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SUMMARY

1. A substantial fraction of the freshwater available in neotropical forests is impounded within the rosettes of bromeliads that form aquatic islands in a terrestrial matrix. The ecosystem functioning of bromeliads is known to be influenced by the composition of the contained community but it is not clear whether bromeliad food webs remain functionally similar against a background of variation in the understorey environment.
2. We considered a broad range of environmental conditions, including incident light and incoming litter, and quantified the distribution of a very wide range of freshwater organisms (from viruses to macroinvertebrates) to determine the factors that influence the functional structure of bromeliad food webs in samples taken from 171 tank-bromeliads.
3. We observed a gradient of detritus-based to algal-based food webs from the understorey to the overstorey. Algae, rotifers and collector and predatory invertebrates dominated bromeliad food webs in exposed areas, whereas filter-feeding insects had their highest densities in shaded forest areas. Viruses, bacteria and fungi showed no clear density patterns. Detritus decomposition is mainly due to microbial activity in understorey bromeliads where filter feeders are the main consumers of microbial and particulate organic matter (POM). Algal biomass may exceed bacterial biomass in sun-exposed bromeliads where amounts of detritus were lower but functional diversity was highest.
4. Our results provide evidence that tank-bromeliads, which grow in a broad range of ecological conditions, promote aquatic food web diversity in neotropical forests. Moreover, although bromeliad ecosystems have been categorised as detritus-based systems in the literature, we show that algal production can support a non-detrital food web in these systems.

Keywords: food webs, French Guiana, invertebrates, microorganisms, phytotelmata, rainforest

Introduction

Bromeliaceae are flowering plants represented by 59 genera and some 2400 species native mainly to the neotropics, with a few species found in the American subtropics and one in West Africa (Mabberley, 1997). The leaves of tank-forming bromeliads are tightly interlocking, forming wells that collect water, leaf litter and other organic detritus. These tanks, or phytotelmata ('plant-held waters'), provide a habitat for aquatic organisms in rainforests where ponds and lakes are naturally scarce. The aquatic food web inhabiting tank-bromeliads consists of micro- and macroinvertebrates (reviewed in Kitching, 2000) and microorganisms such as bacteria (Cochran-Stafira & von Ende, 1998), algae (Laessle, 1961; Maguire, 1971), fungi and protozoa (Carrias, Cussac & Corbara,

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2001; Foissner *et al.*, 2003). Because they can be exhaustively sampled and contain multiple trophic levels, tank-bromeliads and their aquatic biota have recently proven to be ideal model systems for controlled studies of many basic ecosystem processes (Srivastava, 2006), ranging from the rules by which communities are assembled (Céréghino *et al.*, 2010, 2011) to the relationships between diversity and ecosystem function (Leroy *et al.*, 2009; Srivastava & Bell, 2009).

In tank-bromeliads, detritus constitutes a source of nutrients for the aquatic food web as well as for the host plant itself. Debris-chewing invertebrates process incoming litter. Small particles of organic matter, including faeces, are then washed into the plant pools where particulate organic matter (POM) is further processed in the gut of invertebrate collectors and filterers. Dead organisms, litter and faecal particles, which collect in the leaf bases, are utilised by bacteria and other microorganisms. Observations and experimentation have revealed that, at a given site (i.e. a single location), ecosystem functions in bromeliad tanks are strongly influenced by the composition of the community inhabiting them; for instance, nitrogen uptake by the bromeliad is positively influenced by invertebrate species richness (Leroy *et al.*, 2009) while predators facilitate nutrient uptake by limiting the emergence of detritivorous insects that would otherwise represent a loss of nitrogen (Ngai & Srivastava, 2006). However, we do not know whether environmental conditions, such as available understorey light and incoming litter, determine community structure and whether this in turn determines ecosystem function. Moreover, our understanding of the relationships between food web structure and environment in bromeliads primarily comes from ecological studies on a target fraction of the food web (e.g. invertebrates, insects, microorganisms excluding components such as bacteria and viruses).

Taxonomic resolution is inevitably very heterogeneous when dealing with many phyla simultaneously, both because compromises must be made to obtain sufficient information to detect the expected biological responses in the various taxa and because of the cost of obtaining this information (e.g. bacteria versus insects, lack of taxonomic knowledge in tropical areas). Biological traits have the potential to provide additional information on the mechanisms structuring entire communities because they reflect adaptations to environmental characteristics, including spatiotemporal variability and stochasticity (Townsend & Hildrew, 1994). Functional groups (FGs), mostly based on morphological and behavioural adaptations related to food acquisition, aggregate taxa into fewer categories than do species lists (Bonada, Doledec & Statzner, 2007), thus

simplifying *a priori* predictions of the responses of communities to environmental fluctuations.

This study focussed on the tank-bromeliads found in a primary rainforest characteristic of the eastern Amazon. We analysed the functional variability of the aquatic communities extracted from 171 tank-bromeliads ranging from 80 to 420 m above sea level in relation to environmental variables (incident radiation, POM, water volume, position in the host trees). To the best of our knowledge, there is no evidence of species-specific associations between tank-bromeliad species and particular sets of aquatic animals (Benzing, 1990). Instead, when several tank-bromeliads co-occur, the set of plant species present form a metahabitat. Earlier bromeliad studies highlighted the role of habitat characteristics (amount of water, surrounding vegetation) and biological interactions (predation, competition) in shaping species assemblages in these natural microcosms (Armbruster, Hutchinson & Cotgreave, 2002; Srivastava, 2006). Therefore, assuming that the bromeliads that grow in the forest understorey collect leaf litter and nutrients leached from the canopy, we predicted that their detritus-based food webs rely on high abundances of microbial decomposers such as bacteria and/or fungi. Conversely, we expected that bromeliads that grow in open areas would collect lower amounts of detritus, but that higher incident light would promote the growth of algae. Subsequently, we predicted that algae in open areas could support a non-detrital food web (in addition to the detrital food web), thus promoting functional diversity at higher trophic levels.

Methods

Study area

This study was conducted in a primary rainforest characteristic of the eastern Amazon near the Nouragues Tropical Forest Research Station (4°5′N, 52°41′W, French Guiana). The area is totally uninhabited and current anthropogenic disturbance is negligible (see Sarthou *et al.*, 2009 for a detailed description). The Station is located in the Nouragues Nature Reserve (Fig. 1), 100 km as the crow flies from Cayenne, and 40 km from the nearest village (Regina). The area is delineated by hills (elevation <120 m a.s.l.) and by the Balenfois Mountains (maximum elevation: 460 m a.s.l.). The geology of the area is dominated by two types of substrate: Carribean granite and metavolcanic rocks from the Paramaca series (Bongers *et al.*, 2001). A granitic inselberg dominates the Station (maximum elevation: 420 m a.s.l.). The vegetation is composed of primary rainforest with small, naturally
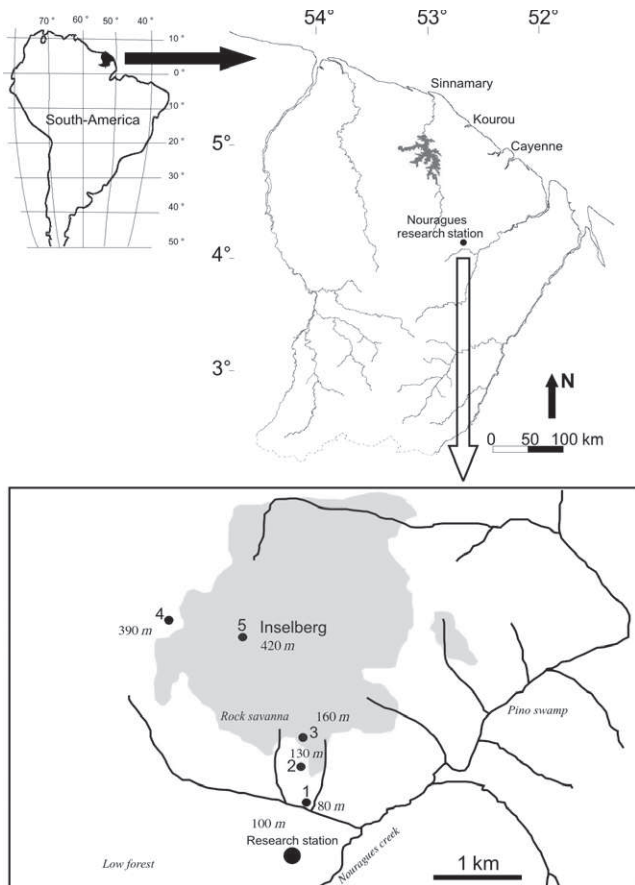
Fig. 1 Map of the study area and location of the five sampling sites (1–5). The grey area delineates the inselberg (maximum elevation 430 m a.s.l.).

occurring stands of palm forest on poorly drained terrain ('pino swamps'), liana forests (probably indicating past Amerindian slash-and-burn agriculture) and bamboo thickets. On the inselberg, patches of savannah ('rock-savannahs') can be found, intermingled with patches of shrubby trees belonging to the Clusiaceae, Myrtaceae and Bombacaceae families (Sarthou, Villiers & Ponge, 2003). The climate is tropical moist with 3000 mm of yearly precipitation distributed over 280 days. There is a major reduction in rainfall between September and November (the dry season) and another shorter and more irregular dry period in March. The maximum monthly temperature averages 33.5 °C (32.1–35.8 °C) and the monthly minimum, 20.3 °C (19.7–21 °C).

Field data and techniques

Sampling was carried out over 12 days, from 23 March to 3 April 2006. We selected five sampling sites located along a gradient of elevation above sea level. We chose the six most common bromeliad species among the 24 that are

present in the area around the Nouragues Tropical Forest Research Station (see Bongers *et al.*, 2001 for a species list). *Guzmania lingulata* (L.) Mez was the only tank-bromeliad at site 1 (80 m a.s.l., Nouragues Creek, rainforest). At site 2 (130 m a.s.l., transition forest), *G. lingulata* co-existed with two other common species, namely *Aechmea melinonii* Hooker and *Vriesea pleiosticha* (Grisebach) Gouda. At site 3 (160 m a.s.l.), *Pitcairnia geyskesii* (L. B. Smith) Varadajaran & Gilmartin, was abundant on a plateau situated at the base of the inselberg. Site 4 (390 m a.s.l.) was a forested area where *Vriesea splendens* (Brongniart) Lemaire was the only tank-bromeliad. Finally, *Catopsis berteroniana* (Schultes f.) Mez was restricted to the summit of the granite inselberg (site 5; 420 m a.s.l.), where it grew as an epiphyte on *Clusia minor* shrubs. Overall, 171 bromeliad individuals (i.e. 171 aquatic communities) were sampled. The number of plants sampled per bromeliad species and their main characteristics are provided in Table 1. To characterise the percentage of total incident radiation above the bromeliads, we used hemispherical photography. Photographs were taken near dusk (to avoid direct sunlight) above every bromeliad. We used a height adjustable tripod and a digital camera (Nikon Coolpix 4500, Tokyo, Japan) equipped with a Nikon Fisheye converter lens (FC-E8 0.21X) that provides a 180° canopy view. We analysed the images using the Gap Light Analyzer (GLA, Burnaby, BC, Canada and Millbrook, NY, USA) 2.0 image processing software to calculate the percentage of total incident radiation (Frazer, Canham & Lertzman, 1999). The percentages of transmitted light are provided in Table 1.

For legal reasons (the Station is located in a protected area), the bromeliads could not be removed from their host trees. Therefore, we used flexible plastic tubes (length 10–30 cm, diameter 2–5 mm) connected to 50-mL syringes and micropipettes (with the end trimmed to widen the orifice) to sample the water retained in the tanks. The elevation above ground (m) was measured for each plant. We then carefully emptied the wells in each plant by sucking the water out using tubes and pipettes of appropriate dimensions. This technique, although less efficient than plant dissection, has already been successfully used by us and others (Céréghino *et al.*, 2010, 2011; Jocqué *et al.*, 2010). It was used for all of the samples, and most of the water (>95%) was collected. The water volume extracted (mL) was recorded for each plant. A subsample of 20% of the collected volume was fixed with 4% (final concentration) formaldehyde for enumeration of microorganisms and detrital particles (see below). The remaining water (and its contents) was preserved in 70% ethanol and used to sort and count the metazoans.

Table 1 Main characteristics of the 171 plants (6 bromeliad species) that were sampled during the study near the Nouragues station (French Guiana) in 2006, and mean densities (individuals mL^{-1}) for the various functional groups

	Guzmania lingulata	Aechmea melinonii	Vriesea pleiosticha	Vriesea splendens	Pitcairnia geyskesii	Catopsis berteroniana
Number of plants sampled per site						
Site 1: rain forest	38	–	–	–	–	–
Site 2: transitional forest	17	30	32	–	–	–
Site 3: inselberg, open area	–	–	–	–	37	–
Site 4: inselberg, forest area	–	–	–	31	–	–
Site 5: summit inselberg, open area	–	–	–	–	–	32
Environmental variables						
Elevation a.s.l. (m)	80–130	130	130	390	160	420
Incident radiation (%, mean ± SE)	15.8 ± 2.3	24.2 ± 3.0	24.2 ± 3.0	16.3 ± 3.0	62.3 ± 7.2	72.5 ± 5.8
Elevation above ground (m)	1.5 ± 0.2	0	0.4 ± 0.1	0	0	0.7 ± 0.1
Water volume (mL, mean ± SE)	16.1 ± 9.6	134.0 ± 105.2	71.7 ± 49.8	50.8 ± 27.8	8.3 ± 1.6	40.6 ± 20.2
Total POM (10^4 particulates mL^{-1})	27.2 ± 6.2	13.5 ± 2.6	14.0 ± 2.5	15.6 ± 3.0	8.2 ± 0.02	3.0 ± 0.05
POM<30 μm (% ± SE)	75.0 ± 2.2	63.4 ± 13.2	69.1 ± 12.4	69.7 ± 13.4	80.3 ± 20.1	57.4 ± 10.6
POM 30–150 μm (% ± SE)	17.8 ± 1.3	20.3 ± 1.9	23.3 ± 4.0	23.1 ± 4.5	15.3 ± 3.8	25.8 ± 4.8
POM 150–300 μm (% ± SE)	7.2 ± 1.1	11.3 ± 2.2	8.6 ± 1.5	7.2 ± 1.4	4.4 ± 1.1	16.9 ± 3.1
Functional groups (ind mL^{-1} ± SE)						
Viruses × 10^7	2.1 ± 0.2	1.2 ± 0.2	1.9 ± 0.3	1.9 ± 0.6	1.8 ± 0.4	1.1 ± 0.2
Bacteria × 10^6	8.6 ± 1.1	6.3 ± 1.2	9.0 ± 1.6	7.5 ± 1.4	9.6 ± 2.4	5.6 ± 1.0
Fungi × 10^2	13.4 ± 6.7	3.1 ± 0.6	7.9 ± 1.4	7.1 ± 1.4	<1.0	7.3 ± 1.3
Algae × 10^2	10.0 ± 8.1	73.0 ± 14.0	0.4 ± 0.08	7.8 ± 1.5	88.4 ± 22.1	25.3 ± 4.7
Ciliates	<1.0	<1.0	8.1 ± 8.0	1.0 ± 1.0	<1.0	2.5 ± 0.5
Rotifers	10 ± 3	26 ± 5	21 ± 4	13 ± 3	221 ± 55	147 ± 27
Insects, filterers	0.15 ± 0.03	0.1 ± 0.01	0.07 ± 0.01	0.08 ± 0.01	–	0.04 ± 0.001
Invertebrates, collectors	0.04 ± 0.01	0.04 ± 0.001	0.03 ± 0.005	0.02 ± 0.01	0.06 ± 0.005	0.08 ± 0.01
Insects, predators	0.05 ± 0.03	0.07 ± 0.01	0.05 ± 0.01	0.1 ± 0.02	–	0.36 ± 0.06

Laboratory analyses

Subsamples for microbial analyses were gently mixed by inversion and the water removed from the supernatant after a 2-min sedimentation period for the larger debris. This procedure enabled us to conduct a thorough microscopic inspection of the samples and prevented size-fractionation and the subsequent loss of fragile microorganisms. For the enumeration of viruses and bacteria, 1-mL subsamples were filtered through 0.02 μm pore size Anodisc filters (Whatman, Whatman International Ltd, Maidstone, UK) using cellulose acetate backing filters (1.2 μm pore size) and were stained with SYBR Green I fluorochrome according to the method developed by Noble & Fuhrman (1998). Slides were prepared using the medium Citifluor (Citifluor, London, UK) amended with c. 20% (v/v) of Vecta Shield (Vector Laboratories, Peterborough, UK), resulting in a highly stable fluorescence of the fluorochrome. The slides were stored at −20 °C before counting. Bacteria were distinguished from virus-like particles on the basis of their relative size and brightness through 40–60 fields of view using an epifluorescence microscope (Leica DC 300F model, Leica microsystems, Wetzlar, Germany) at 1250× magnification. The abundances of algae, fungi, ciliates and rotifers were estimated from settled samples (Utermöhl, 1958) using an inverted Leitz Fluovert FU microscope at 500× magnification by scanning the entire chamber area. Samples with a high detrital particle content were diluted, and total counts were pooled from triplicate subsamples. The abundance of fungi must be considered a density index rather than a real estimate because only the spore stages (conidia) were considered. POM (i.e. detrital particles <300 μm) were also counted from settled samples using the inverted microscope through 30–50 microscopic view settings and separated into three size classes (<30, 30–150 and 150–300 μm). We used particle counts instead of mass because size-fractionation by filtration was not possible with the smallest samples where most of the water permeates the detritus (e.g. P. geyskesii, G. lingulata).

Macroinvertebrates were keyed to genus or morphospecies and counted under a stereomicroscope. They were then partitioned into FGs inspired by the work of Merritt & Cummins (1996). We also relied on the information available in Kitching (2000) for phytotelm organisms. These FGs were filterers (sift fine particulates, including living microorganisms, from the column of water); collectors (gather fine particulates of organic matter from the accumulated debris); and predators (feed on other animals). The macroinvertebrates were largely dominated

by aquatic insects. Other taxa included oligochaetes that were assigned to the collectors. After counting all organisms, density was expressed as the number of individuals per unit volume of water (ind mL^{-1}). It is worth noting that *Dendrobates ventrimaculatus* (Shreve) adults and tadpoles (amphibians) were found in *A. melinonii*, *V. splendens* and *V. pleiosticha*. However, because of their rarity, these organisms were not added to the analyses in this study.

Data analysis

The relationships between all of the environmental variables, bromeliads and abundance of FGs were examined using multivariate ordination. The environmental variables were elevation a.s.l. (m), incident radiation (%), elevation above ground (on the host tree, m), water volume (mL), POM<30 µm (%), POM 30–150 µm (%), POM 150–300 µm (%) and total POM present in the water (number of particulates per mL). Host tree was not included as a factor in our analysis because it was generally confounded by species of bromeliad (e.g. all *C. berteroniana* on *Clusia minor*, *A. melinonii*, *V. splendens* and *P. geyskesii* rooted on the soil). Organism abundance data were log (n + 1) transformed prior to analysis. An initial detrended correspondence analysis (DCA) in CANOCO v4.5 showed that a linear model was the most applicable because of low species turnover (gradient = 0.548) along Axis 1 (Lepš & Šmilauer, 2003); thereafter, a redundancy analysis (RDA) was used to examine functional group relationships with bromeliads and with the eight environmental variables. Forward selection was employed to test which of the eight environmental variables explained significant ($P < 0.05$) proportions of the species variance. The significance of explanatory variables was tested against 500 Monte Carlo permutations.

Results

Axes 1 and 2 of the RDA accounted for 28.7% of the total species variance and 98% of the Functional group (FG)–environment relationship (Fig. 2). Eigenvalues for Axes 1 and 2 were 0.23 and 0.05, respectively. Functional group–environment correlations were 0.667 for Axis 1 and 0.426 for Axis 2. Forward selection identified three variables as explaining a significant amount of the FG variance (bold arrows in Fig. 2a): incident radiation (P = 0.002), percentage of 150–300 µm POM (P = 0.006) and elevation above ground (P = 0.04). Incident radiation accounted for the greatest proportion of total canonical eigenvalues (22%; F = 42.38; P = 0.002).
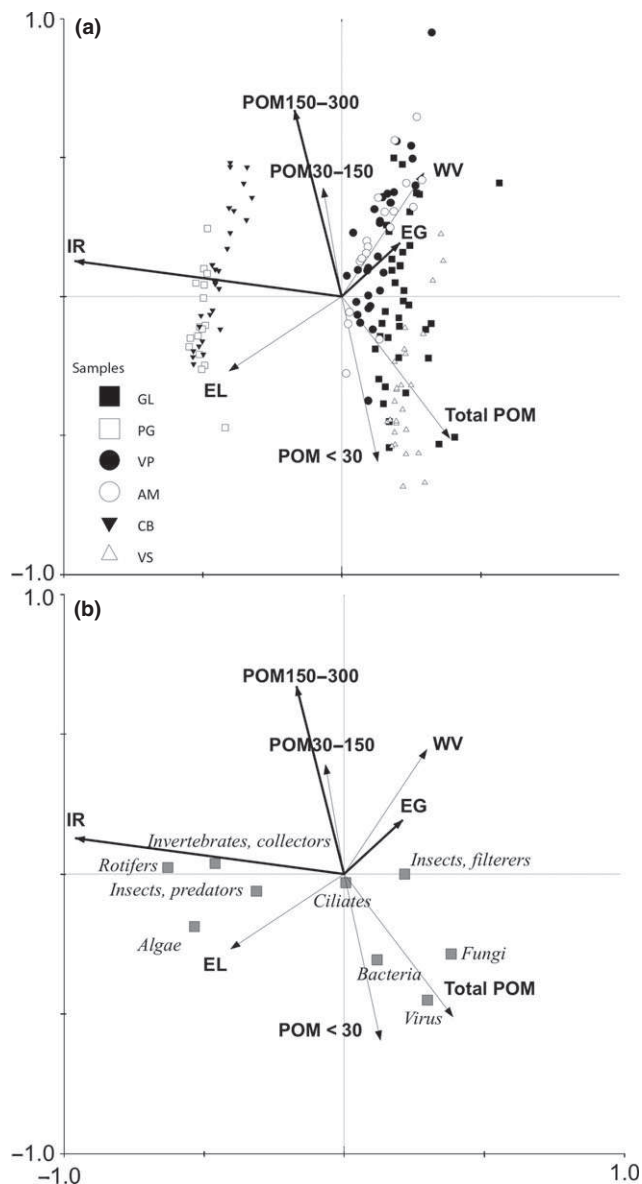
Fig. 2 Redundancy analysis (RDA) biplots. (a) Bromeliads and environmental variables. Environmental variables are represented as vectors; directions show the gradients, arrow length represents the strengths of the variables on the ordination space. Abbreviations are used to identify the bromeliad species (GL = *Guzmania lingulata*; PG = *Pitcairnia geyskesii*; VP = *Vriesea pleiosticha*; AM = *Aechmea melinonii*; CB = *Catopsis berteroniana*; VS = *Vriesea splendens*). (b) distribution of microbial and metazoan functional groups in ordination space. Abbreviations for environmental variables in panels (a) and (b) are as follows: EG = elevation above ground (m); EL = elevation above sea level (m); IR = percentage of total incident radiation above the bromeliads; WV = water volume (mL); Total POM = amount of particulate organic matter (number of particles mL); POM<30, POM 30–150 and POM 150–300 = percentage of particles <30, 30–150 and 150–300 µm in size. Variables explaining a significant ($P < 0.05$) proportion of the functional group variance are represented by bold arrows.

The scatterplot of the RDA segregated two subsets of bromeliads along Axis 1 according to their environmental context, namely forest sites (understorey, low incident radiation, right part of the scatterplot), and the inselberg (overstorey, high incident radiation, left part of the scatterplot) (Fig. 2a). Axis 1 thus displayed a gradient of habitat openness with incident radiation ranging from 15 to 24% and from 62 to 72% in closed and open areas, respectively (Table 1). Axis 2 represented a gradient of POM size [from small (bottom) to large (top)], and, to a lesser extent, a gradient of elevation above the ground [from low (bottom) to high (top)]. In other words, regardless of their location and species, all of the bromeliads were likely to bear small to large amounts of large POM (150–300 μm), but bromeliads at higher elevations in the host trees tended to have larger proportions of large POM. *Guzmania lingulata*, *V. pleiosticha* and *C. berteroniana* contributed to this pattern because they are epiphytes, whereas other bromeliads were rooted in the soil (Table 1).

Algae, rotifers, collectors and predators dominated the bromeliad food web in exposed areas of the inselberg, whereas filterers had their highest densities at forest sites (Fig. 2b, Table 1). More specifically, algal densities reached $88.4 \times 10^2 \pm 22.1 \times 10^2$ and $25.3 \times 10^2 \pm 4.7 \times 10^2$ ind mL^{-1} in *P. geyskesii* and *C. berteroniana*, respectively. *Bumilleriopsis* (Xanthophyceae) dominated the algal assemblage in this area. Algae were apparently abundant in understorey *A. melinonii* bromeliads (forest), but this was due to very high numbers of mixotrophic Euglenophyceae (*Phacus* sp. combining autotrophic and heterotrophic nutrition, mean = $72.9 \times 10^2 \pm 14.0 \times 10^2$ ind mL^{-1}). Rotifer density was 5–20 times higher in the exposed than in the shaded bromeliads. A small bdelloid from the genus *Habrotrocha* (60 μm in length) was the numerically dominant species. Predatory insects (e.g. Veliidae heteropterans, Coenagrionidae odonates, *Toxorhynchites* culicids) and invertebrate collectors (e.g. Chironominae and *Tanytarsus* chironomids, and *Aulophorus superterrenus* Michaelsen Oligochaetes) were three times and 1.5–2 times more abundant in the exposed than in the shaded bromeliads, respectively (Table 1). Conversely, filter-feeding insects (*Wyeomyia* and *Culex* mosquito larvae) were on average 2–3 times more abundant in understorey bromeliads. Microorganisms such as viruses, bacteria and fungi did not show any clear density patterns among the bromeliads (Table 1); however, their densities clearly increased along a gradient of a decreasing percentage of large POM (150–300 μm) in the tanks (Fig. 2b). Ciliates (*Colpoda* sp.) were found in a few plants at low densities, at both open and closed sites.

Discussion

Up to 90% of all primary productivity may enter food webs as dead organic matter or detritus (Moore *et al.*, 2004). In aquatic ecosystems in general, detrital inputs form a strong trophic link between plant production, decomposer microorganisms and larger metazoan detritivores and their predators. The nature and extent of the vegetation that surrounds these systems therefore has a strong influence on food web structure through food quality and availability.

In neotropical forests, a substantial fraction of the freshwater available is impounded within the rosettes of bromeliads that form freshwater islands (i.e. a metahabitat) in a terrestrial matrix. The 171 freshwater communities extracted from six tank-bromeliad species were subject to a wide range of environmental conditions. The first two axes of our RDA explained 98% of the functional groups–environment relationship, using a limited number of variables. This allows us to provide quantitative data on the distribution of a very wide range of freshwater organisms in rainforests and to determine the major factors that influence the functional structure of phytotelm food webs.

A key result of our study is that incident radiation, vertical position on the host trees, and POM size (a series of indicators of habitat openness) explain significant differences in the functional structure of bromeliad food webs in forest environments and, to a lesser extent, between individual bromeliads located at the same site (e.g. epiphytic versus soil bromeliads). Previous studies concluded that water volume (an indicator of habitat size) and the total amount of POM (an indicator of available food at the base of the food web) play key roles in shaping community composition in water-filled bromeliads (Armbruster *et al.*, 2002; Jabiol *et al.*, 2009). Overall, we note that tank-bromeliads show a gradient of detritus-based to algal-based food webs from understorey to overstorey. Our results were used to draw diagrammatic representations of these food webs (Fig. 3). This conceptual framework highlights the dominant taxa and energy pathways and is discussed below.

Tank-bromeliads growing in the forest understorey had higher amounts of detritus in their tanks and displayed higher abundances of filter-feeding insects, while densities of bacteria and fungi increased along a gradient of decreasing POM size. This suggests that leaf-litter breakdown by fungi promotes bacterial growth by increasing the surface area for colonisation (Allan, 1995; Sigee, 2005). Microbial activities are also known to enhance leaf palatability for shredding invertebrates, while microbial
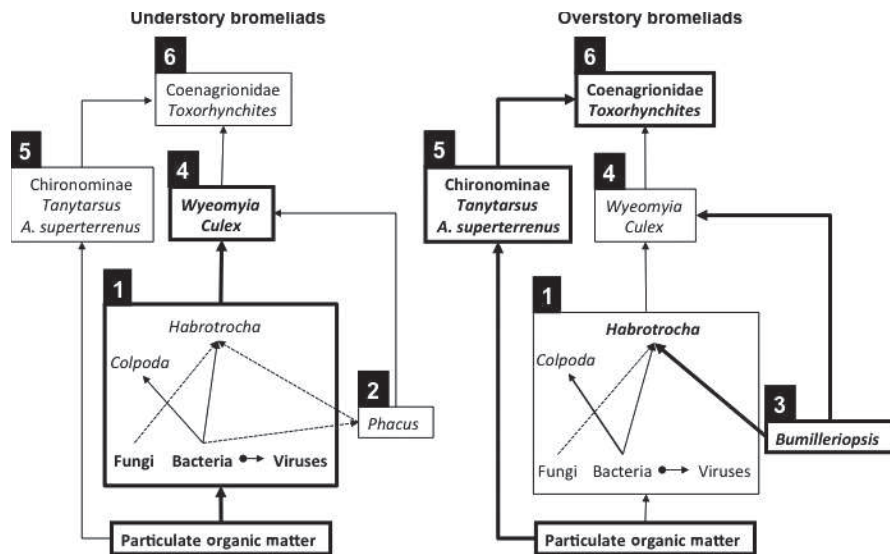
Fig. 3 Diagrammatic representations of the detrital food web (understorey bromeliads, forest sites) and the detrital-algal-based food web (overstorey bromeliads, sun-exposed areas). The numerically dominant organisms are grouped by functional groups (1-6), and arrows show the proposed energy pathways. Bold characters/boxes indicate higher density, and arrow thickness indicates differences in the strength of the relationships. 1 = Heterotrophic microorganisms, 2 = mixotrophic microorganisms, 3 = autotrophic microorganisms, 4 = filter-feeding insects, 5 = macroinvertebrate collectors, 6 = predatory insects.

decomposition may be facilitated by the fragmentation of detritus by insects (Gessner, Chauvet & Dobson, 1999). In our study, the metazoan consumers were largely consumers of bacteria and fungi rather than direct shredders of leaf material. This suggests that POM decomposition is mainly the result of microbial activity in understorey bromeliads, and that microbial and POM consumers are mainly represented by filter feeders in these plants.

Abundances of algae, rotifers, collector and predatory invertebrates increased with greater exposure of the plants to sunlight and lower amounts of detritus on the inselberg. Algae were observed in the earliest limnological studies of tank-bromeliads, especially in plants in the canopy that are exposed to direct sunlight (Maguire, 1971). Laessle (1961) only found algae in bromeliads on open, rocky outcrops in Jamaica. More recent research on bromeliad phytotelmata has frequently ignored algae (but see Brouard et al., 2011; Marino et al., 2011). The current paradigm is that these freshwater microcosms sequester and recycle nutrients to the bromeliad, and therefore, if algae are present and abundant, they should be competing with the bromeliad for dissolved inorganic nutrients. Nitrogen, rather than phosphorus, limits the productivity of bromeliads (Ngai & Srivastava, 2006). Ammonium (NH_4^+) is the primary source of nitrogen for the bromeliad (Inselsbacher et al., 2007), as well as for algae (Sigee, 2005). Ultimately, both algae and collector and filter-feeding invertebrates could form a nitrogen sink in tank-bromeliads. Thus, the high algal density and biomass in exposed bromeliads suggests a trade-off between carbon (light) and nutrient availability. The interactions between bromeliads and algae remain poorly understood (Marino et al., 2011), and further investigations are needed to accurately determine the implications of algae as nutrient competitors of tank-bromeliads. Information on nutrient uptake by freshwater algae comes from studies of taxa isolated from rivers, lakes and other large ecosystems (Sigee, 2005), while the metabolism of bromeliad-dwelling algae is largely unknown. Moreover, mixotrophic Euglenophyceae that are frequent in bromeliads are able to absorb organic rather than inorganic nitrogen.

On the basis of cell volume, we estimate that algal biomass might exceed bacterial biomass in some of the exposed bromeliads: algae represented 22.1% (range: 1.6–104.4%) and 8.5% (0–114.1%) of the bacterial biomass in P. geyskesii and C. berteroniana, respectively. Their role in nutrient cycling as primary producers and prey for metazoan grazers is therefore potentially important, especially in C. berteroniana where amounts of POM are low compared to understorey bromeliads, but where functional diversity is the highest. The same is true of some understorey bromeliads (A. melinonii in our study) that support large numbers of mixotrophic Euglenophyceae. Pitcairnia geyskesii was located in sun-exposed areas but hosted the highest algal densities and did not contain fungi, filterers or predators. This particular situation is

certainly linked to the vegetative traits of this bromeliad which has very narrow leaves and impounds very small volumes of water (8 mL per plant on average), although exposed to a high level of incident light.

Given the small size of the tanks, it is likely that congruent patterns in functional group distributions were also generated through biotic interactions. Most viruses, for instance, are bacteriophages (Fuhrman & Suttle, 1993; Weinbauer & Hofle, 1998) and have patterns that are congruent with bacteria (Weinbauer, 2004). This is also true for tank-bromeliads (this study). The ubiquity and abundance of viruses (10^4 to 10^8 particulates mL^{-1} in lakes according to Bettarel $et\ al.$, 2003; 1.1×10^7 to 2.1×10^7 particulates mL^{-1} in the bromeliads that we studied) suggest that they are heavily involved in the dynamics and functioning of bromeliad food webs. Finally, we did not find clear density patterns for viruses, bacteria or fungi. It should be noted that there are certainly several taxa present within each of these groups, but taxonomic limitations prevented us from obtaining more precise data that would be useful to bring out more specific patterns for the microbial components of the bromeliad food web.

In conclusion, our study provides evidence that tank-bromeliads, which span a broad range of ecological conditions, promote the diversity of aquatic food webs in neotropical forests. The taxonomic composition of the bromeliad food web primarily depends on the plants' vegetative traits (i.e. size, leaf display) (Montero, Feruglio & Barberis, 2010; Céréghino $et\ al.$, 2011), but its functional structure is mainly driven by the surrounding environment (this study). Although detritus is a main source of energy in closed forests (Benzing, 2000), recent bromeliad research has shown that the role of algae as a potential energy source in open habitats is also a topic of interest (Brouard $et\ al.$, 2011; Marino $et\ al.$, 2011). Our results therefore shed new light on the ecology of bromeliad ecosystems, which are usually categorised as detritus-based systems, but where algal production can certainly form the basis of a non-detrital food web.

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