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ECOLOGY

# Rheophytes of the middle Caquetá River, Colombian Amazonia

## Reófitas de la parte media del río Caquetá en la Amazonia Colombiana

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## ABSTRACT

We studied the rheophytic vascular flora of the middle Caquetá River basin in the Colombian Amazon, by sampling along the margins and islands of its two largest rapids, Angostura and Araracuara, along the rapids of the black-water Yarí river, its second largest tributary, and along a swift black-water creek flowing from a small Tepui into the latter. We identified and quantified rheophytes in 12 plots and collected other rheophytic species spotted outside the plots. We found 28 species of rheophytes, belonging to 20 families, mostly herbs and subshrubs. The rheophytic flora of the white-water Río Caquetá only shared three species, with that of the Yarí River; instead, the Yarí River shared no rheophytic species with its tributary creek, despite being just a few meters away. The family Podostemaceae dominates the extreme rheophytic belt, where the current hits the strongest. The most diverse families were Myrtaceae, and Xyridaceae (three species each); Acanthaceae (two species) is the most diverse family in the middle level, whereas Myrtaceae (three species) predominates in the upper rheophytic belt of small trees, and makes up a transition between the truly rheophytic and the riparian floras. The most abundant and frequent species was *Pfaffia iresinoides* (Amaranthaceae). Eight species are endemic to this area, and no species is shared with the other Neotropical areas where rheophytes have been surveyed.

**Keywords:** Aquatic plants, Araracuara, Angostura, rapids, Yarí.

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## RESUMEN

Estudiamos la flora vascular reofítica de la cuenca media del río Caquetá, en la Amazonía colombiana. Muestreamos a lo largo de los márgenes y las islas de sus dos rápidos más grandes, Angostura y Araracuara, también a lo largo de los rápidos de aguas negras del río Yarí, segundo tributario más grande y a lo largo de una quebrada rápida de aguas negras que fluye desde un pequeño Tepui hacia este último. Se determinaron y cuantificaron los reófitos en doce parcelas y se recolectaron otras especies localizadas fuera de las parcelas. Se encontraron 28 especies de reófitos, que se pueden agrupar en 20 familias; principalmente son hierbas y subarbustos. La flora reofítica de los ríos de aguas blancas del medio Caquetá comparte solo tres especies con la del Yarí; en cambio, el río Yarí no comparte ninguna especie con su arroyo tributario, a pesar de estar solo a unos pocos metros de distancia. Podostemaceae domina el cinturón reofítico extremo, donde la corriente golpea fuertemente. Las otras familias más diversas son Myrtaceae y Xyridaceae (tres especies cada una). Acanthaceae (dos especies) es la más diversa en el nivel medio, mientras que Myrtaceae (tres especies) predomina en el nivel superior, habitando con árboles de pequeño porte, que se encuentran en la transición entre el cinturón reofítico superior y la vegetación riparia. La especie con mayor abundancia y frecuencia fue *Pfaffia iresinoides* (Amaranthaceae). Ocho especies son endémicas en esta área y ninguna especie es compartida con las otras áreas neotropicales donde se han estudiado las reófitas.


**Palabras clave:** Plantas acuáticas, Araracuara, Angostura, rápidos, Yarí.

## INTRODUCTION

Rheophytes are plants that grow on the margins of swift waters and are adapted to withstand the strong currents that occur during floods. Although they were recognized long ago as a particularly different ecological group (van Steenis 1981, 1987), in the Neotropics they remain mostly overlooked (Hoyos and Bernal 2018) and the species are often cited as riparian by collectors and in catalogs and floras (e.g., Madriñán *et al.* 2017).

However, there are strong differences between riparian and rheophytic plants. Many plant species from open environments often grow along river margins in the Amazon plain, and some of them can tolerate long floods, as in many areas of the Amazon várzea. For these plants, however, the strength of the current plays a minimal role, and it is their ability to withstand long floods that determines their persistence along the river margins. Rheophytic plants, on the other hand, have to deal, either permanently or during flash floods, with strong currents that would dig up or damage most plants. They have developed particular traits to withstand the strong currents and to establish themselves in new sites, for instance narrow-leaved species, bowed trunks towards the current, specialized roots (van Steenis 1981).

Because of their adaptation to swift streams and flash floods, rheophytes are particularly abundant along mountain rivers and steep canyons. However, they occur also along the rapids and falls that form in areas that are mostly flat. In such areas, the rheophytic flora is restricted to the swift portion of the river, being replaced upstream and downstream by the common, riparian flora (van Steenis 1981).

The Caquetá River, known in its Brazilian stretch as Japurá, originates at 3956 m in the Andes of southern Colombia, and flows for 2280 km until joining the Amazon. In its middle basin, the river marks the border between the Colombian departments of Caquetá and Amazonas, and it is ca. 350-600 m wide at this point. The flora of this area, centered in the small village of Araracuara, has been relatively well studied, and a preliminary checklist is available (Sánchez 1997). However, no mention of rheophytic plants is made in this checklist.

While traveling along the Caquetá River, it becomes obvious that the common riverine flora growing along the margins in flat areas, where the river is broad and the stream is slow, is replaced by a specialized flora in areas where the river forms canyons, the stream is faster, and the margins are rocky (pers. obs.). In the middle Caquetá there are two

such areas –the Angostura and the Araracuara Canyons, where the river channel narrows down to 80-150 m, and is flanked by vertical cliffs of the Guiana Shield. It is in this area that rheophytes occur.

The Yarí is a black water river that originates in the western parts of the Guiana Shield in Colombia and runs for 620 km through the rocky plateaus of the Chiribiquete National Park, and flows into the Caquetá River 17 km downstream from Araracuara, where it is ca. 300 m wide. It is the second largest tributary of the Caquetá. As with the Caquetá, the Yarí River is mostly a broad, slow-flowing river. It forms strong rapids in the areas where the surrounding plateaus form deep canyons. The first of such canyons, the Gamitana Canyon, is located 56 km upstream from the confluence with the Caquetá and stretches for 7 km. At this canyon, the river channel narrows down to 30-50 m wide, and it is also in this area that rheophytes appear.

Rheophytic flora is mostly unknown, especially in South America (van Steenis 1981), the authors have been working in documenting different basins of Colombia (Hoyos and Bernal 2018), looking forward to understand and describe this new and incredible ecosystem that had been remaining unexplored for many years.

## MATERIALS AND METHODS

We studied the rheophytic flora of the middle Caquetá by establishing twelve plots (Fig. 1) along the margins of the Angostura (5 plots; Fig. 2a) and Araracuara canyons (5 plots; Fig. 2b), and at the lower end of the Gamitana Canyon (1 plot), in the Yarí river (Fig. 2c). Additionally, we established one plot along a small, unnamed creek that flows from the Tepui into the Yarí River, just at the upper extreme of the Gamitana Canyon (Fig. 2d). This creek, ca. 3 m wide at its confluence with the Yarí, is mostly slow-flowing, but forms small rapids along its course. The plots were established in March 2019, just at the end of the dry season, during six days in the field making two plots per day.

Our plots followed the method used by Hoyos and Bernal (2018), and consisted of a strip 20 m long, its width being defined by the width of the rheophytic belt, which is itself determined by the slope of the river margin and the flood level at that point (Fig. 3). At each plot we recorded all species occurring from water level up to the upper flood level. For each species we recorded its presence/absence, abundance in terms of coverage, level of occupancy above the river level, and kind of substrate where the plant grew.


**Figure 1.** Location of the sites where rheophytes were studied along the middle Caquetá river in Colombia. **a**, Angostura Canyon. **b**, Araracuara Canyon. **c**, Gamitana Canyon. **d**, Unnamed creek.

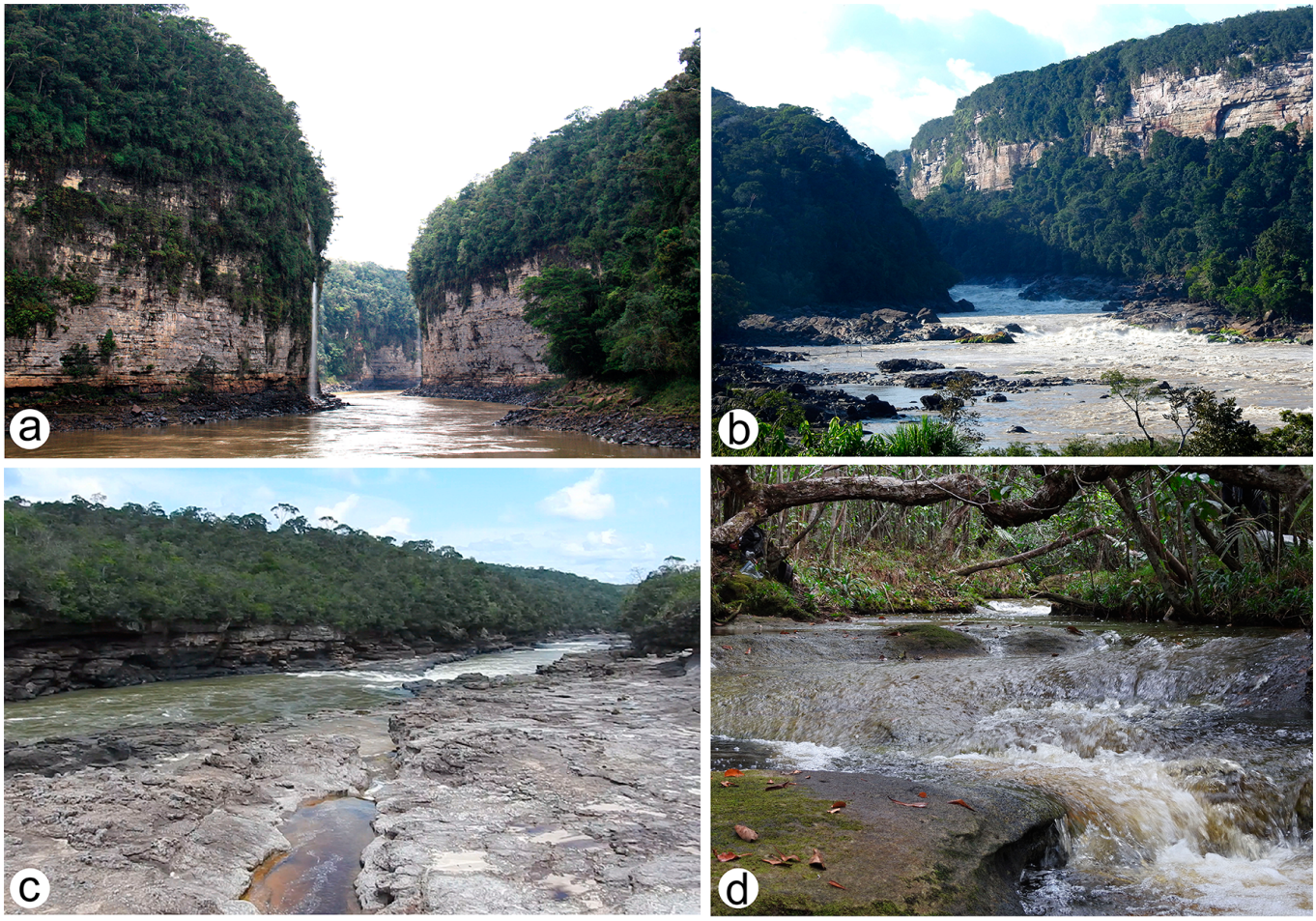


**Figure 2.** Sites where rheophytes were studied along the middle Caquetá river in Colombia. **a**, Angostura Canyon. **b**, Araracuara Canyon. **c**, Gamitana Canyon. **d**, Unnamed creek.

Abundance was measured in a subjective scale from 1-5 (rare, occasional, frequent, common, abundant). Each researcher independently assigned a value to each species, and the final value was calculated as the average of the two individual values. Overall abundance was calculated as the sum of the species' abundance at each of the twelve plots, and thus it can range from 0 (absent from all plots) to 60 (occurring at all plots, with abundance 5 at each). The level of occupancy was recorded in a visual scale that divides the usual range of the river's flash floods at each plot into three regions: lower, intermediate, and high. The kind of substrate was recorded as rock, wall or sand.

Besides the plots, we explored every rheophytic species spotted along the rocky margins, or in the middle of the stream, either by walking among the passable areas or by navigating the rapids in a kayak. Vouchers of each species were collected and deposited at COL, HUA, JAUM, and MEDEL. For most species, identifications were made by specialists (see acknowledgements).

## RESULTS

We found 28 species of rheophytic vascular plants, that can be grouped in 20 families (Table 1). They include 25 species or flowering plants, and three species of pteridophytes. The most diverse families were Myrtaceae, and Xyridaceae (3 species each), and Acanthaceae, Eriocaulaceae, Fabaceae, and Pteridaceae (2 species each).

There were three rheophytic species shared between the Caquetá and the Yarí (*Apinagia* sp., *Eugenia* sp.1 and *Borreria* sp. nov.), and no species was shared between the small creek and either of the rivers. The most frequent species was *Pfaffia iresinoides* (Kunth) Spreng., which occurred at seven plots, whereas twelve species were found only at one plot.

Most rheophytic species were herbaceous (50%), whereas subshrubs (28.6%) and treelets (21.4%) had a lower representation. The lower rheophytic belt was occupied mostly by the herbaceous, thalloid *Apinagia* sp. (Podostemaceae), which grew exclusively attached to rocks, either on the margins or in the middle of the river (Fig. 4a). The intermediate belt was occupied mainly by the reduced subshrub *Pfaffia iresinoides* (Amaranthaceae) which grows among rocks and crevices, and produces a short, woody stem that breaks during strong floods and reiterates during low waters. Other species occupying this same intermediate level include *Dicranopygium* sp. (cf. *D. schultesii* (Cyclanthaceae), *Justicia comata* and *J. pectoralis* (Acanthaceae), and the ferns *Adiantum latifolium* and *Pityrogramma calomelanos* (Pteridaceae).

In open areas outside the canyons, the upper rheophytic belt is dominated by subshrubs or small trees, including *Myrcia salicifolia*, *Myrciaria dubia*, and *Eugenia* sp. 1 (Myrtaceae), and the legumes *Inga nobilis* and *Calliandra trinervia* (Fig. 4b). These treelets make a transition to the riparian flora at the extremes of the rapids, where the stream is smooth and with laminar flow. In the canyons, depending on the width, the upper belt can reach different levels (Fig. 4c). In the Araracuara canyon, for instance, water level rises up to 8 m during floods, whereas in the Angostura canyon it can reach up to 17 m on extraordinary events (Duivenvoorden and Lips 1993). In these areas, the upper portion of the rheophytic belt is dominated by the rupicolous *Nautilocalyx pallidus* (Gesneriaceae), and the endemic bromeliad *Navia acaulis*.

In the small creek that flows from the Tepui into the Yarí River (Fig. 4d), we found six species of monocot rheophytes, all of them in the order Poales: *Syngonanthus umbellatus* (Eriocaulaceae), *S. tenuis* (Eriocaulaceae), *Rapatea elongata* (Rapateaceae), *Abolboda grandis, Xyris esmeraldae,* and *X. fallax* (Xyridaceae).

Some of the rheophytes found are substrate-specific. For instance, *Apinagia* sp. (Podostemaceae) grows only on rocks under strong currents. *Dicranopygium* cf. *shultesii* (Cyclanthaceae) grows also on rocks, but in the intermediate level, whereas the gesneriad *Nautilocalyx pallidus* grows on the rocky walls of the canyon, at the upper rheophytic belt. Other species thrive both on rocks and sand, like *Pfaffia iresinoides* (Amaranthaceae), *Adiantum latifolium* (Pteridaceae), and *Myrcia salicifolia* (Myrtaceae).

**Figure 3.** Views of the plot for the study of rheophytes at Puerto Arturo, Caquetá River, Colombia.

**Table 1.** Rheophytic plants of the middle Caquetá River basin, Colombia. Collection number with an asterisk (*) means rheophytic species collected outside the plots. H= herb, SS= subshrub, T= tree, R= rock, C= crevices, S= sand, W= wall.

| Species | Voucher Saúl E. Hoyos-Gómez | Habit | Global distribution | Plots in which found | Overall abundance | Substrate |
|---|---|---|---|---|---|---|
| **ACANTHACEAE** | | | | | | |
| *Justicia comata* (L.) Lam. | *SEHG 3680* | H | Mexico to Argentina; 0-2280 m | 2,3,4,9 | 8.5 | R |
| *Justicia pectoralis* Jacq. | **SEHG 3715* | H | Tropical South America; 50-600 m | general collection | | R |
| **AMARANTHACEAE** | | | | | | |
| *Pfaffia iresinoides* (Kunth) Spreng. | *SEHG 3744, 3655* | SS | Mexico to South America; 0-2500 m | 1,3,4,5,6,7,8,9,10 | 24 | R, C |
| **ASTERACEAE** | | | | | | |
| *Wedelia iners* (S.F.Blake) Strother | *SEHG 3745* | H | Nicaragua to Colombia; 200-2550 m | 4 | 1.5 | R |
| **BROMELIACEAE** | | | | | | |
| *Navia acaulis* Schult. & Schult.f. | **SEHG 3706* | H | Guiana and Serranía de La Macarena; 100 - 650 m | general collection | | R |
| **CYCLANTHACEAE** | | | | | | |
| *Dicranopygium sp.* (cf. *D. schultesii* Harling) | *SEHG 3686, 3737* | H | Amazonia; 100 - 400 m | 4,6,7,8,9 | 9.5 | R |
| **ERIOCAULACEAE** | | | | | | |
| *Syngonanthus umbellatus* (Lam.) Ruhland | *SEHG 3696* | H | Guiana Shield, Brazil, Colombia, Venezuela; 220 m | 11 | 3 | S |
| *Syngonanthus tenuis* Moldenke | **SEHG 3697* | H | Brazil, Colombia, Venezuela; 50-300 m | general collection | | S |
| **FABACEAE** | | | | | | |
| *Calliandra trinervia* Benth. | *SEHG 3678* | T | South America; 100-2200 m | 9 | 1 | R |
| *Inga nobilis* Willd. | *SEHG 3675* | T | Mexico to Brazil;0-2890 m | 1,9 | 3.5 | S, R |

*(Continúa)*

| Species | Voucher Saúl E. Hoyos-Gómez | Habit | Global distribution | Plots in which found | Overall abundance | Substrate |
|---|---|---|---|---|---|---|
| **GESNERIACEAE** | | | | | | |
| *Nautilocalyx pallidus* (Sprague) Sprague | *SEHG 3682* | H | Tropical South America; 65 - 1500 m | 2 | 2.5 | W |
| **LINDERNIACEAE** | | | | | | |
| *Lindernia crustacea* (L.) F.Muell. | *SEHG 3733* | H | Tropical and subtropical; 0-1000 m | 6,9 | 2 | S |
| **LOGANIACEAE** | | | | | | |
| *Spigelia hamelioides* Kunth | *SEHG 3716* | SS | Honduras to northern South America; 75 - 1000 m | 4 | 2.5 | R |
| **LYTHRACEAE** | | | | | | |
| *Cuphea beneradicata* Lourteig | **SEHG 3701* | SS | Colombia, Amazonia, Guiana and Serranía de La Macarena; 290-600 m | general collection | | R |
| **MYRTACEAE** | | | | | | |
| *Eugenia* sp. 1 | *SEHG 3674, 3676, 3711, 3741,* | T | South America; | 9,1 | 3.5 | R, C |
| *Myrcia salicifolia* DC. | *SEHG 3739* | T | Colombia, Perú, Brasil; 200-250 m | 1,4,6,7 | 12 | R |
| *Myrciaria dubia* (Kunth) McVaugh | SEHG 3677 | T | Colombia, Venezuela, Guianas, Brasil, Perú, Bolivia, Amazonian lowlands; 100-150 m | 8 | 2.5 | R |
| **PLANTAGINACEAE** | | | | | | |
| *Conobea* cf. *scoparioides* (Cham. & Schltdl.) Benth. | *SEHG 3685* | SS | Mexico to Brazil;0-1500 m | 4,8,9 | 5.5 | S,R |
| **PODOSTEMACEAE** | | | | | | |
| *Apinagia* sp | *SEHG 3669, 3681, 3690, 3691, 3700, 3713, 3714, 3720* | H | South America, Amazonia; 0-400 m | 1,2,3,10,12 | 20.5 | R |

*(Continúa)*

| Species | Voucher Saúl E. Hoyos-Gómez | Habit | Global distribution | Plots in which found | Overall abundance | Substrate |
|---|---|---|---|---|---|---|
| **PTERIDACEAE** | | | | | | |
| *Adiantum latifolium* Lam. | *SEHG 3687, 3742* | SS | Neotropics; 100-1500 m | 4,6,7,8,9 | 9.5 | S,R |
| *Pityrogramma calomelanos* (L.) Link | *SEHG 3688, 3729* | SS | U.S., Antilles to Argentina, Paleotropical; 0-2700 m | 4,6,7,9 | 8 | S,R |
| **RAPATEACEAE** | | | | | | |
| *Rapatea elongata* G.Schulze | *SEHG 3695* | H | Brazil, Colombia; 20 - 650 m | 11 | 2 | S |
| **RUBIACEAE** | | | | | | |
| *Borreria* sp. nov. | *SEHG 3743* | SS | Colombia; 150-200 m | 6 | 1 | S |
| **SALICACEAE** | | | | | | |
| *Ryania angustifolia* (Turcz.) Monach. | **SH 3712* | T | Colombia, Venezuela, Guianas, Brasil, Perú, Amazonian lowlands; 80-250 m | general collection | | R,S |
| **TECTARIACEAE** | | | | | | |
| *Tectaria pilosa* (Fée) R.C.Moran | *SEHG 3659, 3750* | SS | Costa Rica y Antillas a Bolivia y Brasil; 0-1900 m | 6,8,9 | 8 | S,R |
| **XYRIDACEAE** | | | | | | |
| *Abolboda grandis* Griseb. | *SEHG 3692* | H | Brazil, Colombia, Guiana, Suriname, Venezuela; 130-550 m | 11 | 4 | S |
| *Xyris esmeraldae* Steyerm | *SEHG 3693* | H | Colombia, Venezuela; 120-400 m | 11 | 4 | S |
| *Xyris fallax* Malme | *SEHG 3643* | H | Brazil, Colombia, French Guiana, Suriname Venezuela; 130-580 m | 11 | 2.5 | S |

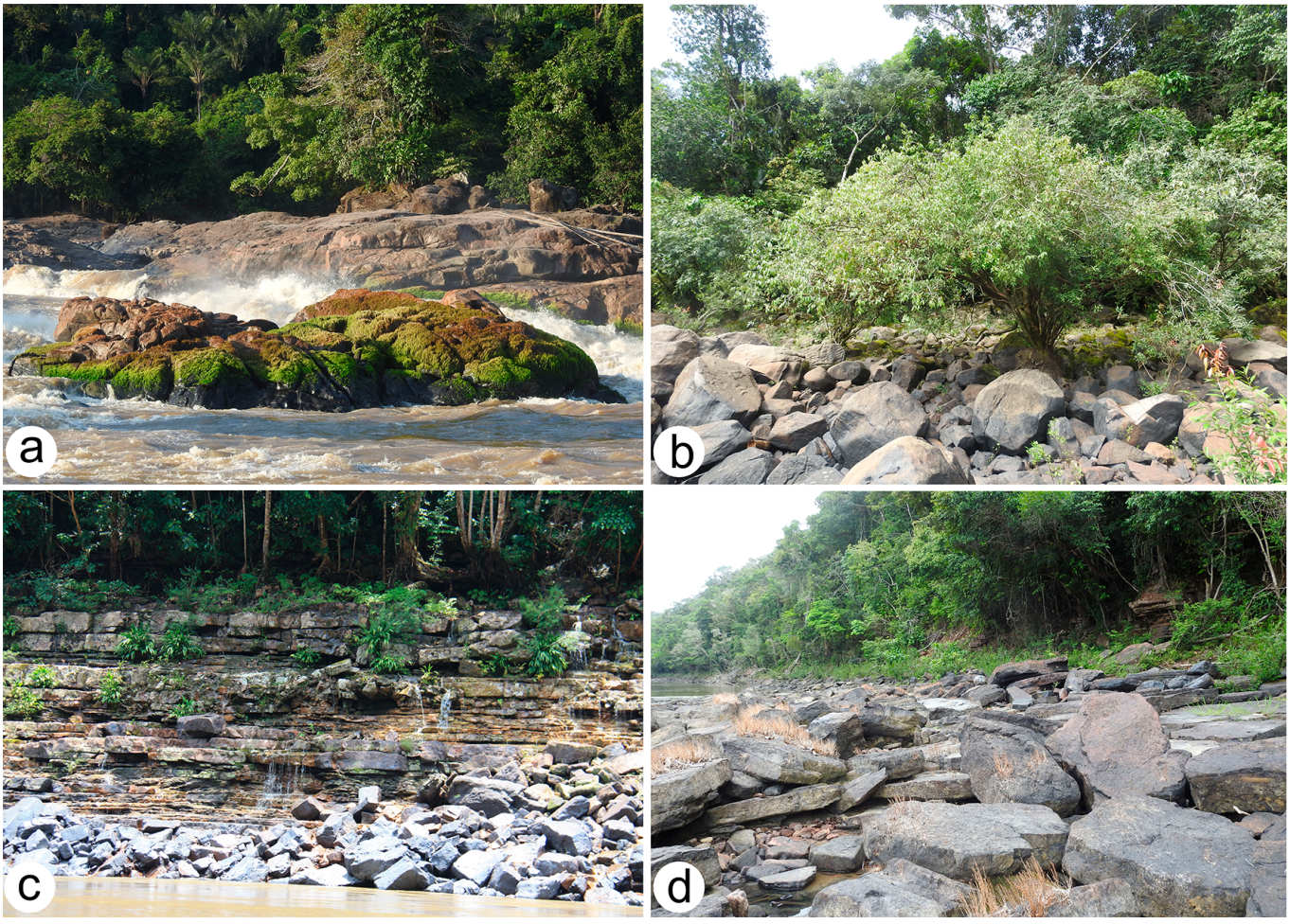


**Figure 4.** Some rheophytic communities of the middle Caquetá River, Colombia. **a**, *Apinagia* sp. 1 on rocks at the Araracuara Canyon. **b**, shrubby community dominated by three species of Myrtaceae, at the mouth of the Araracuara Canyon. **c**, Rocky walls of the Angostura Canyon, on the Caquetá River. **d**, At the mouth of the Gamitana Canyon, on the Yarí River.

## DISCUSSION AND CONCLUSIONS

Because our sampling took place at the end of a long dry season, the river was at its lowest level, and several non-rheophytic plants, besides the rheophytes themselves, grew along the rocky margins of the turbulent, fast-flowing streams. These included several species typical of swampy areas, like *Tonina fluviatilis* Aubl. (Eriocaulaceae), three species of *Ludwigia* L. (Onagraceae), *Montrichardia linifera* (Arruda) Schott (Araceae), *Aeschynomene rudis* Benth. (Fabaceae), *Sauvagesia erecta* L. (Ochnaceae), *Biophytum amazonicum* R. Knuth (Oxalidaceae), and *Phyllanthus caroliniensis* Walter (Phyllanthaceae). They all are herbaceous or subshrubs species with short life cycles, which thrive in small, sandy pools that form among the rocks on wet margins, but do not tolerate the strong currents when the water level rises. This is evident from their scattered occurrence in the river margins, and from the easy way they are detached from their substrate.

An interesting finding is the occurrence of *Pfaffia iresinoides* as a rheophyte, as no member of this family had been explicitly recorded so far to have this biotype (van Steenis 1981, 1987; Ameka *et al.* 1996; Bernardes 2012; Köhler *et al.* 2016), until recently by Kuetegue *et al.* (2019). This plant produces a short, thick, woody stem strongly attached to crevices, from which short branches up to 30 cm tall are produced. When the branches are broken by the turbulent water during floods, the stem produces reiterations, and the stem becomes thicker (Fig. 5).

Despite exhaustive exploration in the area near Araracuara (see, e.g., Sánchez 1997), this plant has been found only as a rheophyte associated to the rapids (Agudelo 2008). However, although *Pfaffia iresinoides* is recorded as a widely

distributed species ranging from Mexico to Perú and Brazil, and from sea level to 2500 m, none of the Colombian specimens examined by us is recorded as being rheophytic. We do not rule out the possibility that the rheophytic plants represent a different, undescribed and cryptic species, as recently shown with *Aiphanes argos* (Bernal *et al.* 2017), a rheophytic palm that had been erroneously treated as *Aiphanes parvifolia*. Molecular data have shown that this rheophytic taxon is indeed different from its forest allies (Bernal *et al.* 2019).

The rheophytic flora of the middle Caquetá River basin is half as rich as that of the Samaná, an Andean river (58 species in 29 families) (Hoyos and Bernal 2018). We compare the rheophytic flora of the Samaná and Caquetá Rivers, to show differences between basins, and also, because no other study of the rheophytic flora in Colombia and south America has been done. This comes as no surprise, as there are many more rapids along the Samaná. There were 11 plant families shared by both sites, and the proportion of life forms was roughly similar. It is good to highlight that both rivers had one species of rupicolous Bromeliaceae - *Pitcairnia fluvialis* in the Samaná, and *Navia acaulis* in the Caquetá, each of them endemic; the genus *Cuphea* (Lythraceae) had also one endemic species (Graham 2009, 2019), whereas the genera *Justicia* (Acanthaceae), and *Calliandra* (Fabaceae), had one species at each river. However, some important and diverse tropical families occurring in the rheophytic flora of the Samaná, Piperaceae and Arecaceae, do not occur at the Caquetá. Conversely some families found in the Caquetá and Yarí did not occur at the Samaná, notoriously Eriocaulaceae, Rapateaceae, and Xyridaceae, which are more diversified in the Guiana Shield than in the Andes (Huber 1987).

The number of plants that could not be determined to species, even by specialists (15%), as well as the discovery of a new species of *Borreria* (Rubiaceae; Roberto M. Salas, pers. comm.), reveals the poor understanding we still have of the Neotropical rheophytes. Although almost forty years have passed since van Steenis' (1981) seminal work on the rheophytes of the world, rheophytic floras for most areas are still unavailable, although an updated checklist of the world's rheophytic seed plants was recently compiled (Costa *et al.* 2020). Getting to know the rheophytic floras


**Figure 5.** *Pfaffia iresinoides*, the most frequent rheophyte at the Caquetá River, Colombia. **a**, Habit, among rocks at the Araracuara Canyon. **b**, Lignified stem that breaks during strong floods and reiterates during low waters. (photos Saúl E. Hoyos-Gómez).

is just the first step for understanding the evolutionary processes underlying this unique biological group.

## AUTHORS PARTICIPATION

All authors SEHG, JD and RB participated in the conception, design, data collecting, analysis and writing of the paper.

## ACKNOWLEDGEMENTS

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## CONFLICT OF INTEREST

The Authors declare that there is no conflict of interest.

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