or Laurentian) is the oldest craton, characterized by ancient Paleoproterozoic to Neoarchean metamorphic and igneous rocks (Chapman & Putnam, 1984). In South America, the cratons from Guyana, Brazil, and Patagonia comprise the Archean and Proterozoic islands of this continent. The the Guyana and Brazilian Shields as constituents of the ancient continent of Gondwana (Kroonenberg & de Roever, 2010) are parts of the immense Amazon Craton, composed of crystalline igneous and metamorphic rocks from the Proterozoic (Hammond et al., 2007; Potapov et al., 2017).

The Guiana Shield covers approximately 13% of Northeastern South America (Hammond, 2005a), including territories in northern Brazil, southern Venezuela, eastern Colombia, Guyana, Suriname, and French Guiana. It accounts for approximately 26% of the Amazon's surface area

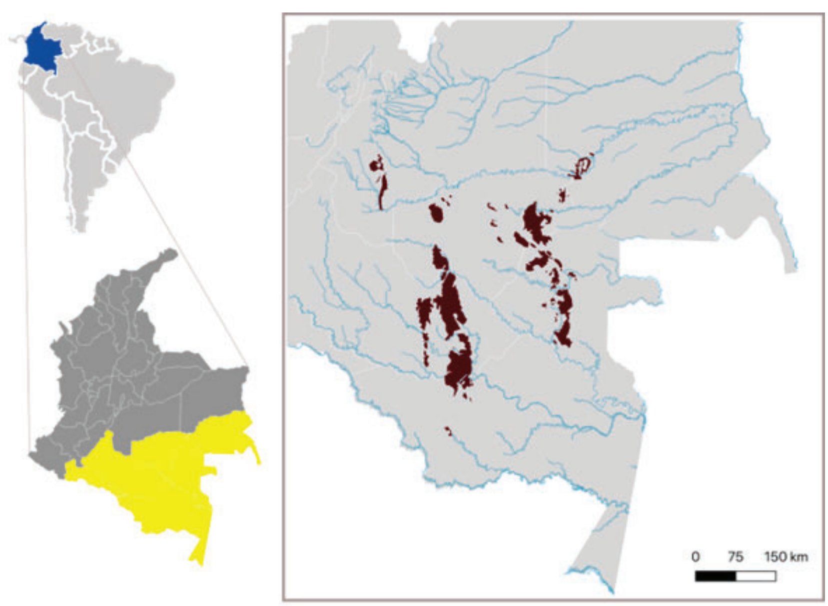

Figure 1. Geographic distribution of Colombian cratons and Guiana shield systems (colored in red). The area of Colombia is shown in blue, and the area of the Orinoco-Amazonian region where Guiana shield systems are found is shown in yellow. *Distribución geográfica de los cratones colombianos y los sistemas del escudo guayanés (coloreados en rojo). La zona de Colombia se muestra en azul, y la zona de la región Orinoco-Amazónica donde se encuentran los sistemas de escudos de Guayana se muestra en amarillo.*

(Bovolo et al., 2018). The Guiana Shield has a complicated geological history, from ca. 2130 Myr around the Equator, moving towards the Pole ca. 2050 Myr, and returning to the Equator by ca. 1970 Myr (Theveniaut et al., 2006). These displacements are associated with strong geological links outlining the transamazonian orogeny between 2.1 and 1.9 Myr (Potapov et al., 2017). Before the Andean uplift, the main rivers in the west likely flowed into the Pacific Ocean and did not reverse their flow to the Atlantic until about 8-10 million years ago (Lujan & Armbruster 2011).

Cratonic rocks have been recognized as a primary source of minerals, including gold, of porphyry (Cu, Mo, Au) or epithermal (Au, Ag) types (Hammond, 2005a). These findings are consistent with the rising development of small-scale mining areas scattered throughout the region. Up to 47 rivers of middle and large size drain the region. They account for a global discharge of 2792 km^3/yr (Hammond, 2005a; Lujan & Armbruster, 2011). These include both very large and smaller river systems, as well as fluvial lakes ("madreviejas") and wetlands ("morichales" and "canaguchales").

In Colombia, one of the best-known areas within the Guiana Shield is the Serranía La Lindosa (Fig. 1), with approximately 300 km^2 surface area and a cracked morphology due to the meteorization of sandstones that generates large blocks, arches, bridges, caves, and steep walls (Nivia et al., 2011; Arango et al., 2011). Most of the observations we provide in this paper derive from studies in this mountain range.

FRESHWATER ECOSYSTEMS IN THE GUIANA SHIELD

Hydrological and geomorphological characteristics

One of the most distinctive characteristics of freshwater ecosystems in the Guiana Shield is their remarkable hydrological stability (Fouquet et al., 2015). Water flow patterns are associated with the tropical regime that persistently alternates from dry (low water) to wet (high water) periods. This remarkable hydrological homogeneity also includes the occurrence of higher than usual water flow during La Niña events, or lower than usual flow under El Niño events (Labat et al., 2012). Overall, there is a lower number of catastrophic floods or persistent droughts, and the systems are characterized by periodical lateral expansions and contractions of watercourses within the river system.

The river and stream ecosystems in the Guiana Shield account for remarkable geomorphological stability. Sediment deposition in the northwestern Amazonia was dominated in the early Miocene by a moderately braided, low sinuosity fluvial system, with sediments from the crystalline rocks of the region (Hoorn, 1994) that currently configure the geomorphology of large river systems. Rivers draining the Guiana Shield show a multiplicity of exposed Proterozoic structures that perform as hydrological and physical barriers within the river channels. The described dynamics of expansion and contraction in high-order rivers facilitate the existence of large areas of alluvial materials associated with the main channel (Fig. 2a). These floodplains are larger when the slope and inclination are very low and are composed of unconsolidated clays and sands. Within these alluvial areas, meanders, lagoons, and horseshoe lakes exist, some evolving into swamps and shallows (i.e., areas of a river, lake, or coastal zone where the water is relatively shallow compared to surrounding areas) after long-term silt deposition (Junk et al., 2012).

Some low-order rivers flowing over extensive Precambrian slabs have simplified and less sinuous channels with fractures that interrupt the uniformity of the substrata and allow the formation of pools and rapids (Fig. 2c). In these low-order rivers, slabs alternate with sand bars and marginal and ephemeral pools, along with aquatic plants, which together contribute to a large diversity of riverine habitats (Rodrigues-Filho et al., 2017; Córdoba-Ariza et al., 2020; González-Trujillo et al., 2021). These geomorphological structures and the absence of substantial hyporheic sediments causes these systems to stop flowing during the low water period, this being particularly remarkable in those of lower order streams (i.e., small, headwater streams that are the first and smallest tributaries in a river system). However,

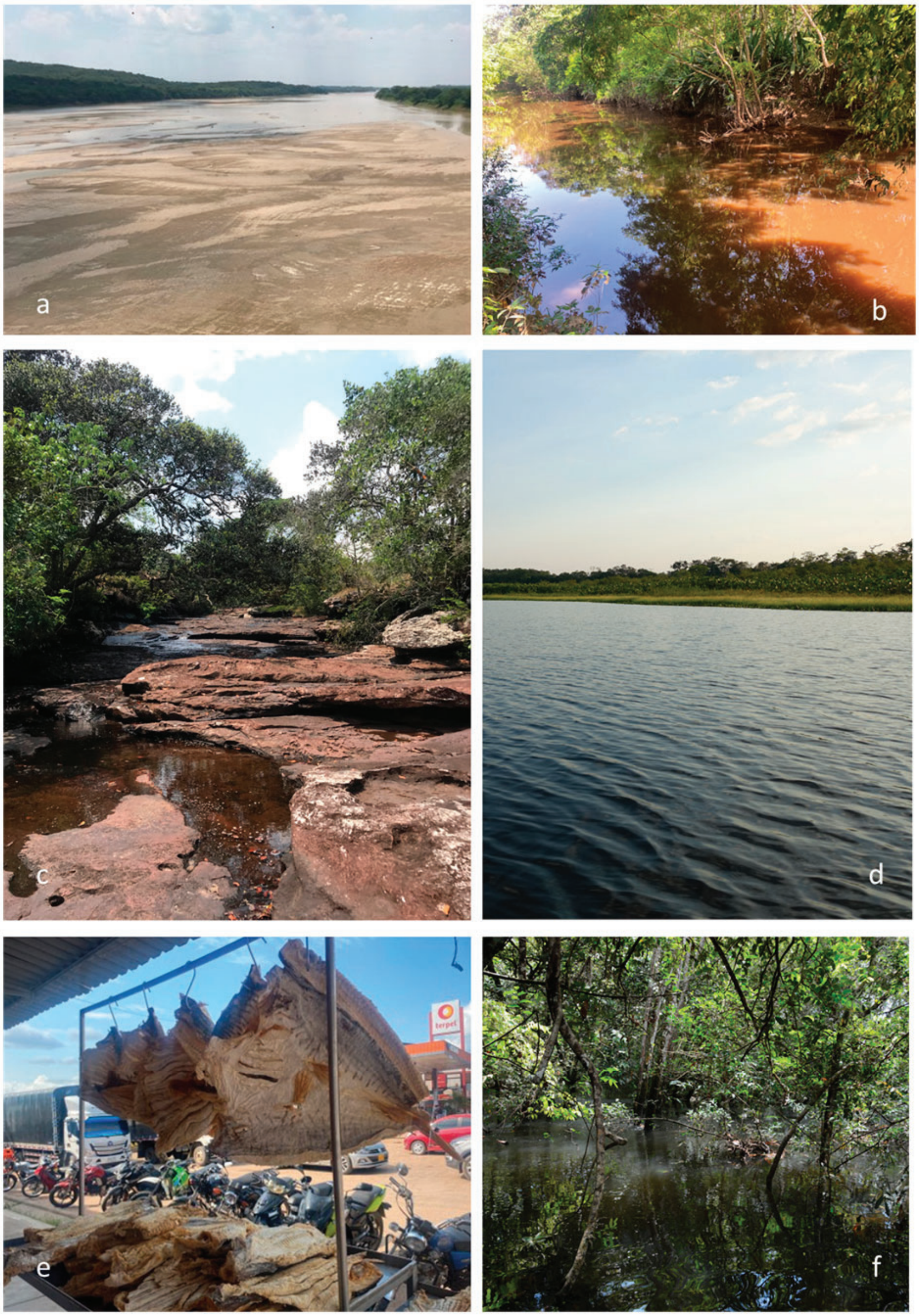

Figure 2. Freshwater ecosystems in the Colombian Guiana Shield. a) The river Guaviare at San José de Guaviare; b) Caño Retiro, a dark waters stream; c) Lindosa stream, a clear water stream; d) Laguna Negra, an oxbow lake; e) fish exposed at the San José market; f) a "cananguchal" wetland. *Ecosistemas de agua dulce en el Escudo Guayanés Colombiano. a) El río Guaviare en San José de Guaviare; b) Caño Retiro, arroyo de aguas negras; c) arroyo Lindosa, arroyo de agua clara; d) Laguna Negra, meandro; e) pescado expuesto en el mercado de San José; f) Humedal "cananguchal".*

other low-order streams flowing through forests and sedimentary materials might reduce their water flow during the dry period, but do not become temporary (Fig. 2b).

Riparian vegetation and water chemical characteristics

Overall, the geographical expanse of this area gives rise to a remarkable juxtaposition of forests and savannas housing diverse vegetation types like savannas under perpetual and seasonal flooding, high plain savannas, riparian or gallery forests, palm forests, and swamps (Borghetti et al., 2020; Rosales et al., 1999). Gallery forests foster environments of considerable biodiversity along the banks of streams and rivers (Veneklaas et al., 2005) and contribute substantial inputs of organic material and large woody debris materials along the river courses (Graziano et al., 2022). These riparian habitats (Fig. 2f) that are transitional zones between terrestrial and aquatic systems are characterized by the presence of vegetation adapted to high disturbance regimes and wet soils. This vegetation not only provides stability and protection to the watercourses by stabilizing slopes and preventing erosion, but it also serves as an important resource and habitat for a variety of species (Luque et al., 2019).

Within the predominant savanna vegetation, a notable presence of C4 grasses and herbs adapted to nutrient scarcity and fire (Huber, 2006) intermingle with scattered woody plants. Riparian cover in savanna regions is low, so both the terrestrial inputs as well as shading that contributes to watercourses remain poor.

Regarding their biogeochemistry, the fluvial ecosystems of the Guiana Shield are highly diverse. Water types respond to visible physical characteristics (termed as black or clear waters) that also correspond to specific chemical properties (Table 1). Rivers that have their headwaters in the Guiana Shield may either have medium water transparency when they flow over forests ("black waters") or be transparent when they flow over Precambrian slabs and savannas ("clear waters"). The main rivers draining this region include the Negro, Essequibo, Orinoco, Guaviare, and Caquetá (Lujan, & Armbruster, 2011). Overall, these are oligotrophic systems (Lewis, 1988), which may become ultraoligotrophic during periods of heavy rainfall (Hernes et al., 2017).

Table 1. Typologies and environmental characteristics of the river systems in the Guiana Shield, with examples from the Lindosa Mountains Range and areas of influence in San José del Guaviare. *Tipologías y características ambientales de los sistemas fluviales del Escudo Guayanés, con ejemplos de la Serranía de Lindosa y áreas de influencia en San José del Guaviare.*

	Guiana Shield origin "Black water"	Lagoon "Black water"	Guiana Shield Origi "Clear waters"	Guiana Shield origin "Clear waters" Cananguchal
Geological setting	Clays	Clays	Sands	Sands
Geomorphological characteristics	Gently dissected denudation plain	Gently dissected denudation plain	Strongly dissected denudation plain	Strongly dissected denudation plain
Hydrological patterns	Permanent	Permanent	Temporary	Mostly permanent
Water cond. (µS/cm)	≥ 10 ≤ 23	≥ 5.5 ≤ 7.5	≥ 5.5 ≤ 10	≥ 2.5 ≤ 5.5
pH	≥ 4.5 ≤ 5.8	≥ 3.9 ≤ 4.2	≥ 3.6 ≤ 6	≥ 4.0 ≤ 4.5
Water transp (m)	≥ 0.5 ≤ 1.5	≥ 2.3 ≤ 4.0	≥ 2.7 ≤ 4.5	≥ 0.1 ≤ 0.5
P-PO_4 (mg/L)	≥ 0.01 ≤ 1.5	≤ 0.05	≤ 0.015	≥ 0.01 ≤ 1.5
Algae and Macroinvertebrate	Diatoms Filamentous Cyanobacteria Chironomidae	Chrysophyceae Dinoflagellates Chironomidae	Rhodophyceae Desmids Hydropsychidae	Diatoms Desmids Leptohyphidae
	Negro and Retiro streams	Laguna Negra	Cristalina and La María streams	Cananguchal Lajas

Waters have low conductivity (<20 µS/cm), low concentrations of dissolved inorganic carbon (Jepsen & Winemiller, 2007), acidic pHs (3.5-6), and high O_2 values (Lewis et al., 1987; Lewis & Saunders, 1990). Those of black waters (Fig. 2d) are characterized by containing higher concentrations of dissolved organic matter (Sobieraj et al., 2002), mostly humic and fulvic acids, derived from organic matter decomposition (Mora et al., 2010). Overall, the chemical signals of rivers in the Guiana Shield are influenced by both the primary weathering of silica-rich materials (Hammond, 2005a) and by the extent of interaction with the terrestrial vegetation (Lewis & Weibezahn, 1976; Lujan & Armbruster, 2011). The different biogeochemical patterns of the rivers draining the Colombian Guiana Shield are fundamental for understanding the diversity of the biological communities inhabiting these waters (González-Trujillo et al., 2020a, 2020b). Overall, they are adapted to weak mineralization, acidity, high temperatures, potential water intermittency, and oligotrophy (Bowman et al., 2008; Neff & Jackson, 2013).

FRESHWATER ECOSYSTEMS IN THE GUIANA SHIELD: THEIR TYPOLOGY AND BIODIVERSITY

The complex Neogene tectonic events and Pleistocene climatic changes, together with marine transgressions during the Late Cretaceous and Cenozoic, have created a unique diversity of fluvial and associated freshwater habitats throughout the Guiana Shield region. Overall, the freshwater ecosystems in the Guiana Shield can be structured along two main axes, regardless of their size: i) their permanent or temporal character that remains associated with their geomorphological characteristics, and ii) the physical and chemical attributes of their water that in turn is related to the higher or lower influences of the riparian vegetation. The Colombian portion of the Shield's river ecosystems contains different water types (white, black, clear, and mixed), as well as diverse associated ecosystems (varzea, igapos, meanders, and lagoons). In the former case, factors such as basin geology, lithology, suspended solids, and vegetation (both riparian and terrestrial) influence the water types; while geomorphology, flooding patterns, vegetation, erosion, and sediment deposition contributes to the formation of river-associated ecosystems. Table 1 presents the typology as well as some examples from the Lindosa Range and areas of influence in San José del Guaviare.

Altogether, river networks perform as connectors for large, mobile organisms such as fish; they also perform as barriers that limit the dispersal of species (Rodrigues-Filho et al., 2017; Rodrigues-Filho et al., 2018). In the long-term, this has caused the isolation and redistribution of elements throughout lowland and highland areas (Huber & Renno, 2006), promoting species divergence (endemism) via processes of vicariance and allopatric divergence (Lundberg et al., 1998; González-Trujillo et al., 2021; Melo et al., 2021). Several keystone vertebrate species exemplify the complex geological, climatic, and evolutionary history in the region. Neotropical fish diversity can be traced back to higher endemic clades from the Cenozoic era (Lundberg et al., 1998; Albert et al., 2020). There is 80%-95% endemism in various lineages of the rheophilic loricariid catfishes (Lujan & Armbruster, 2011), Gymnotidae (Lehmberg et al., 2018), Characiformes (Lópes et al., 2020), Loricaridae (Collins et al., 2018), and Siluriformes (Hayes et al., 2020). This high endemism is a result of genetic evolution under constrained ecological space that limited their dispersal (Lujan & Armbruster, 2011; de Souza et al., 2020). The specific geomorphological characteristics of these fluvial systems have also been essential for establishing the genetic diversity and dispersal of many amphibian species, such as *Hysiboas* and *Stefanias* (Fouquet et al., 2015; Kok et al., 2016).

The aquatic invertebrate communities of the Colombian Guiana Shield exhibit remarkable diversity, comparable to that of fish communities. Over 90 macroinvertebrate genera have been recorded in areas such as Serranía La Lindosa and Serranía de La Macarena (Granados-Martínez et al., 2018; Córdoba-Ariza et al., 2020). The taxonomic composition of aquatic macroinvertebrates in the Guiana Shield differs significantly from that of surrounding ecoregions such as the Andes, Amazon, and Eastern plains. This dissimilarity can be attributed to the historical isolation and unique physical and chemical characteristics of the tributaries in the Guiana Shield (González-Trujillo et al., 2021). However, despite this isolation, it has been observed that some genera found in the Andean and Amazonian regions can be also found in the region; these include genera such as *Scaphydra*, *Parametriocnemus*, *Leptohyphodes*, and *Tricorythopsis* (Córdoba-Ariza et al., 2020), indicating some degree of connection between these ecoregions.

As stated above, the water biogeochemistry and hydrological conditions define river typologies and are strong environmental filters for the spatial and temporal distribution of aquatic invertebrates. Córdoba-Ariza et al., (2020) observe low spatial and temporal variability in the community composition that is attributable to the high specialization of taxa to specific environmental conditions. Notably, greatest variability is observed in invertebrates inhabiting the endemic macrophyte formations in the region, particularly those associated with the Podostemaceae *Rhyncholacis clavigera* (P. Royen) B.R.Ruhfel & C.T.Philbrick. This suggests that these non-perennial macrophytes might play a significant role in maintaining high benthic species diversity, an aspect that deserves further investigation.

Past events of geographical isolation and present-day water chemistry also account for the composition and diversity of diatom communities observed in the Guiana Shield rivers. Diatom assemblages in these systems encompass a high number of cosmopolitan taxa together with other rarer species, such as *Encyonopsis frequentis* Krammer, 1997, or *Eunotia rhomboidea* Hustedt 1950 (González-Trujillo et al., 2020b). Acidophilous diatoms are accompanied by a wide number of Desmids (such as the genera *Actinotaenium* sp., *Micrasterias* sp., *Cosmarium* sp., *Euastrum* sp., and *Staurastrum* sp.), and a few freshwater red algae (*Audouinella* sp.) and filamentous green algae (*Mougeotia* sp., *Spirogyra* sp., *Klebsormidium* sp.).

As mentioned above, some of the smaller river systems flowing through the high savannas over the Precambrian slabs may naturally dry out periodically. In the process of complete drying, isolated pools probably remain in the stream bed, or small water volumes are retained in the crevices among the rocks. In these conditions, high light insulation may cause large daily temperature fluctuations (ranging between 20°C to 40°C). While there is still water, these areas could function as refugia for species adapted to these extreme temperature conditions, low water levels, and high irradiance. These include algae (particularly euglenophytes, and to a lesser extent diatoms) and cyanobacteria (*Doliocatella* sp.) with a narrow-range distribution, together with some well-adapted macroinvertebrate families (such as Chironomidae, Elmidae and Culicidae).

FRESHWATER ECOSYSTEMS IN THE COLOMBIAN GUIANA SHIELD: IMPLICATIONS FOR CONSERVATION

The Guiana Shield is currently affected by logging (Bovolo et al., 2018), mining (Hammond et al., 2007), road construction (Armenteras et al., 2009), fisheries, and water contamination (Suarez et al., 2020). Although several decades ago deforestation in the Colombian Guiana Shield was still low in comparison to other parts of the ecoregion (Hammond, 2005a), more recent studies (Clerici, et al. 2020) show increases in the percentages of change (5.1%) in deforestation (i.e., Serranía de Chiribiquete). The forest cover in the Lindosa mountain range has been reduced 17% during 2012-2016, corresponding to an increase in secondary vegetation and pastures (Monroy et al., 2019). Still, the protected area in relation to human density is very high in the Colombian part (60.1 ha protected per local inhabitant; Hammond, 2005a). This gives some hope for conservation.

The impact of freshwater fisheries is high in the most populated areas (e.g., around San José de Guaviare, Fig. 2e), and has led to the depletion in catches of some of the large fish species (such as catfish and arapaima; Watson & Stewart, 2020), particularly in the alluvial areas as well as in clear and black water streams. Additionally, there is a rising interest in fish trade for the colorful Cichlids and Loricariids which thrive in small rivers of clear and black water, because of the demand for ornamental fishes for aquaria by American and European collectors (Ortega-Lara & Luján, 2020).

These still have only moderate impacts; the real threat occurs in other areas of the Guiana Shield but could be mirrored in Colombian parts in the near future. Alerts of relevant impacts should be taken now (Fig. 3). Human impacts in nearby areas of the Guiana Shield include a significant rise in gold mining activities (Miller et al., 2003; Hammond et al., 2007; Lainig, 2019); these may cause silting and heavy metal (mercury) contamination to the nearby rivers (Hilson & Vieira, 2007; Miller et al., 2003). Mining activities are responsible for 41% of the region's total forest losses (Alvarez-Berrios & Aide, 2015; Dezecache et al., 2017; Bovolo et al., 2018). Mining increases the mortality rates of fish species and causes lower turnover rates, resulting in the proliferation of smaller fish that negatively impact the productivity and water quality of low-order rivers (Brosse et al., 2011). Other associated risks are the logging of certain tree species with high economic value (Verıssimo et al., 2008), as well as infrastructure development, usually associated with logging activities (Armenteras et al., 2009). Regional model predictions suggest that widespread forest clearing would lead to a twofold increase in rainfall and runoff in lowland forests, as well as an average temperature rise of up to 2.2°C in the savannas (Bovolo et al., 2018). Deforestation in less than a third of the Guiana Shield and in areas threatened by mining, logging and agricultural activities, could result in significant changes in the water cycle throughout the continent (Oliveras & Mahli, 2016). The consequences for freshwater ecosystems under this scenario could include a general disruption of the quoted hydrological stability, likely leading to an increase in water intermittency (already present in some small streams of the region) as well as a decrease in water quality, two prospects that directly might affect the current biodiversity of freshwater in the region.

The vulnerability of the species inhabiting the freshwater Guiana Shield ecosystems is related to the known state-range of the environmental characteristics to which they are adapted (Perujo et

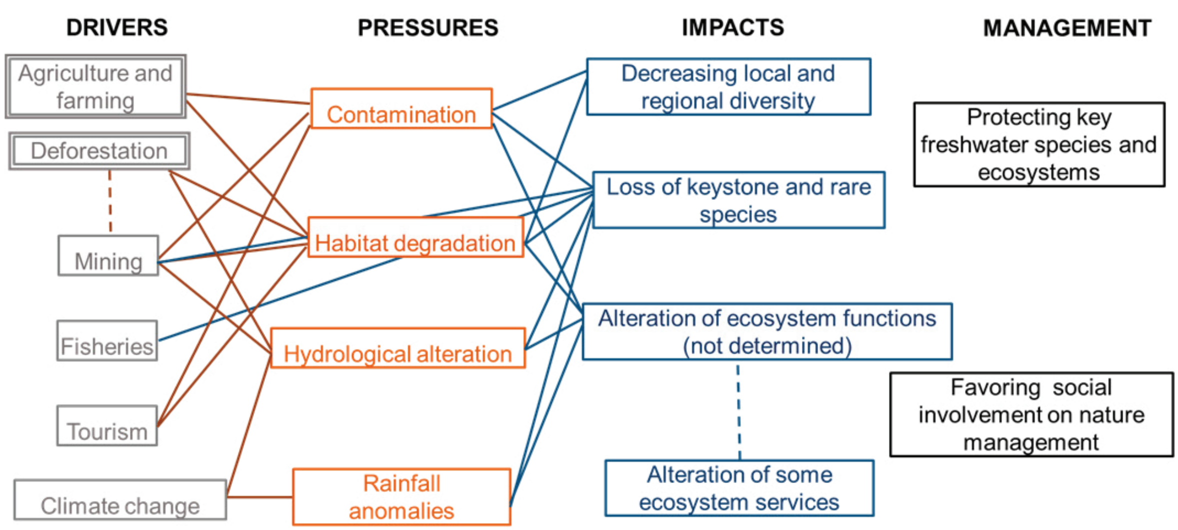

Figure 3. Conceptual relationship between the drivers, pressures and impacts which potentially may affect the Colombian Guiana Shield. Among the drivers, agriculture, farming and deforestation are outlined as the most relevant current drivers, causing habitat degradation, contamination, and local hydrological alteration. Impacts freshwaters concern biodiversity, functions and ecosystem services. Some management clues to minimize current or future impacts are also indicated. *Relación conceptual entre los factores, las presiones y los impactos que potencialmente podrían afectar al Escudo Guayanés Colombiano. Entre los factores, la agricultura, la ganadería y la deforestación se destacan como los más relevantes en la actualidad, causando degradación del hábitat, contaminación y alteración hidrológica local. Los impactos en las aguas dulces afectan la biodiversidad, las funciones y los servicios ecosistémicos. También se indican algunas estrategias de gestión para minimizar los impactos actuales o futuros*.

al., 2022). The state-range is the natural variability that species may withstand and implies that those more sensitive species (the case of those inhabiting the Guiana Shield freshwaters) may be particularly affected by abrupt changes. The infrequent natural extreme events occurring in the Guiana Shield contrasts with other areas in the Neotropics that historically have suffered from geological catastrophes (Hoorn, 1994; Hoorn et al., 2009). The region is characterized by its high endemism and species diversity, likely a result of the stable geological landscape and the scarce occurrence of large-scale natural disturbances (Hammond, 2007). This has forged biological communities adapted to low frequency (rare) disturbances that are highly susceptible to human-associated changes (Hammond, 2005b). Therefore, abrupt hydrological changes (e.g., desiccation or extended low flows) caused by logging, mining, climate change, occurrence of contaminants (such as heavy metals or organic micropollutants from mining or untreated urban sewage), or habitat degradation (i.e., through siltation after mining, logging, or infrastructure construction), can displace species from their adapted range and complicate maintaining their diversity and functions (Fig. 3). The alteration of ecosystem functions (not yet measured in freshwater ecosystems of the area) may give rise to unwanted effects on ecosystem services such as water depuration with direct effects on human settlements depending on the river (Sabater et al., 2021). The effects might be stronger than in systems elsewhere adapted to periodical disturbances (Sabater et al., 2021).

To be effective, mitigation of impacts requires a confluence of environmental awareness (Cabello et al., 2015), stewardship (Pahl-Wostl et al., 2012), and governance (Carvalho et al., 2019). These elements guide the social involvement of natural resource management (Fig. 3). Some attempts to coordinate these factors already exist in some parts of the Colombian Guiana Shield. As such, locally supported tourism is a reliable alternative to illicit crops and are a means of promoting peace in the region (Unigarro-C, 2020), as well as preserving the region's cultural and natural diversity (Montenegro-Perini, 2022). Some initiatives already exist, based on local communities organized as worker cooperatives that successfully promote low-impact tourism. However, tourism alone may not be sufficient to mitigate the effects of other drivers of degradation like deforestation, fisheries, or mining. To make this more effective, the region should develop a framework to make social development and conservation of natural resources compatible. This requires common scrutiny of the threats and effects from where appropriate management may stem. At present, low human densities, reduced human activity, and some local tourism initiatives are preserving local biodiversity (Del Cairo et al., 2018); but the existence of human activities in nearby parts of the Guiana Shield in Brazil and Venezuela is a warning about the problems ahead for the Colombian Guiana Shield. Expanding our knowledge of biological diversity, and the associated ecological functions of freshwater ecosystems is a necessary step forward to promote the conservation of these systems. Such actions subsequently define the opportunities for local developments that might be respectful of the rich biological diversity in the region. Threats to freshwater ecosystems by climate change, agriculture, mining, and livestock may reduce aquatic biodiversity in the future. Conservation of these ecosystems is a priority not only for maintaining regional biodiversity, but also for them to be considered in formulating management plans and designing protected areas. It is advisable to map the different types of rivers and streams, as well as their associated ecosystems (varzeas, igapos, meanders, lagoons, floodplain forests, among others) in the region, accompanied by a thorough characterization of referenced biological communities (benthic algae, macroinvertebrates, fish) in each habitat, and coupled to the detailed physical and chemical variables which define their environmental range.

CONCLUSIONS

The Colombian Guiana Shield has a gradient of environmental, geomorphological, and geological conditions that generate freshwater ecosystems unique to their limnological properties as well as to their aquatic biodiversity. However, anthropogenic activities and pressures compromise the ecological integrity of the

Colombian Guiana Shield. Although there are already initiatives in local communities, it is necessary to promote the conservation of the region's natural resources by means of more rigorous policies and local involvement (peasants and indigenous people) addressed to empower them on the sustainable use of resources and biodiversity. Related research in Colombian parts of the Guiana Shield has been significantly delayed compared to other areas of Colombia, thereby impeding further generalizations of the causes and consequences of biodiversity.

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AUTHOR CONTRIBUTIONS

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