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TANK BROMELIADS : aquatic life at the heart of plants



On the edge of the forest in Guiana, catching a glimpse of the guests living in the tanks formed by the leaves of the bromeliad *Aechmea mertensii* (photo C. Leroy).

« *Assuredly a small thing may give an example [...] leading to the knowledge of great things.* »

Lucretius
(*On the Nature of Things*, 1st century BC).

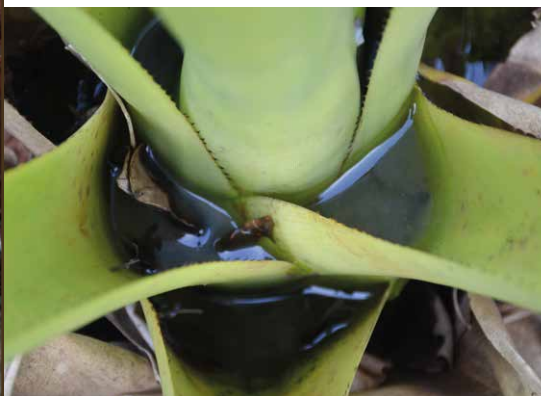
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THE INTERLOCKING LEAVES OF TANK BROMELIADS ARE HOME TO SMALL BUT GENUINE AQUATIC ECOSYSTEMS. THESE MICROWORLDS ARE USED BY RESEARCHERS AS MODELS TO TEST HYPOTHESES, ESPECIALLY IN EXPERIMENTAL STUDIES SIMULATING THE EFFECTS OF CLIMATE CHANGE.



The bromeliad family, native to the Guiana Shield, includes 3 475 species of flowering plants. Its most famous representative is pineapple (*Ananas comosus*). Apart from a single species, *Pitcairnia feliciana*, which “recently” arrived in West Africa (probably two million years ago), the family’s natural distribution ranges from tropical to subtropical America. Bromeliads grow either on soil or on rock (lithophytes), and very often on a supporting tree (epiphytes). They occur in environments as different as tropical forests or coastal deserts, from sea level up to an elevation of 4 000 metres.

Bromeliads have alternate leaves arranged in a spiral that forms a “rosette”. About half of the species (known as “tank bromeliads”) show tightly interlocking leaves that collect rainwater and form actual tanks, a central tank being formed by the youngest leaves. Depending on the species and age of the plant, a tank bromeliad will retain more



Close-up on the peripheral tanks of a bromeliad. Dead leaves can be seen in the left tank : they are the primary source of energy and nutrients in the aquatic micro-ecosystem (photo B. Corbara).

or less water, a few dozen litres being an absolute record among giants such as *Glomeropitcairnia*. The resulting freshwater habitat is unique : still waters without fish are quite uncommon in the tropics and therefore tank bromeliads represent aquatic habitats of major ecological importance. In some locations, all the bromeliads together may sequester up to 50 000 litres per hectare. While studying the ecology of these plants for more that fifteen years, our team has been particularly interested in the living beings they host, and in the aquatic micro-ecosystems to which these beings contribute.

A wide variety of aquatic organisms

The tanks of the bromeliads are home to many aquatic life forms, which are often dependent on this habitat. The detritus (mainly dead leaves) that enters the tanks is the main source of energy and nutrients. There, it is subject to the activity of microscopic decomposers such as fungi, bacteria and archaea* which improve its nutritional quality.



Depending on the size and morphology of their leaves, bromeliads retain more or less water (photos B. Corbara).

At the top, *Werauhia sintenisii* and its distinct "rosette" morphology. The tanks are filled with rainwater. They interconnect with each other thanks to the water overflowing from the center to the peripheral leaves (El Yunque National Forest, Puerto Rico).

Above, *Pitcairnia geyskesii* can only retain 5 ml of water in one plant (The Nouragues inselberg, French Guiana).

Opposite, *Aechmea polyantha* and its vertical leaves ("Savane-roche" Virginie, French Guiana).



Two detritivorous organisms from the tanks : a Chironomidae larva (Diptera) on the left, and a *Contacyphon* larva (Scirtidae beetle) opposite (photos F. Azémar).

Detritivorous macroorganisms* also contribute to litter breakdown, from coarse to finer elements that accumulate at the bottom of the tanks. These detritivores (mostly larvae of terrestrial adult insects) can be divided into shredders such as Tipulidae, and scrapers such as Scirtidae (beetles feeding on large algae attached at the surface of the litter). Collectors such as Chironomidae feed on fine deposited organic matter, and filter-feeders such as mosquito larvae sift fine particles from the water column. All of these inhabitants produce fecal pellets that further feed microorganisms and, once they decompose and mineralise, provide nutrients that the plant partly retrieves through specialised trichomes*.

All this microbial richness inevitably attracts predators. Protists and small metazoa such as rotifers constitute the first predatory level, particularly at the expense of bacteria. Then, these microorganisms are largely preyed upon by filtering mosquito larvae, which, as most detritivorous macroinvertebrates, become prey for various-sized predators – from the small *Corethrella* larvae (dipterans, similar to mosquitoes) to large top predators, such as

larvae of *Toxorhynchites* mosquitoes or damselflies. Predators help enrich the tanks by preventing their prey from becoming adults and leaving the aquatic environment. In a way, the energy in the bodies of prey is retained in the bromeliad food web, both directly through predator's growth, and indirectly through the production of fecal pellets.

"Brown pathway" and "green pathway"

Depicted above in a simplified form, the bromeliad food web is based on detritus, and is therefore considered a "brown pathway" for the flow of nutrients. But it can also include a chlorophyllous pathway or "green pathway". Some bromeliad-held waters indeed host large amounts of microscopic algae that are autotrophic (they do not depend on organic matter to grow). With their higher nutritional quality compared to detrital particles, these algae are integrated into the bromeliad food web, and are mostly consumed by filter feeders. Besides, we found that algae are only partly responsible for photosynthetic activity

Three predatory organisms from the tanks. Left to right : a *Corethrella* larva (Diptera), a *Toxorhynchites* larva (Diptera) and a damselfly larva (photos F. Azémar and B. Corbara).

* **Archaeon**: unicellular prokaryotic (with no nucleus) microorganism, genetically distinct from bacteria.

* **Macroorganisms**: organisms that are visible to the naked eye (in opposition to microorganisms).

* **Trichome**: absorptive leaf structure, enabling the plant to retrieve water and nutrients.



in the tanks : in French Guiana, bromeliads are home to a great variety of surprisingly abundant bacteria containing bacteriochlorophyll*. Thanks to this pigment, they are able to achieve photosynthesis in the absence of oxygen, and may therefore grow in the poorly oxygenated bottoms of the tanks.

We still have to clarify how brown and green pathways combine in bromeliad ecosystems, and how they fluctuate over time. Studies have shown that their relative importance depends on incident light, and thus on the degree of canopy cover above the plants. However, the role of photosynthetic organisms in supporting the bromeliad food web is probably still strongly underestimated.

The dynamics of the bromeliad ecosystem

Until recently, there was no information on temporal changes in aquatic communities in terms of species turn-over or biomass production. Only “snapshots” were available (recorded only occasionally, at different times of the year). We felt that such knowledge, available for decades for much



On the Nouragues inselberg in French Guiana, the bromeliads *Aechmea melinonii* (opposite) and *Catopsis berterionana* (top right), which sometimes grow only a few metres away from each other, host very different algal communities in their tanks (photos B. Corbara).



larger aquatic environments (lakes or rivers), would be useful to understand the ecological importance of tank bromeliads. We chose a typical plant from the understorey of the primary forest in the Guiana Shield : *Lutheria splendens*. This bromeliad, whose clonal cultivars are now popular in garden centers all over the world, is (as its name suggests) a splendid species recognisable with its zebra-striped foliage. In French Guiana, where we sampled its associated fauna every two weeks over an entire year, it is frequently encountered either as an epiphyte or rooted on the soil, close to creeks. At our study site, *Lutheria*, whose largest specimens retain each *ca.* 0.23 liters of water, is inhabited by 22 macroinvertebrate species, 11 of which are present throughout the year. Among the latter, despite seasonal fluctuations in air temperature and precipitation, only a few species show a peak in population density once or twice a year; the others are present at almost constant abundances. Where scraper detritivores such as *Contacyphon* (Scirtidae beetles) or *Elpidium* (small

* **Bacteriochlorophyll** : photosynthetic pigment found in certain bacteria.



Tank bromeliads sometimes host vertebrates seeking for moist refuges or, like amphibians, spending part of their life cycle as aquatic stages. On the leaf of this *Lutheria splendens* from Guiana, the frog *Osteocephalus oophagus*, a species known to lay its eggs inside the tanks of bromeliads. The female can lay eggs in several plants that she then regularly visits to supply its tadpoles with trophic eggs (photo B. Corbara).

crustaceans from the class *Ostracoda*) develop slowly with less than five generations per year, filter-feeding mosquitoes such as *Wyeomyia* can go through 22 generations per year! With so many generations massively and continuously recruiting, bromeliad invertebrate biomass as a whole is produced in somewhat important quantities. We estimated it around 24 grams of animal dry matter per square metre of tank surface, which is comparable to what can be found in lakes and rivers worldwide. Another extrapolation, despite the uncertainty inherent to such exercises, allowed us to conclude that on one hectare at our study site, *Lutheria* plants annually produced 225 grams dry weight of invertebrates. It seems few, but let's not forget it is mostly tiny mosquitoes.



Like other mosquitoes, *Toxorhynchites* have aquatic larvae and terrestrial adults. However, whilst most mosquito larvae are filter-feeders, *Toxorhynchites* larvae are top predators. The adult is a large, non-biting mosquito, which feeds on nectar. Here, an adult male *Toxorhynchites haemorrhoidalis* from French Guiana (photo C. Bonhomme).



The bromeliad *Aechmea mertensii* only grows in ant gardens. Characterized by large inflorescences with bright red bracts, the plant looks different depending on which ant species initiated the garden. On this garden hosting the ants *Camponotus femoratus* and *Crematogaster limata*, the plant shows long leaves spreading almost horizontally (photo B. Corbara).

Ants and tank inhabitants

Let's leave *Lutheria splendens* on the banks of the creeks they appreciate, and reach the edge of this Guianese rainforest. There, another bromeliad is frequent : *Aechmea mertensii*, whose presence is sometimes revealed by the superb bright red bracts decorating the base of its inflorescences. Throughout the Amazon and the Guianas, *A. mertensii* grows on "ant gardens". In these peculiar associations, the seeds of a few epiphytes (including those of our *Aechmea*) are attractive to ants, which incorporate them in the walls of their arboreal nest, built with a rich loamy "carton". Germinating on a suitable substrate, the seedlings grow firm roots, wrapping the branch and anchoring the nest on the supporting tree. The epiphytes keep on growing, and so does the nest and the ant colony (and the supporting tree), thereby ending up with a reinforced site for long-term nesting. *Aechmea mertensii* are found in "gardens" initiated by the ant *Neoponera goeldii*, or by two ant species living together in parabiosis*, *Camponotus femoratus* and *Crematogaster limata*. The parabiotic

associates usually establish their common nest (and therefore their garden) under the shade on the edge of a forest. In order to get as much sunlight as possible under these conditions of relative low light, each *Aechmea* grows very long leaves, spreading them almost horizontally. Together, these leaves form a very effective "catchment basin". Provided with a lot of water, the tanks also collect large amounts of organic matter coming from the overhanging tree foliage. Conversely, being a pioneer ant species, *Neoponera goeldii* builds its nests on small trees along the edge of the forest. Its gardens develop in full light, and the *Aechmea* growing there develop in an amphora shape : their short leaves grow vertically, so as to minimise the harmful effects of excessive exposure to sunlight. The usable area of their catchment basin is reduced, and little water enters the tanks which, in addition, are faced with a strong

Aechmea mertensii from an ant garden inhabited by *Neoponera goeldii*. Here, the plant has a typical amphora shape (photo B. Corbara).



* **Parabiosis** : the association of two ant societies from different species, which share their nest and foraging trails (but keep their broods in separate locations).

risk of evaporation. For the same reason, the plants collect little organic matter, also because the overhanging tree foliage is scarce.

Therefore, depending on which ant species initiated the garden, the *Aechmea* tanks are supplied with more or less nutrients. Consequently, they host different aquatic communities : *Neoponera goeldii*-associated *Aechmea* have smaller tanks, containing fewer macroinvertebrate species (and individuals), than those growing in the gardens of *Camponotus* and *Crematogaster*.

By associating with this tank-forming plant, ants are leading the way for ecologists : by placing a single bromeliad species in various locations subject to various ecological conditions (sometimes only a few metres away from each other), they create a nearly-perfect experiment. Studying these two contrasting conditions in which ants initiate their gardens helped us better understand how aquatic micro-ecosystems work, and how the latter interact with the plants. Indeed, this natural circumstances inspired our “real” experiments on other tank bromeliads!

Experimental models

Biologists are accustomed to reasoning and generalising from model species : we know how much genetics owes to *Drosophila* and peas, for instance. For about fifteen years already, and especially since the work of Diane Srivastava from the University of British Columbia in Vancouver, the miniature ecosystem hosted by bromeliads is regarded as a relevant model system for field experiments and the testing of predictions.

First, the ecosystem being physically enclosed in the tanks of a plant, it is easy to define its boundaries and, therefore, what comes in or gets out. Moreover, since bromeliad tanks host rather simple communities, it is easy to exhaustively record the macroorganism species found in a plant. Regarding microorganisms, a single tank is however in itself a whole universe. Besides, even if they often occur in patches on a same location where they form genuine aquatic metacommunities*, bromeliads can be easily moved for experimental purposes.



Overview of the understorey vegetation from the Guianese forest, with a specimen of the bromeliad *Lutheria splendens* at the base of a tree trunk. This epiphytic species can be easily recognised thanks to its zebra-striped foliage, and is typical of humid lowlands (photo B. Corbara).

All these criteria enable the plants together to be submitted to controlled conditions in the field, and in which it is possible, for instance, to experimentally change the number of detritivores, predators, and so on.

A fundamental ecological process

Detrital decomposition of organic matter is an ecological process of major importance. Therefore, in most experimental studies conducted in bromeliads, decomposition rate is often examined as a relevant indicator of ecosystem functioning.

In an experiment carried out in French Guiana, we introduced carefully measured dead leaf pieces into bromeliad tanks, either allowing the detritivorous macroorganisms (shredders, scrapers and collectors) to access the leaf resources, or preventing them from doing so by using a fine-mesh net. In both cases, microorganisms could reach the leaf pieces. It turned out that regardless of the surrounding environment (under the shade of the understorey or in full sunlight) or the leaf species we tested, significant variations in the composition and biomass of the detritivorous invertebrates did not significantly affect leaf litter decomposition.

* **Metacommunities**: set of local communities interacting through the dispersal of individuals.

In fact, microorganisms ensure most of the decomposition process in the Guianese bromeliads. Compared to other locations in tropical and subtropical America, there are relatively few leaf shredders living in these bromeliads. Hence, whilst our results cannot be generalised to the Neotropics, they show the importance of carrying out comparative studies on a continental scale.

A network to study networks

The knowledge of bromeliad ecosystems made great progress during the last decade in part because it benefited from collaborative research within an international network, the *Bromeliad Working Group* (BWG). Once constituted, this group of researchers decided, amongst other goals, to replicate standardized experiments on the aquatic communities of bromeliads in different countries covering the Neotropical region. Supported by the Agence Nationale de la Recherche (ANR, French National Research Agency), the Rainwebs program falls within the same approach. In a context of global climate change, Rainwebs aims at studying how shifts in precipitation patterns can impact the functioning of the bromeliad ecosystems in French Guiana, Puerto Rico and Costa Rica. Overall, according to our first results, the functioning of bromeliad ecosystems should better resist changes in precipitation patterns,

A database for ecological data

One of the goals of the *Bromeliad Working Group* (BWG) was to create and maintain a database of species living in bromeliad tanks, covering the entire neotropical range of bromeliads, and including as much biological and environmental information as ecologists can use. BWG members are supported in this task by the french Centre for the synthesis and analysis of biodiversity (CESAB), through the FunctionalWebs program. FunctionalWebs aims at organising and analysing data on the functional traits* of the aquatic organisms living in bromeliads. The database is regularly updated with new or complementary

information regarding body size, morphology, dispersal mode, desiccation tolerance, but also respiration, locomotion, defensive morphologies, etc.

More than 850 macroorganism species (more exactly morpho-species*), collected from bromeliads sampled from Mexico to Argentina, have been recorded in the database thus far. They belong to 46 insect families and 11 non insect taxa, 60 % of the insects being Dipterans. Among them, culicid mosquitoes unsurprisingly dominate the charts, with more than 120 morphospecies listed.

* **Functional traits**: biological, physiological and ecological attributes which predict how species interact with their environment.

* **Morphospecies**: a collection of individuals with similar morphology.



Using a pipette to remove the contents of the tanks without destroying the plant, here a *Vriesea pleiosticha* in French Guiana (photo B. Corbara).

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and particularly drought episodes, in regions of the world where invertebrate communities show higher species richness. On the basis of climate scenarios for the next century, the inhabitants of the tanks should be able to maintain functional food webs. Nonetheless, this prediction only applies if their surrounding environmental conditions, such as the integrity of the forest, are sufficiently preserved.

Most aquatic larvae living in the tanks belong to species that also spend part of their life cycle as terrestrial adults, and the tank microworlds only function because they are connected through the dispersal of adults.

In order to properly take this aspect into account, in a next stage in our research we will consider bromeliads as island archipelagos, where adult individuals (for instance females born in one bromeliad and laying eggs in another one) establish metacommunities. A true experimental challenge we are eager to take up. ■

This article is dedicated to the memory of Raphaël Boulay (1973-2018), our late myrmecologist colleague and fellow through our adventures in French Guiana.

Learn more

- > **Dézerald O., Leroy C., Corbara B., Dejean A., Talaga S. & Céréghino R., 2016** – “Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads”, *Freshwater Biology*, 62, p. 229-242 (doi : 10.1111/fwb.12862).
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- > **Leroy C., Carrias J.-F., Céréghino R. & Corbara B., 2016** – “The contribution of microorganisms and metazoans to mineral nutrition in bromeliads”, *Journal of Plant Ecology*, 6, p. 241-255 (doi : 10.1093/jpe/rtv052).
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