

The contribution of microorganisms and metazoans to mineral nutrition in bromeliads

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Abstract

Aims

One critical challenge for plants is to maintain an adequate nutrient supply under fluctuating environmental conditions. This is particularly true for epiphytic species that have limited or no access to the pedosphere and often live in harsh climates. Bromeliads have evolved key innovations such as epiphytism, water-absorbing leaf trichomes, tank habit and Crassulacean acid metabolism (CAM) photosynthesis that enable them to survive under various environmental conditions. Bromeliads encompass diverse ecological types that live on different substrates (they can be terrestrial, epilithic or epiphytic) and vary in their ability to retain water (they can be tank-forming or tankless) and photosynthetic pathway (i.e. C3 or CAM). In this review, we outline the nutritional modes and specializations that enable bromeliads to thrive in a wide range of nutrient-poor (mostly nitrogen-depleted) environments.

Important Findings

Bromeliads have evolved a great diversity of morphologies and functional adaptations leading to the existence of numerous nutritional modes. Focusing on species that have absorptive foliar trichomes, we review evidence that bromeliads have evolved multi-faceted

nutritional strategies to respond to fluctuations in the supply of natural nitrogen (N). These plants have developed mutualistic associations with many different and functionally diverse terrestrial and aquatic microorganisms and metazoans that contribute substantially to their mineral nutrition and, thus, their fitness and survival. Bacterial and fungal microbiota-assisted N provisioning, protocarnivory, digestive mutualisms and myrmecotrophic pathways are the main strategies used by bromeliads to acquire nitrogen. The combination of different nutritional pathways in bromeliads represents an important adaptation enabling them to exploit nutrient-poor habitats. Nonetheless, as has been shown for several other vascular plants, multiple partners are involved in nutrient acquisition indicating that there have been convergent adaptations to nutrient scarcity. Finally, we point out some gaps in the current knowledge of bromeliad nutrition that offer fascinating research opportunities.

Keywords: digestive mutualism, insect-assisted nutrients, leaf $\delta^{15}\text{N}$, multiple N sources, myrmecotrophy

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INTRODUCTION

In many ecosystems, the low availability of nitrogen (N) limits plant growth and development and is critical to photosynthetic carbon gain (Berendes and Aerts 1987; Field and

Mooney 1990). One of the most vital challenges for plants is thus to maintain an adequate supply of nutrients under such conditions. Plants have evolved both autonomous pathways (i.e. uptake systems) and association pathways (i.e. interactions with diverse mutualistic microorganisms and

metazoans) that contribute to their mineral nutrition (Kraiser *et al.* 2011). Nutritionally beneficial plant–bacteria (i.e. nitrogen-fixing plants), plant–fungi (i.e. mycorrhizal plants) and plant–arthropod interactions can, however, increase nutrient accessibility and uptake in the most nutrient-poor environments. Some vascular plants (i.e. carnivorous plants) have also evolved remarkable adaptations enabling them to utilize nutrients derived from animals.

To acquire and conserve nutrients, plants can use a great variety of strategies (Bloom *et al.* 1985). This is particularly true for epiphytic species. These plants have no (or limited, in the case of ‘suspended soils’) contact with the pedosphere, so they need to draw nitrogen from rainfall, throughfall and stemflow water and/or from decomposing canopy organic matter. Epiphytes have, thus, evolved numerous remarkable morphological, anatomical and physiological adaptations such as litter-trapping leaf arrangements (i.e. *Asplenium* ‘trash-basket’ ferns), water-storing phytotelmata (e.g. tank bromeliads), water-absorbing leaf trichomes (i.e. *Tillandsia* spp. bromeliads), velamen radicum (i.e. the spongy multiple epidermis of the aerial roots in the Orchidaceae), slippery walls (e.g. insectivorous pitfall bromeliads such as *Brocchinia reducta* and *Catopsis berteroniana*) and domatia (e.g. *Myrmecodia tuberosa*, Rubiaceae, whose name literally means ‘tuberous ant house’) that facilitate water and nutrient acquisition (Benzing 1990; Benzing and Renfrow 1974; Lüttge 2008; Pridgeon 1987). Bromeliads, one of the largest and most widespread families of vascular plants in the Neotropics, display many of these adaptations.

The Bromeliaceae family (Fig. 1) comprises ca. 3140 species and 58 genera distributed between three subfamilies: the Bromelioideae, Tillandsioideae and Pitcairnioideae (Benzing 2000; Crayn *et al.* 2004; but see Givnish *et al.* 2011 for recent systematic updates). Bromeliads are distributed throughout the entire tropical and subtropical regions of the Americas, from the southern USA to northern Argentina and one species (i.e. *Pitcairnia feliciana*) is found in tropical West Africa (Mabberley 1997). The Bromeliaceae family arose in the Guiana Shield and spread to other tropical and subtropical regions (Givnish *et al.* 2011) with an ecological range that includes extremes of moisture availability (from rain forests to arid coastal sands), elevation (from sea level to ca. 4000 m a.s.l) and exposure to sunlight (fully exposed to shaded forest understory). The ecological success corresponding to this wide geographic distribution may be explained by the development of key innovations such as epiphytism, water-absorbing leaf trichomes, tank habit and Crassulacean acid metabolism (CAM) photosynthesis that enable bromeliads to survive under different environmental conditions. Bromeliads live on different substrates (they can be terrestrial, epilithic or epiphytic) and vary in their ability to retain water (they can be tank-forming or tankless) and photosynthetic pathway (i.e. C3 or CAM photosynthetic pathways).

Bromeliads were classified by Benzing (2000) into five ecological types or life forms based on morphological and

functional attributes (Table 1). Bromeliads show varying degrees of dependency on roots *versus* leaves for nutrient acquisition. With the exception of nutritionally root-dependent terrestrial species, a unique feature of the bromeliad family is that many species are capable of absorbing water and nutrients thanks to their foliar trichomes (Fig. 2), reducing the roots to a purely mechanical support function: attaching the plants to the substrate (Martin 1994; Winkler and Zotz 2009). Therefore, their foliar trichomes have played a pivotal role in the adaptive radiation of the Bromeliaceae (Benzing 2000). This specificity motivated us to compile the present review wherein we provide an overview of the nutritional modes and specializations that enable bromeliads to thrive in a wide range of nutrient-poor (mostly nitrogen) or pulse-driven habitats. In this review, we thus focus on species that have absorptive foliar trichomes (i.e. life forms II, III, IV and V; Table 1) and exclude species with the conventional mode of nutrient absorption *via* their roots (i.e. life form I).

Nitrogen (N) and phosphorus (P) are often considered to be limiting nutrients for plant growth and reproduction (Chapin 1980). Since most studies on bromeliad nutrient acquisition principally examine nitrogen levels through stable isotope analysis (SIA) (Dawson *et al.* 2002; Stewart *et al.* 1995), we therefore focus this review on the means by which bromeliads acquire nitrogen. If terrestrial bromeliads obtain nitrogen mainly through the absorption of inorganic nitrogen from the soil *via* the root system, epiphytic bromeliads preferentially absorb organic forms (Endres and Mercier 2001). There is evidence, compiled from the available literature, that many bromeliads which do not have absorptive roots and are not supplied with inorganic soil nitrogen by microorganisms are involved in complex associations with other organisms (from microorganisms to metazoans) that provide them with nutritional inputs. Hence, it is imperative to review the latest findings and the less frequently covered aspects regarding the contribution of both terrestrial and aquatic microorganisms and metazoans to bromeliad nutrition.

ADAPTIVE SPECIALIZATION OF BROMELIADS FOR NUTRIENT ACQUISITION

Multiple environmental sources of nitrogen

The potential nitrogen sources for epiphytic bromeliads are various. Atmospherically derived nitrogen includes exogenous dry deposition (i.e. wind-borne dust, nitrogenous gases, aerosols containing ammonium and nitrate) and wet deposition (i.e. rainfall). Clouds and mist also deliver substantial inputs, in part because they contain concentrations of nutrients several fold higher than the concentrations in rainwater (Coxson and Nadkarni 1995). Atmospheric nitrogen deposition consists of dissolved inorganic nitrogen (DIN) forms such as ammonium (NH_4^+) and nitrate (NO_3^-) (Stewart *et al.* 1995) and dissolved organic nitrogen (DON) forms such as urea,



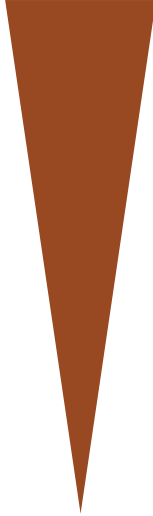
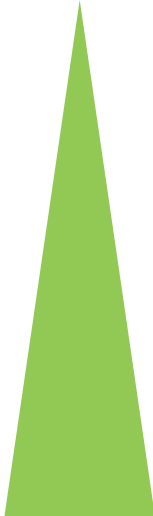
Figure 1: some representative species of bromeliads from French Guiana. Images are at different scales. (A) *Bromelia agavifolia* Brongn. and (B) *Disteganthus basilateralis* Lem. are both terrestrial bromeliads from the Bromelioideae subfamily. (C) *Pitcairnia geyskesii* L.B.Sm. (Pitcairnioideae) is a lithophytic species found on inselbergs. (D) *Tillandsia tenuifolia* (Tillandsioideae) have a silvery leaf appearance. (E) *Tillandsia bulbosa* Hook. is a Tillandsioideae often inhabited by ants. (F) *Tillandsia flexuosa* Mez. is a Tillandsioideae, i.e. found in dry habitats. (G, H) *Aechmea aquilega* (Salisb.) Griseb. is a Bromelioideae that can either be an epiphyte (G) or a lithophyte (H). (I) *Vriesea pleiosticha* (Griseb.) Gouda and (J) *Vriesea splendens* (Brongn.) Lem, both from the Tillandsioideae subfamily, have an extensive water-holding tank. (K) *Catopsis berteroniana* Mez. (Tillandsioideae) is a (proto)carnivorous tank bromeliad found in inselberg habitats. Photo credits: Céline Leroy.

amino acids, small polypeptides and other nitrogen-containing molecules (Cape et al. 2011). Canopy-derived nitrogen may also be involved, which includes DON leached from canopy leaves, stems or epiphytes or deriving from decomposing canopy organic matter (e.g. canopy soils, litter in tanks). Nitrogen can also derive from free-living, atmospheric nitrogen microbial fixers. Finally, bromeliads benefit from external sources of biotic nitrogen *via* the insects and vertebrates foraging, reproducing and spending part-time in the plants (see later chapters). In addition to this wide range of nitrogen sources, the delivery of nutritive inputs varies according to the season. Nutrient supply is thus temporally largely restricted to the wet season. Although precipitation tends to be higher in nutrient concentrations during the dry season compared with the wet season (Nadkarni 1984), the greater volume of wet-season

rainfall considerably decreases dry-season contributions to total inputs (Gonçalves et al. 2011; Romero et al. 2010).

Given such heterogeneous nitrogen availability, Benzing (1990) defined two functional groups ranging from pulse-supplied atmospheric bromeliads (life form V) to continuously supplied tank bromeliads (life forms III and IV). For atmospheric bromeliads, nutrients are only available during precipitation events, which are followed by dry periods of very low nutrient availability. The bromeliads growing in such nutrient pulse-supplied environments are thought to be adapted to these conditions: they can also take up inorganic nitrogen (and other nutrients) and show effective nutrient retention strategies (Chapin 1980). During precipitation events, bromeliads with these traits can absorb nutrients in excess of their immediate growth

Table 1: life forms and ecophysiological types of Bromeliaceae (according to Benzing 2000)

Life forms	Characteristics	Water and nutrient acquisition by the roots	Water and nutrient acquisition by the leaves
1	Terrestrial bromeliads belonging to the Pitcairnioideae (CAM and C3) and many Bromelioideae (CAM) that use roots to acquire water and nutrients, the trichomes being non-absorbent		
2	Terrestrial Bromelioideae (CAM) with leaf bases that form a rudimentary watertight 'tank' into which some axillary roots may grow		
3	Terrestrial or epiphytic Bromelioideae, the roots of which have less importance in water and nutrient acquisition with the leaf bases forming an extensive water-holding tank—predominantly crassulacean acid metabolism (CAM) photosynthetic pathways, with trichomes that have the capacity to take up water and nutrients		
4	Tank-forming epiphytes belonging to the Tillandsioideae and some Brocchinia—predominantly C3 photosynthetic pathways and with high densities of trichomes on the leaf bases that are highly effective at water and nutrient uptake, the roots functioning primarily as holdfasts		
5	Atmospheric CAM photosynthetic pathway Tillandsioideae that are epiphytic or lithophytic, with leaf hairs taking up water directly over the entire leaf surface (without a tank) and possessing holdfast roots, if any		

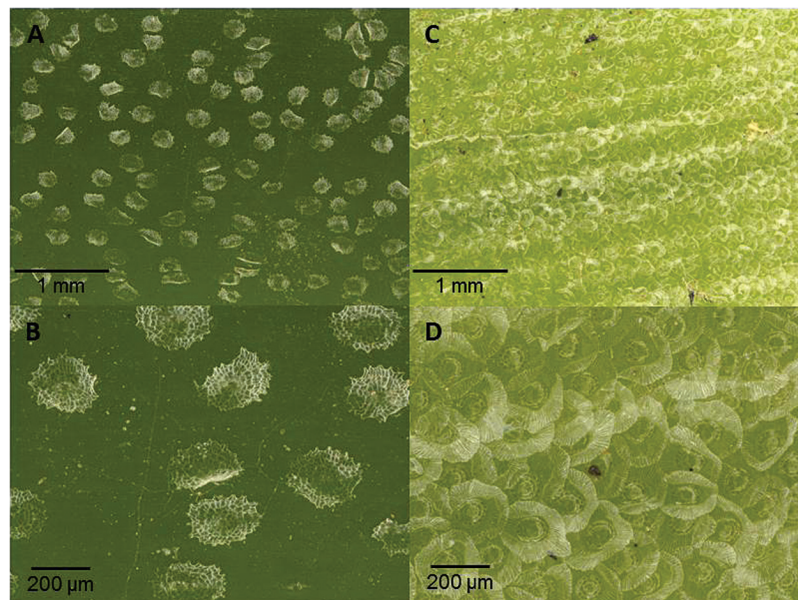


Figure 2: leaf blade surfaces of the tank bromeliad *Aechmea mertensii* Schult.f (A, B) and the atmospheric *Tillandsia tenuifolia* L. (C, D) illustrating various trichome densities. Observations were made with a macroscope (Leica Z16 APO, Nanterre, France) and photographs taken with a digital camera (Leica DFC 450, Nanterre, France). Photo credits: Céline Leroy.

requirements. Thereafter, these reserves are used to support growth when nutrients for plant uptake are scarce (i.e. 'luxury consumption'; Chapin 1980). On the other hand, continuously supplied bromeliads can store water and nutrients to buffer the plant against irregular precipitation inputs, thus reducing water and nutrient stresses. Besides nitrogen, rainwater may contain other elements, such as magnesium (Mg), potassium (K) and phosphorus (P) that are also available for epiphytes (Schroth *et al.* 2001).

Atmospheric bromeliads: the fundamental role of water-absorbing trichomes

Life form V bromeliads are the atmospheric bromeliads. They represent an extreme life form capable of absorbing water and nutrients directly from atmospheric sources thanks to foliar trichomes (Benzing 1990) which are absorptive and serve as one-way valves, allowing moisture and nutrients to enter into the plant and preventing moisture loss (Benzing 1976; Benzing and Burt 1970). Bromeliad trichomes are complex multicellular

structures composed of a shield of empty cells and a stalk of several living ones located in a concavity within the foliar epidermis (Benzing 2000). When rainwater moistens a leaf, the dead cells of each trichome cap fill and the liquid is then directly absorbed by the live cells of the trichome stalk. When the leaf surface dries, the cap cells drain and a vapor lock is established, preventing further water loss from the live stalk cells. Atmospheric bromeliads have a high density of trichomes that cover the entire leaf surface, allowing a high level of light reflectivity when the leaf surface is dry and producing the silvery appearance of the leaves (Fig. 2). Water-absorbing trichomes and the fine roots of other terrestrial plants, although very different in morphology and anatomy, share comparable biochemical properties and autonomous uptake mechanisms (Winkler and Zotz 2010).

Atmospheric bromeliads are the most strongly ^{15}N depleted (i.e. have the most negative $\delta^{15}\text{N}$ values; Table 2) and are thus thought to obtain nitrogen from ^{15}N -depleted atmospheric sources (i.e. precipitation, fog), whereas more ^{15}N -enriched values may originate from organic host tree matter (e.g. leaf litter, decomposing bark), the canopy soils found on tree branches and trunks or from animal detritus (e.g. feces,

decaying invertebrates) (Hietz et al. 1999; Stewart et al. 1995). Differences in foliar $\delta^{15}\text{N}$ may also be related to environmental conditions. The most relevant abiotic factor that affects epiphyte nutrition and, thus, growth is the availability of water (Zotz and Hietz 2001). The leaf $\delta^{15}\text{N}$ of epiphytes may also vary with elevation (Cardelus and Mack 2010; Hietz et al. 1999). Greater elevation leads to ^{15}N depletion that could be caused by changes in atmospheric versus terrestrial nitrogen sources. The position of epiphytic bromeliads in the canopy may also affect nitrogen nutrition and $\delta^{15}\text{N}$ values. The nitrogen sources that are available for the epiphyte and their $\delta^{15}\text{N}$ signature differ from the lower to the upper canopy. Leaves sampled from different canopy strata provide evidence of a vertical $\delta^{15}\text{N}$ gradient ranging from more positive values in the lower zones to more negative values in the upper ones (Wania et al. 2002). The lower canopy receives more runoff from branches and leaves, and more litter from the host tree accumulates there compared with the upper canopy. A horizontal N and $\delta^{15}\text{N}$ gradient has also been shown. As a result, epiphytes in the outer crowns have lower nitrogen concentrations and more negative $\delta^{15}\text{N}$ values than do those in the

Table 2: nitrogen stable isotopes of different bromeliad species according to biotic and/or abiotic variations

Life forms	Species	Subfamily	Biotic and/or abiotic variations	Leaf $\delta^{15}\text{N}$ (‰)	References
2	<i>Ananas comosus</i>	Bromelioideae	Spiders (dry → wet season)	+1.71 → +5.19	Gonçalves et al. (2011)
2	<i>Bromelia balansae</i>	Bromelioideae	Spiders (absence → presence)	+1.88 → +3.21	Romero et al. (2006)
2	<i>B. balansae</i>	Bromelioideae	Spiders (low → high density)	1.1 → +4.83	Romero et al. (2008)
2	<i>B. balansae</i>	Bromelioideae	Spiders (dry → wet season)	+1.84 → +6.66	Gonçalves et al. (2011)
2	<i>Streptocalyx longifolius</i>	Bromelioideae	Ants (<i>Camponotus femoratus</i>)	-0.40	Leroy et al. (2013)
3	<i>Aechmea aquilega</i>	Bromelioideae	No	-0.19	Leroy et al. (2013)
3	<i>Aechmea bromeliifolia</i>	Bromelioideae	No	+0.55	Leroy et al. (2013)
3	<i>Aechmea distichanta</i>	Bromelioideae	Spiders (dry → wet season)	-1.03 → +14.57	Gonçalves et al. (2011)
3	<i>Aechmea mertensii</i>	Bromelioideae	Ants (<i>Neoponera goeldii</i> → <i>C. femoratus</i>)	+0.54 → +1.64	Leroy et al. (2009a)
3	<i>Neoregelia cruenta</i>	Bromelioideae	No	-2.7	Reinert et al. (1997)
4	<i>Catopsis berteroniana</i>	Tillandsioideae	(Proto)carnivorous	-1.05	Leroy et al. (2013)
4	<i>Guzmania lingulata</i>	Tillandsioideae	No	-0.56	Leroy et al. (2013)
4	<i>Guzmania monostachia</i>	Tillandsioideae	Ontogenetic shift (atmospheric → tank)	-6.6 → -0.8	Reich et al. (2003)
4	<i>Vriesea bituminosa</i>	Tillandsioideae	Frogs (absence → presence)	-0.5 → +0.1	Romero et al. (2010)
4	<i>Vriesea gladioliflora</i>	Tillandsioideae	Ontogenetic shift (atmospheric → tank)	-6.6 → +0.6	Reich et al. (2003)
4	<i>Vriesea pleiosticha</i>	Tillandsioideae	No	-0.19	Leroy et al. (2013)
4	<i>Vriesea sanguinolenta</i>	Tillandsioideae	Size class (small tank → large tank)	-2.2 → -1.3	Wanek and Zotz (2011)
4	<i>Vriesea splendens</i>	Tillandsioideae	No	+0.64	Leroy et al. (2013)
5	<i>Tillandsia butzii</i>	Tillandsioideae	No	-12.2	Hietz and Wanek (2003)
5	<i>Tillandsia juncea</i>	Tillandsioideae	No	-12.6	Reich et al. (2003)
5	<i>Tillandsia landbeckii</i> ^a	Tillandsioideae	Fog (low → high intensity)	-4.01 → +0.32	Latorre et al. (2011)
5	<i>Tillandsia punctulata</i>	Tillandsioideae	No	-10.4	Reich et al. (2003)
5	<i>Tillandsia stricta</i>	Tillandsioideae	No	-11.2	Reinert et al. (1997)
5	<i>Catopsis sessiliflora</i>	Tillandsioideae	No	-5.8	Reich et al. (2003)

$\delta^{15}\text{N}$ data are given as means or as mean ranges (→) depending on the biotic and/or abiotic variations.

^aThe establishment of the terrestrial *Tillandsia landbeckii* was possible thanks to moisture from fog in a desert condition (Gonzalez et al. 2011). Because these plants do not have functional roots and acquire all of their moisture from fog, they are considered atmospheric bromeliads.

inner crowns likely due to the lower nitrogen concentrations and the more ^{15}N -depleted isotope signatures of rainfall as it reaches the epiphytes in the outer crown (Hietz *et al.* 2002).

Tank bromeliads

The leaves of tank bromeliads (i.e. life forms III and IV) are tightly interlocking, forming compartments that collect considerable amounts of water and debris, which in turn attract a great variety of terrestrial and aquatic organisms (Frank and Lounibos 2009). The contents of the tanks have often been considered organic soils rich in nutrients which are available to the epiphyte (Pittendrigh 1948). Although less abundant than in the case of atmospheric bromeliads, the water-absorbing trichomes that are present on the leaf surfaces of tank bromeliads (Fig. 2) ensure that moisture and nutrients are absorbed *via* the autonomous pathway. The basal and apical parts of the leaf are generally exposed to distinct environmental conditions in terms of light, shade, water and nutrients and, accordingly, these foliar regions carry out different physiological functions (Freschi *et al.* 2010; Medina *et al.* 1994; Popp *et al.* 2003; Takahashi and Mercier 2011; Takahashi *et al.* 2007; Zotz *et al.* 2002). The leaf bases, characterized by numerous trichomes with large shields, are in direct contact with the water and nutrients that accumulate in the tank and they have the ability to absorb these resources. The top portions of the leaves, with low trichome density and numerous stomata, are more exposed to light and are devoted to gas exchange (Benzing 2000).

The $\delta^{15}\text{N}$ values for tank bromeliads are much higher than for the atmospheric ones, reflecting the contribution of the terrestrial litter inputs and decomposition activities of the aquatic food web to nutrient acquisition (Table 2). Inter- and intra-specific variations in foliar $\delta^{15}\text{N}$ may be due to ultimate (i.e. biotic and abiotic factors; see below) and proximal causes (i.e. the plant's developmental stage). It has been shown that both foliar N and $\delta^{15}\text{N}$ shift with plant ontogeny in the Tillandsioideae (Hietz and Wanek 2003; Reich *et al.* 2003; Zotz *et al.* 2004) but not in the Bromelioideae (Petit *et al.* 2014). Young tillandsioid bromeliads that have not yet developed tanks depend on atmospheric inputs and are more ^{15}N depleted compared with older plants that form a tank (Hietz and Wanek 2003).

THE CONTRIBUTION OF ROOT- AND LEAF-ASSOCIATED ORGANISMS

Nutritional assistance from bacteria and fungi

Bromeliads nutritionally benefit from associations with free-living bacteria (e.g. diazotrophs, decomposers) and fungi (e.g. mycorrhizae, fungal decomposers). Some atmospheric *Tillandsia* have been found to harbor free-living, N_2 -fixing bacterial microflora on their leaf surfaces (Brighigna *et al.* 1992). Nitrogen fixation in the atmospheric *Tillandsia* phyllosphere occurs only under specific conditions (i.e. a wet environment) probably because the nitrogen-fixing bacteria living on these leaves are soil or water inhabitants that are not completely adapted to a foliar environment (Brighigna

et al. 1992). Moreover, terrestrial bromeliads, such as *Bromelia balansae* (life form II) that have well-developed roots in contact with the soil, can absorb nutrients through their leaves. In this species, the mineralization of organic compounds by phyllospherical bacteria highly contributes to plant nutrition (Gonçalves *et al.* 2014). Potentially diazotrophic bacteria have recently been found in the phyllosphere of tank bromeliads (Giongo *et al.* 2013).

Another possible source of nitrogen may be the presence of arbuscular mycorrhizal fungi (AMF) in epiphytic bromeliads (Janos 1993). The occurrence of AMF in epiphytic bromeliad species is strongly dependent on the quantity of the substrate and the bromeliad species. Rabatin *et al.* (1993) found *Glomus tenue* to be the main AMF species associated with bromeliad species such as *Aechmea lasserii*, *Vriesea splendens* and *Vriesea platynema* (life forms III and IV) in a Venezuelan cloud forest. Rowe and Pringle (2005) showed that the Costa Rican montane cloud forest epiphyte *Vriesea werkleana* (life form IV) is also associated with AMF species mainly belonging to the genus *Glomus*. In a Brazilian Atlantic rain forest, Grippa *et al.* (2007) found only three bromeliad species associated with AMF among 13 species from the genera *Aechmea*, *Bilbergia*, *Nidularium*, *Tillandsia* and *Vriesea*. Finally, Allen *et al.* (1993) did not find any AMF associated with the epiphytes *Tillandsia bartramii*, *Tillandsia balbisiana* (both life form V) and *Catopsis nutans* (life form IV) in a Mexican tropical forest. Lugo *et al.* (2009) showed that epiphytic bromeliads, from an arid area in central Argentina, were not associated with AMF but rather with dark septate endophytes (DSE), whereas the terrestrial ones formed AMF-DSE associations. DSEs may be involved in host nutrient acquisition and therefore may have a mutualistic, mycorrhiza-like relationship with their host plants (Jumpponen and Trappe 1998). In any case, the relatively low occurrence of mycorrhizal associations with epiphytic bromeliads might be explained by the dry and exposed habitat and/or low photosynthetic activity, not sufficient to support symbiotic fungi (Lesica and Antibus 1990).

Bromeliads fed by ants: myrmecotrophy

Interactions between ants and plants are widespread in the Tropics. The plants greatly benefit from the anti-herbivory effect of ants, and bromeliads provide habitat and shelter to a great variety of ant taxa (e.g. Hammill *et al.* 2014). The strength of the ant–bromeliad interaction ranges from a few strictly ‘myrmecophytic’ bromeliad species with morphological modifications to more commonly ‘non-myrmecophytic’ species such as typical tank bromeliads (Davidson and Epstein 1989; Huxley 1980). Besides protection, the ants may also provide direct nutritional benefits (known as ‘myrmecotrophy’) to the plant (Beattie 1989).

Some epiphytic species from various taxa, including the tank bromeliad *Aechmea mertensii*, occur only in association with arboreal ant gardens that are a particular type of ant–plant interaction frequent in both the Neotropics and Southeastern Asian Paleotropics (see the review by Orivel and Leroy 2011).

In French Guiana, ant gardens are initiated either by the ant *Neoponera goeldii* (until recently known as *Pachycondyla goeldii*; Schmidt and Shattuck 2014) or by *Camponotus femoratus* (Corbara and Dejean 1996; Orivel and Leroy 2011). Leroy et al. (2012) have provided evidence that these two ant species may play a direct role in supplying nutrients to *A. mertensii*. The results from a ^{15}N -enrichment experiment indicated that *C. femoratus*-associated plants had higher leaf $\delta^{15}\text{N}$ values compared with *N. goeldii*-associated bromeliads. This indicates that *C. femoratus* ants might be better able to pass nitrogen to the host plant compared with *N. goeldii*. While it has commonly been stated in the literature that the roots of epiphytic (both atmospheric and tank forms) bromeliads have no nutrient-absorbing function, this experiment demonstrated that a tank bromeliad, *A. mertensii*, in an ant garden is able to acquire nutrients through its roots. The study by Petit et al. (2014) supports this idea as the leaves of the seedlings are characterized by a lack of absorptive trichomes (which is not the case for young Tillandsoid bromeliads) and, thus, water and nutrient acquisition are only possible *via* the roots. Overall, although ants have a positive influence on the supply of nutrients to bromeliads (Leroy et al. 2013), the species of associated ant is of great importance and may play a key role in shaping plant fitness and evolution.

Myrmecotrophy has been demonstrated for various taxonomically distinct epiphytic species inhabited by ants (Bazile et al. 2012; Beattie 1989; Gegenbauer et al. 2012; Treseder et al. 1995; Watkins et al. 2008), but just once (*A. mertensii*) for tank bromeliads (Leroy et al. 2012). Some atmospheric *Tillandsia* spp. (Frank et al. 2004; Huxley 1980) and tank bromeliads from the *Aechmea*, *Guzmania* and *Vriesea* genera (Blüthgen et al. 2000; Dejean and Olmsted 1997; Dejean et al. 1995) are known to form close, mutualistic associations with ants. These ants either nest in the dry outer leaf axils of plants that retain water in their inner axils, in domatia at the base of the leaf consisting of chambers containing absorptive trichomes, or in a central waterproof cavity. By storing food, gathering debris or through defecation, ants can accumulate organic matter in their nesting sites (Beattie 1989) and contribute to the nutrition of plants by supplying nitrogen, something that leads us to assume that myrmecotrophy may be more widespread and probably more prevalent than previously thought, and, thus, certainly requires much more study.

THE PHYTOTELM AND AQUATIC BIOTA

A discrete detritus-based ('brown') food web: biota-assisted, saprophytic tank bromeliads

Phytotelmata are defined as water bodies held and enclosed by living plants (Kitching 2000). These small pools provide discrete freshwater habitats for specialized invertebrates (Frank 1983; Kitching 2000; Richardson 1999), vertebrates such as anurans and diverse microorganisms such as bacteria (Cochran-Stafira and von Ende 1998), algae (Brouard et al. 2011; Laessle 1961; Maguire 1971), fungi (Brouard et al.

2012) and protozoa (Carrias et al. 2001; Foissner et al. 2009), which altogether constitute an aquatic food web (Fig. 3). Detritus (i.e. wind-borne particulates, feces and dead leaves and animals) is the main source of energy and nutrients for the macroinvertebrates and microbial food webs living in tank bromeliads (Benzing 1990, 2000; Richardson 1999) as well as of nutrients for the host plant itself (Inselsbacher et al. 2007; Reich et al. 2003). Aquatic macroinvertebrates are the major contributors to litter breakdown at all stages, from coarse particulate organic matter (CPOM; >1000 μm in size) to the fine particulate organic matter (FPOM; <1000 μm in size) which is washed into the base of the phytotelm. Detritivores can be divided into shredders (e.g. Psychodidae, Tipulidae) and scrapers (e.g. Scirtidae) that feed on CPOM,

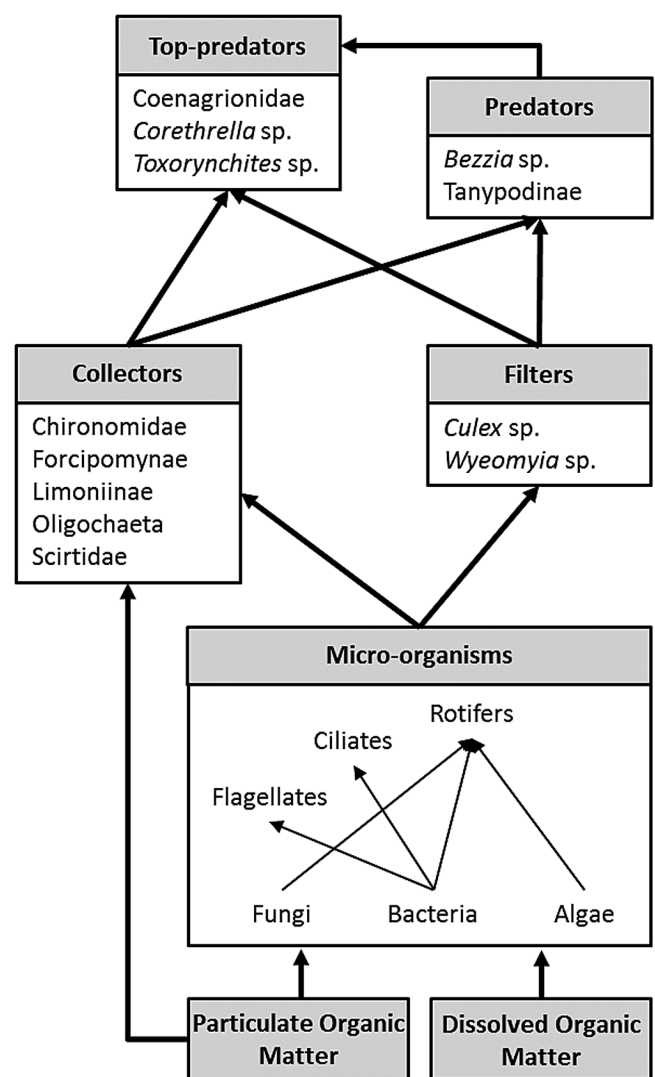


Figure 3: diagrammatic representations of the detrital food web of a hypothetical tank bromeliad. The dominant organisms are presented according to functional groups (i.e. micro-organisms, filter-feeders, collectors, predators and top predators) and arrows show the proposed energy pathways (adapted from Brouard et al. 2012).

and collectors (e.g. Chironomidae, Naididae) and filter feeders (e.g. Culicidae) that feed on FPOM. All of these aquatic invertebrates produce fecal pellets that fuel the microbial compartment, which then decomposes and mineralizes the organic matter into organic and inorganic N compounds and release CO₂ and other nutrients alongside that can be absorbed directly by the bromeliads. A great variety of microorganisms are also capable of decomposing lignin, pectin and cellulosic materials as well as chitin (Manuchavora 2009) that are the main components of the leaf litter and the exoskeletons of arthropods. Bermudes and Benzing (1991) demonstrated the presence of cyanobacteria in the phytotelmata of both terrestrial and arboreal *Aechmea*, *Guzmania*, *Tillandsia* and *Vriesea*. A combination of constant moisture and nutrients (e.g. K, P) released by the litter accumulated in the tank may favor atmospheric N₂ fixation by cyanobacteria that significantly ameliorates bromeliad nutrition in terms of nitrogen. This N₂ fixation by microorganisms living in the tank might to some extent account for the ¹⁵N depletion in the bromeliad (Bermudes and Benzing 1991). Moreover, several fungi from basidiomycetous and ascomycetous species have been reported within the phytotelmata of bromeliads (Araújo *et al.* 2012; Safar *et al.* 2013).

Bacterivorous organisms (mainly phagotrophic protists and rotifers) constitute the first predatory level in the phytotelma food web. Also, protists are mediators of certain fundamental processes (Corliss 2002); e.g. phagotrophic forms are known to control microbial prey and release large amounts of DIN (Sherr and Sherr 2002). Their fundamental roles derive from their small size and high growth rates, and the fact that they provide essential organic nutrients to higher trophic levels (Arndt 1993; Stoecker and Capuzzo 1990). This detrital microbial food web is largely controlled by filtering mosquito larvae (Addicott 1974; Frank 1983). Nitrogen is made available to the plant through the bacterial decomposition of organic matter, and the presence of arthropod predators (e.g. Odonata Coenagrionidae; Diptera Corethrellidae, Culicidae Toxorhynchitini) in the phytotelmata food web most likely accelerates nitrogen cycling and leaf assimilation (Ngai and Srivastava 2006). Indeed, most detritivorous insect larvae pupate rapidly and constitute a loss of litter-derived nitrogen for bromeliads when they emerge and leave the tank. Predators limit this loss by preying upon them and defecating in the tank (Table 2).

A complementary 'green' food web

In addition to detritus, a few studies have reported the presence of algae in tank bromeliads (Brouard *et al.* 2011, 2012; Laessle 1961; Maguire 1971; Marino *et al.* 2011). For the carnivorous pitcher plant *Sarracenia purpurea* (Sarraceniaceae), Gebuhr *et al.* (2006) found a significant algal community growing in the pitchers, suggesting that algae might constitute an important complementary food source for predators and an indirect supply of nutrients for the plant. While the role of detritus in bromeliad aquatic food webs ('brown' food

webs) is well known, the role of algae as a potential energy source has been poorly documented. Recently, Brouard *et al.* (2011) found that algae are able to develop in the tanks of different species of bromeliads. Interestingly, the bromeliad species plays a significant role in shaping the algal community and its diversity (Carrias *et al.* 2014). The highest occurrence of algae was found in bromeliads exposed to light where the algae act as primary producers. They represent a relevant functional community and might form the basis of a complementary non-detrital food web (the 'green' food web), therefore increasing the complexity of the entire aquatic food web (Brouard *et al.* 2012). Algae, indeed, represent a significant source of organic carbon for filter-feeders such as mosquito larvae. However, the role of algae in tank-bromeliad nutrition and how the algae and the bromeliad interact are still largely unexplored topics.

An alternative pathway to prey digestion by carnivorous plants

The most common example of metazoans that contribute to plant nutrition concerns carnivorous plants (Adamec 1997; Anderson 2005). The carnivorous syndrome in angiosperms corresponds to plants that attract, trap and digest prey and absorb the nutrients from that prey (Givnish 1984). Plants that do not possess the digestive function are referred to as 'protocarnivores', 'subcarnivores' or 'paracarnivores' (Darnowski *et al.* 2006; Rice 2011). However, some studies suggest that plants do not need conventional digestive organs to be considered carnivorous (Anderson and Midgley 2003; Nishi *et al.* 2013). To date, the use of 'protocarnivory' or 'true carnivory' to define certain cases is still under debate in the scientific community. Although this is not the core subject of this review, deep thought must be given to the definition of 'carnivorous' plants.

Among the Bromeliaceae, three tank bromeliads are considered (proto)carnivorous species: *Brocchinia reducta* Baker and *Brocchinia hechtiioides* Mez. (life form II) from the Pitcairnoideae subfamily and *C. berteroniana* (Schult. & Schult.f.) (life form IV) from the Tillandsioideae (Frank and O'Meara 1984; Givnish *et al.* 1984; Król *et al.* 2012). The leaves of these bromeliads are coated with a powdery wax that plays a central role in attracting and trapping insects in the pitfall-like plant (Gaume *et al.* 2004). Whereas all other tank bromeliad species have the same leaf organization, they are considered non-carnivorous because their nutrition is litter rather than animal-based (Rice 2011). Because these three (proto)carnivorous bromeliads do not produce enzymes to digest prey, they depend on the aquatic biota to carry out digestive functions, a process that occurs in the water of all tank bromeliads. The digestion of prey requires enzymes secreted by bacteria, fungi or even the digestive apparatus of other aquatic biota that feed on trapped prey, a situation which, to a certain degree, may be comparable with the widespread symbioses occurring between metazoans and their digestive microorganisms (Gilbert *et al.* 2012; McFall-Ngai *et al.* 2013). Thus, prey digestion by aquatic biota occurs over multiple trophic levels. This alternative method

of prey digestion to the carnivorous syndrome reduces the costs of having to produce digestive structures and enzymes (Anderson and Midgley 2003).

Carnivorous plants, which derive nitrogen from ^{15}N -rich insect tissues, are usually characterized by higher $\delta^{15}\text{N}$ values compared with non-carnivorous plants (Moran et al. 2001; Schulze et al. 1997). *Catopsis berteroniana*, which relies on decaying insects (Frank and O'Meara 1984) for its nutritional needs, does not have high $\delta^{15}\text{N}$ values as expected but rather low $\delta^{15}\text{N}$ (Table 2). Such low $\delta^{15}\text{N}$ values indicate that *C. berteroniana* depends on ^{15}N -depleted sources. On a sun-exposed inselberg, the plants may harbor bacteria or/and cyanobacteria in their tanks that are able to fix the ^{15}N -depleted N_2 (Bermudes and Benzing 1991) responsible for foliar $\delta^{15}\text{N}$ close to 0‰ (Robinson 2001). Another possibility might concern trapped ants or ants living on the inselberg that might themselves consume ^{15}N -depleted food and therefore be isotopically depleted. Based on these assumptions, *C. berteroniana* tank bromeliads may likely depend on multiple nutrient sources that cannot be identified properly only by examining the natural abundance of leaf ^{15}N .

TERRESTRIAL—AQUATIC LINKAGE

Nutritional contribution of terrestrial animals and digestive mutualisms

If a great number of terrestrial animals are occasional visitors (i.e. they hunt on or hide in the plants), some others inhabit the bromeliad and are involved in mutualistic associations (Frank and Lounibos 2009). Some examples include web-spinning spiders which construct their trap right over the bromeliad (Romero and Vasconcellos-Neto 2004), frogs that breed in tank bromeliads (Romero et al. 2010), ants that live inside the leaf axil or between the roots of bromeliads (Corbara and Dejean 1996; Dejean and Olmsted 1997) and snails that estivate or spend the hottest hours of the day in the leaf axil (C Leroy, R Céréghino and B Corbara, personal observation). All of these species benefit from their association with the bromeliads in that they obtain water, a breeding habitat or a moist refuge to buffer climatic variations. In turn, these terrestrial species release fecal pellets and liquid excretions into the tanks or leaf axils that quickly decompose and thereby become available to the plants either directly (liquid excretions) or thanks to aquatic decomposers. This terrestrial animal–plant interaction is known as a digestive mutualism (i.e. mutualisms involving arthropods that contribute to plant nutrition; Anderson and Midgley 2003).

The Neotropical jumping spider *Psecas chapoda* (Salticidae) inhabits and breeds on bromeliads such as *B. balansae* (Romero and Vasconcellos-Neto 2004) or *Ananas comosus* and *Aechmea distichantha* (Gonçalves et al. 2011). This spider indirectly contributes ~15% to the total nitrogen input of its host bromeliad (Table 2) and the amount of nitrogen varies depending on spider density (Romero et al. 2008) and the season (Gonçalves et al. 2011). It was experimentally demonstrated that bromeliads associated with a high abundance of spiders obtain

more ^{15}N compared with those with a lower density of spider presence (Romero et al. 2008). Also, these spiders make a greater nutritional contribution during the wet season than during the dry season, generating a conditional outcome in this digestive mutualism (Gonçalves et al. 2011). In addition to spiders, the treefrog *Scinax hayii* (Hylidae), which breeds in *Vriesea bituminosa* (Tillandsioideae), indirectly contributes ~30% of the nitrogen flux to the bromeliads by defecating in the tanks (Romero et al. 2010).

Besides fecal pellets, the liquid excretions of terrestrial animals provide a direct nutritional input to the bromeliad. Indeed, the considerable activity of urease is associated with the cell walls and membranes of *Vriesea gigantea* (Cambui et al. 2009). Inselsbacher et al. (2007) also further demonstrated that there is probably an efficient urea uptake by aquaporins when urea is present in high concentrations in the tank water. Epiphytic bromeliads have the capacity to take up urea and amino acids at a higher rate than inorganic forms and accumulate the highest biomass when fertilized with urea (Mercier et al. 1997; Nievola et al. 2001) or amino acids (Endres and Mercier 2003) compared with terrestrial bromeliads. This may be related to the presence of a relatively higher concentration of organic rather than inorganic nitrogen in the water of the tank bromeliad under natural conditions (Endres and Mercier 2003). Tank bromeliads further reflect the presence of an adaptive functional strategy linked to the association with terrestrial biota.

We suspect that the water reservoir has a role in bromeliad nutrition that has been overlooked. Indeed, it attracts terrestrial allies which, through their fecal pellets and urine, concentrate nutrients inside the leaf rosette, certainly providing great nutritional benefits to the plant. Further field and experimental studies are, however, needed to verify such hypotheses. Moreover, what is considered less often in freshwater habitats is that the outer leaf axils contain wet litter at different stages of decomposition that forms semiterrestrial habitats. These bromeliad terraria are constantly occupied by many terrestrial arthropods (e.g. Blattodea, Coleoptera, Formicidae, Orthoptera and Scorpionida; Frank and Lounibos 2009). If bromeliads are essential to the existence of many of these insect species, their nutritional input for the plants has been overlooked.

Ants mediate the aquatic biota structure and tank bromeliad nutrition

In addition to the direct contribution of ant-garden ants to the mineral nutrition (i.e. myrmecotrophy) of the tank bromeliad *A. mertensii*, the two ant species, *N. goeldii* and *C. femoratus*, also played an indirect role in plant performance by generating changes in the plant's architecture and phytotelmatic biota. The ants indirectly influence nutrient acquisition by the bromeliad through a kind of plant-invertebrate-plant feedback loop (Fig. 4). Nitrogen supply and acquisition were significantly higher in *C. femoratus*-associated *A. mertensii* compared with *N. goeldii*-associated *A. mertensii* (Leroy et al. 2009a, 2009b, 2012; Table 2).

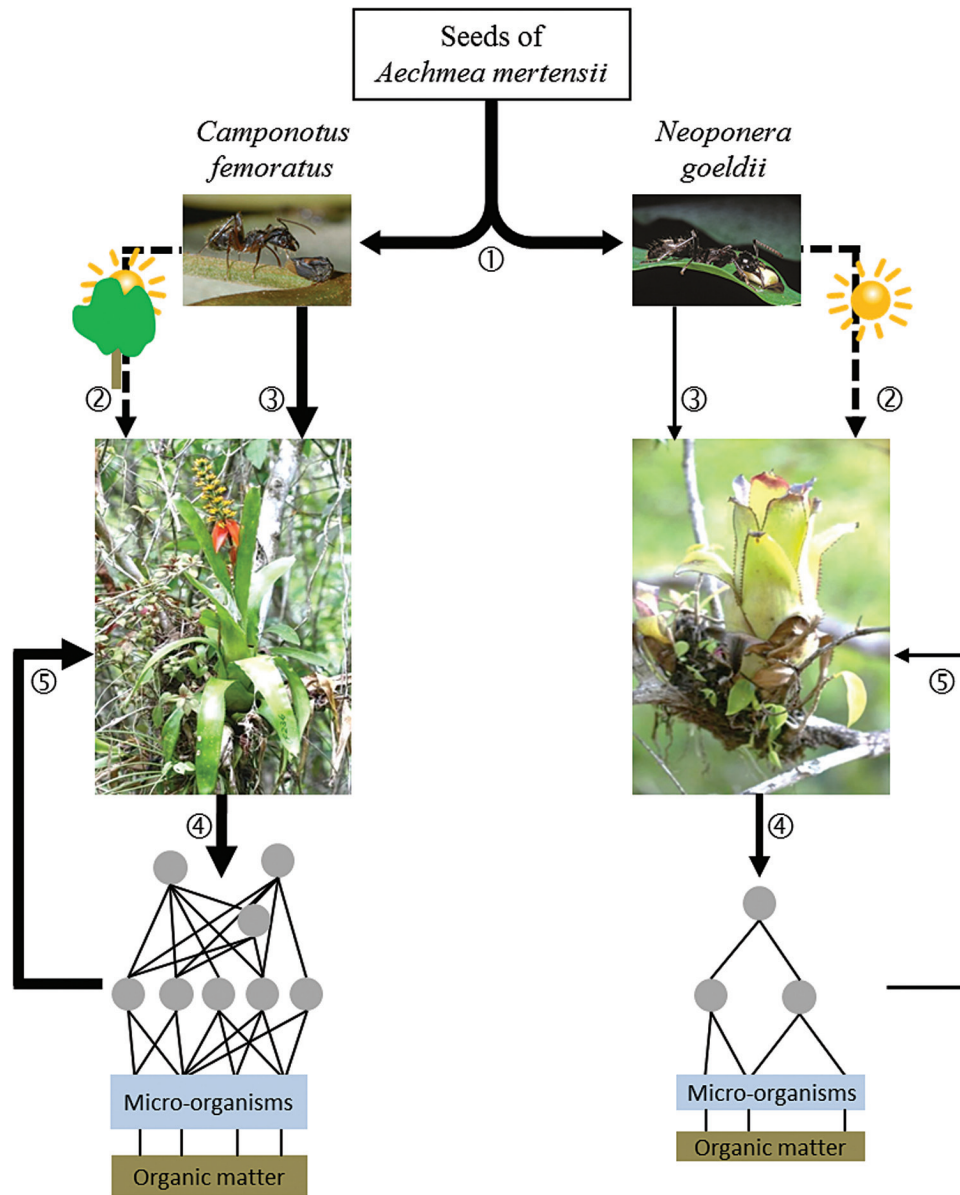


Figure 4: summary of the interactions between the tank bromeliad, *Aechmea mertensii*, the two ant species, *Camponotus femoratus* and *Neoponera goeldii* and the aquatic biota living in the tanks of bromeliads found in ant gardens. (1) The seeds of *A. mertensii* are integrated into the carton of either *C. femoratus* or *N. goeldii* ant gardens (dispersal mutualism). (2) Because of different ecological preferences, *C. femoratus* colonize shaded areas whereas *N. goeldii*-associated bromeliads are located in sun-exposed environments. By positioning the seeds in two contrasting light environments, the ants indirectly affect the shape of *A. mertensii*. (3) The two ant species also play a direct role in nutrient transfer to the bromeliads that thus benefits from myrmecotrophy. (4) These two ant species generate, directly and indirectly, a gradient of space (i.e. tank size and water volume) and food (amount of organic matter) for the aquatic biota. Both the specific and functional diversity of macro- and micro-organisms are differently affected by the two ant species. (5) By determining a more complex food-web structure, *C. femoratus* indirectly generates a greater nutrient supply for the *A. mertensii* tank bromeliads in comparison to *N. goeldii*. The black lines indicate the direct effects and the dotted lines indicate the indirect effects of the presence of ants for the plant. The thickness of the lines translates minor (thin line) to major (thick line) effects.

The difference in nutrient supply by the two ant species can be explained by their distinct ecological preferences. *Neoponera goeldii* preferentially colonizes small trees in sun-exposed environments, whereas *C. femoratus* rather colonizes larger trees in more shaded areas. Such a difference in ant habitat preferences influences the structural plasticity of both the vegetative and floral traits of *A. mertensii* (Leroy *et al.* 2009a, 2012). The sun-exposed

bromeliads associated with *N. goeldii* are smaller and limit direct light incidence by adopting an amphora shape, whereas those growing in partial shade and associated with *C. femoratus* are larger and forage for light by developing a wider canopy (Leroy *et al.* 2009a). This phenotypic plasticity in the shape of the bromeliad has a direct influence on the amount of rainwater and leaf litter intercepted by the tank-forming leaves.

By coexisting on a local scale, the two ant species generate a gradient in habitat conditions (i.e. space and food) for bromeliads and aquatic invertebrates, and the diversity of invertebrate communities increases with greater volumes of water and fine detritus in *C. femoratus*-associated *A. mertensii* (Céréghino et al. 2010). In that study, *N. goeldii*-associated bromeliads experienced water- and nutrient-stressed conditions. Because the plants were located in exposed areas, they mostly obtained wind-borne nutrients and their water-to-FPOM volume ratio was on average two times lower than in the *C. femoratus*-associated bromeliads. Moreover, the traits of the aquatic invertebrates in *C. femoratus*-associated bromeliads suggest that habitat occupancy and resource use are favored by a larger body size and a higher diversity of feeding groups compared with bromeliads associated with *N. goeldii* (Céréghino et al. 2011). The dominant invertebrate functional groups in *C. femoratus*-associated plants were collectors and filterers. These communities strongly relied on litter supply and the decomposition of particulate organic matter by microorganisms, something which suggests a bottom-up influence on community structure. On the contrary, the *N. goeldii*-associated communities contained a higher proportion of predators. The association of *A. mertensii* with one or the other of these two ant species was also shown to affect the microbial community structure (Carrias et al. 2012). Indeed, the heterotrophic and autotrophic protists inhabiting *C. femoratus*-associated bromeliads exhibited greater richness and abundance than those in *N. goeldii*-associated bromeliads which is mainly explained by variations in detritus content, tank size and incident radiation.

Variations in some vegetative traits were related either to the process of acclimation to light (i.e. the size and shape of the bromeliad) or to nutrient-stressed environments linked to the species of associated ant (i.e. leaf thickness and leaf mass per unit area). Whereas the incident radiation reaching the plants might explain the phenotypic plasticity in the vegetative traits, Leroy et al. (2012) showed that the floral traits of *A. mertensii* are not primarily influenced by light, but rather by nutrient stress. Indeed, *C. femoratus*-associated bromeliads have the potential to allocate more nutrients to the inflorescences, flowers and seeds than do *N. goeldii*-associated plants (Leroy et al. 2012). *Camponotus femoratus* is thus a better mutualistic ant partner in terms of bromeliad performance when compared with *N. goeldii*.

CONCLUSION AND OUTLOOK

This review shows that bromeliads have evolved a great diversity of morphologies and functional adaptations leading to the existence of numerous nutritional modes (Table 3) and points out that bromeliads rely on wide variety of organisms to assist them in obtaining nutrients. These plants have developed loose and mutualistic associations with many different and functionally diverse terrestrial and aquatic microorganisms that contribute substantially to their mineral nutrition and, thus, their fitness and survival. Indeed, mutualisms are

an integral component of the means by which bromeliads obtain nutrients. Bacterial and fungal microbiota-assisted nitrogen provisioning, protocarnivory, digestive mutualisms and myrmecotrophic pathways are some of the main strategies used, separately or combined, by bromeliads to acquire nutrients (Table 3). Because nitrogen is particularly important to plant growth and reproduction, bromeliads have thus established multi-faceted nutritional strategies to respond to natural fluctuations in nitrogen which represent an important adaptation for the exploitation of nutrient-poor habitats. Nonetheless, only a relatively small number of bromeliad species have been studied to date. We thus find ourselves asking if the nutritional strategies found in a bromeliad species might be transposed to other bromeliads with the same life form and if there is some convergence in functional traits and nutritional strategies within habitats.

In this review, we also highlight gaps in the current knowledge that offer fascinating research opportunities to study the nutritional ecology of bromeliads and, more generally, numerous epiphytic taxa or nutrient-poor soil species. We point out that the presence of multiple nitrogen sources with overlapping isotopic values makes it difficult to identify nitrogen sources based only on the natural abundance of leaf $\delta^{15}\text{N}$ (as we showed for *C. berteroniana*; Leroy et al. 2013). The limits of the isotopic approach are even more significant because temporal and spatial variations in the availability of nitrogen, ontogeny and changes in plant needs can all influence plant $\delta^{15}\text{N}$ (Dawson et al. 2002). In that case, the use of ^{15}N -enriched tracers may help to quantify nitrogen fluxes from one potential nitrogen source to the bromeliads. Future research should more closely consider the nutritional importance of the fecal pellets and urine of terrestrial animals for both the aquatic biota and the bromeliad. In addition to digestive mutualisms, the direct absorption of DON by the bromeliad might be a complementary short pathway, i.e. still being underestimated. Also, myrmecotrophy in bromeliads is another topic which has been neglected so far and deserves to be studied in greater depth. Moreover, symbioses (i.e. mycorrhiza, Rhizobia) which have great importance for terrestrial flora have nearly unknown effects on arboreal flora (Benzing 1990) and remain overlooked. Future research will be necessary to evaluate the absorptive role of roots and the presence of fungal associations in bromeliads. Finally, how algae and bromeliads interact and what their respective roles are in the functioning of phytotelms are still open questions.

All biotic interactions that change the availability of nutritional resources by creating novel opportunities might increase the size of the plant's fundamental niche (Rodríguez-Cabal et al. 2012). Indeed, it has been shown that positive interactions between several vascular plants and root symbionts (e.g. mycorrhiza) extend the range of abiotic conditions (e.g. water, nutrients) in which the plants can survive and expand their geographical distribution (Stachowicz 2012). If the majority of terrestrial plants rely on one main type of mutualistic interaction (e.g. mycorrhiza, Rhizobia) to enhance nutrient

Table 3: overview of the different nutritional pathways reported in this review and summarized with a hypothetical bromeliad (i.e. mixture of atmospheric and tank forms)

Bromeliad parts	Absorbing organs	N sources	N forms	Nutritional assistance	Functional pathway
Aerial part	Leaf trichomes [Atmospheric (and tank) forms]	Wet deposition	NH ₄ ⁺ , NO ₃ ⁻	—————→	Autonomous pathway
		Dry deposition	N ₂	—————→ N2-fixing bacteria	→ Association pathway
		Faeces, humus	Urea, amino acids	-----→ Mutualistic ants	-----→ <i>Myrmecotrophic pathway</i>
Tank part	Leaf trichomes [Tank forms]	Wet deposition	NH ₄ ⁺ , NO ₃ ⁻	—————→	Autonomous pathway
		Leaf litter	Pectin, cellulose	→ Aquatic biota	→ Association pathway
		Faeces	Urea, amino acids	↔ Terrestrial biota	→ Digestive mutualism pathway
		Decaying insects	Chitin	→ Aquatic biota	→ (proto)carnivorous pathway
		Dry deposition	N ₂	—————→ N2-fixing bacteria	→ Association pathway
Root system	Root hairs [Atmospheric and tank forms]	Wet deposition	NH ₄ ⁺ , NO ₃ ⁻	-----→	<i>Autonomous pathway</i>
		Organic matter	Pectin, cellulose	→ Fungi	→ Mycorrhizal pathway
		Faeces	Urea, amino acids	↔ Mutualistic ants	→ <i>Myrmecotrophic pathway</i>
				-----→	<i>Autonomous pathway</i>

The bromeliad has been divided into three spatially distinct zones (i.e. aerial, tank and root parts). For each part is indicated the water and absorbent organs, potential N sources, available N forms, nutritional assistance, if any and, finally, the functional pathway for N supply. Solid arrows and functional pathways written in italics indicate that this pathway has been proven to exist only once. Dotted arrows and functional pathways written in italics indicate that this pathway is likely to be, but has not yet been proven.

accessibility and uptake, some have evolved alternative nutritional strategies. Indeed, the maintenance of various sources of nitrogen through multiple mutualistic partners may represent a valuable strategy for constantly obtaining nutrients despite nutrient-poor soils or in epiphytic habitats. Bromeliads are thus not really unique in their nutrient acquisition strategies: by developing a diversity of nutrient-acquisition mechanisms, several species of unrelated plant families have evolved convergent adaptations to nutrient scarcity. For example, Bazile *et al.* (2012) showed that the carnivorous plant *Nepenthes bicalcarata* (Nepenthaceae) combines carnivory and myrmecotrophy. Also, Nishi *et al.* (2013) pointed out the role of multiple partners in a digestive mutualism for the protocarnivorous *Paepalanthus bromelioides* (Eriocaulaceae). The biggest challenge now is to concentrate on unrelated species that share similar strong selective pressures (i.e. nutrient-poor habitats) to obtain a more complete picture of animal-assisted plant nutrition.

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