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Summary

1. Our understanding of the contribution of interspecific interactions to functional diversity in nature lags behind our knowledge of spatial and temporal patterns. Although two-species mutualisms are found in all types of ecosystems, the study of their ecological influences on other community members has mostly been limited to third species, while their influence on entire communities remains largely unexplored.

2. We hypothesized that mutualistic interactions between two respective ant species and an epiphyte mediate the biological traits composition of entire invertebrate communities that use the same host plant, thereby affecting food webs and functional diversity at the community level.

3. *Aechmea mertensii* (Bromeliaceae) is both a phytotelm ('plant-held water') and an ant-garden epiphyte. We sampled 111 bromeliads (111 aquatic invertebrate communities) associated with either the ant *Pachycondyla goeldii* or *Camponotus femoratus*. The relationships between ants, bromeliads and invertebrate abundance data were examined using a redundancy analysis. Biological traits information for invertebrates was structured using a fuzzy-coding technique, and a co-inertia analysis between traits and abundance data was used to interpret functional differences in bromeliad ecosystems.

4. The vegetative traits of *A. mertensii* depended on seed dispersion by *C. femoratus* and *P. goeldii* along a gradient of local conditions. The ant partner selected sets of invertebrates with traits that were best adapted to the bromeliads' morphology, and so the composition of the biological traits of invertebrate phytotelm communities depends on the identity of the ant partner. Biological traits suggest a bottom-up control of community structure in *C. femoratus*-associated phytotelmata and a greater structuring role for predatory invertebrates in *P. goeldii*-associated plants.

5. This study presents new information showing that two-species mutualisms affect the functional diversity of a much wider range of organisms. Most biological systems form complex networks where nodes (e.g. species) are more or less closely linked to each other, either directly or indirectly, through intermediate nodes. Our observations provide community-level information about biological interactions and functional diversity, and perspectives for further observations intended to examine whether large-scale changes in interacting species/community structure over broad geographical and anthropogenic gradients affect ecosystem functions.

Key-words: ant gardens, biodiversity, bromeliads, community functions, forest, French Guiana, invertebrates, phytotelmata, two-species mutualism

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Introduction

Our understanding of the contribution of interspecific interactions to the distribution of biological diversity in nature lags behind the increasingly vast knowledge of spatial and temporal ecological patterns in general (e.g. Lamoreux *et al.* 2006). This is certainly owing to the fact that ecological research on biodiversity has primarily focused on species richness and/or community composition (Bascompte 2009), while biologists have mostly considered the outcomes of two-species interactions or interactions between only a few species (Schmitt & Holbrook 2003). Biological interactions result in the formation of complex ecological networks where all species are more or less closely linked to each other, either directly or indirectly, through intermediate species (Montoya, Pimm & Solé 2006). However, our understanding of the indirect impact (i.e. mediated by intermediate species) on biological diversity primarily comes from studies on behavioural and chemical interactions in intertidal, marine communities (Menge 1995) and, to a lesser extent, from studies on herbivory (Ohgushi 2005). Herbivory, for example, can participate in modifying the vegetative traits of some terrestrial plants and thus indirectly influence the distribution of many invertebrates that utilize these plants (Ohgushi, Craig & Price 2007). Although the influence of two-species mutualisms on communities was poorly explored (Savage & Peterson 2007), preliminary observations made on a single location suggested that mutualistic ants can influence the shape and size of their associated plants by determining the distribution of the seedling along gradients of incident light (Leroy *et al.* 2009), thereby affecting the taxonomic composition of invertebrate communities that depend on the same plant (Céréghino *et al.* 2010). While these results show that two-species mutualisms can determine the local distribution of other species, they do not tell us whether most of the variation in the plant-associated community is attributable to geography or to the ant–plant interaction. More importantly, they do not tell us whether changes in invertebrate distributions from local to regional scales change ecosystem functions or whether convergence in community structure ensures that invertebrate food webs are functionally similar.

The rosettes of many bromeliads (Bromeliaceae) form wells that collect water and organic detritus (phytotelmata), and provide a habitat for specialized aquatic organisms ranging from prokaryotes to invertebrates (Laessle 1961; Carrias, Cussac & Corbara 2001; Franck & Lounibos 2009). The invertebrate food web–inhabiting water-filled bromeliads is especially amenable to studies of aquatic–terrestrial interactions (Romero & Srivastava 2010), food web structure (Kitching 2000) and ecosystem function (Srivastava 2006), because it is small in size, can be exhaustively sampled and is naturally replicated throughout the neotropics. Some tank bromeliads such as *Aechmea mertensii* Schult.f. are involved in mutualistic associations with arboreal ants called ant gardens (AGs, reviewed in Orivel & Leroy 2011). In tropical America and Southern Asia, some ants build arboreal carton nests by agglomerating organic material (Kaufmann & Maschwitz 2006). The ants then incorporate seeds of selected epiphytes on the carton nests (Orivel & Dejean 1999; Benzing 2000). As the epiphytes grow, their roots intertwine and anchor the carton nest in the supporting tree. In turn, the plants benefit from seed dispersal and protection from herbivores. In French Guiana, the tank bromeliad *A. mertensii* is only found in arboreal AGs initiated either by the ant *Camponotus femoratus* Fabr. or by *Pachycondyla goeldii* Forel (Corbara & Dejean 1996). Both ant–bromeliad associations can coexist on a local scale and the aquatic communities that depend on these AG-bromeliads are sensitive to ant-mediated environmental gradients (Leroy *et al.* 2009; Céréghino *et al.* 2010). To the best of our knowledge, there has been no previous evidence provided for an indirect plant-mediated impact upon the functioning of entire animal communities as a result of mutualistic interactions. This system is thus relevant to studies of cross-scale interactions because it includes both non-trophic and trophic interactions (with multiple trophic levels).

Because two-species mutualisms are widespread in nature (Vázquez *et al.* 2009), investigations should go beyond the search for evidence of the intermediate species-mediated impact upon community composition (Céréghino *et al.* 2010) to address the functional implications of such indirect effects. In addressing the role of interspecific relationships in the maintenance of ecological networks and functions in nature, we focused on how one scale of species–species interactions (ant–bromeliad mutualisms) can interact and influence the nature of other ecological interactions (notably the resulting food webs within the bromeliad phytotelm). Assuming that ants mediate the foliar structure of the tank bromeliad *A. mertensii* (Leroy *et al.* 2009) and that habitat is the template for ecological strategies (Southwood 1977), we hypothesized the following: (i) for a given ant partner, the composition of the biological traits of the aquatic invertebrates housed by *A. mertensii* is independent of geography, despite a spatial turnover in the taxonomic composition, and (ii) on a local scale, the composition of the biological traits of invertebrate phytotelm communities depends on the identity of the ant partner. Subsequently, we predicted that the impact of ant–bromeliad mutualisms upon phytotelm communities overrides the influence of geography on the functioning of *A. mertensii* ecosystems.

Materials and methods

STUDY AREA, ANT GARDENS AND BROMELIADS

This study was conducted in French Guiana in October 2008 in secondary forest formations (pioneer growths) located along roads. Two distinct geographical areas were selected. We sampled 63 bromeliads along a 11-km-long dirt road near the Petit-Saut Dam (latitude: 5°03′43″N; longitude: 53°02′46″W; elevation a.s.l.: 80 m; hereafter 'Petit-Saut') and 48 bromeliads along a 17-km-long section of the D6 road starting from the Kaw marsh (latitude: 4°30′52″N; longitude:

52°03'58"W; elevation a.s.l.: 250 m; hereafter 'Kaw'). The distance between Petit-Saut and Kaw is 125 km as the crow flies. The climate of French Guiana is moist tropical, with 3000 mm of yearly precipitation at Petit-Saut and 4000 mm in the Kaw area. There is a major drop in rainfall between September and November (dry season) and another shorter and more irregular dry period in March. The maximum and minimum monthly temperatures average 33·5 and 20·5 °C at Petit-Saut and 32 and 21 °C at Kaw.

All of the samples were taken from *A. mertensii* bromeliads rooted on well-developed AGs inhabited either by the ants *C. femoratus* and *Crematogaster levior* ($n = 71$) or by *P. goeldii* ($n = 40$), hereafter '*C. femoratus* samples' and '*P. goeldii* samples'; Fig. 1. *Camponotus femoratus* is a polygynous (multiple queens), arboreal formicine species living in a parabiotic association with the myrmicine species *C. levior*, i.e. to say, they share the same nests and trails but shelter in different cavities of the nests (Orivel, Errard & Dejean 1997). Their large polydomous (multiple nests) colonies and aggressiveness identify them as territorially dominant, arboreal species in Neotropical rain forest canopies. Conversely, *P. goeldii* is a monogynous (single queen) arboreal ponerine species with comparatively smaller populations, although the colonies may be polydomous (Corbara & Dejean 1996).

There are six *Aechmea* species in French Guiana (Mori *et al.* 1997), and *Aechmea mertensii* is the only tank-forming species found in association with AGs in French Guiana (Madison 1979; Belin-Depoux, 1991; Benzing 2000). In *Aechmea mertensii*, leaf display and plant size differ markedly according to the associated ant species (Leroy *et al.* 2009). The plants are *c.* 20–60 cm tall, forming either a '*subbulbous or crateriform rosette*' (Mori *et al.* 1997). We compared inflorescences and flowers (two characters for the identification of bromeliad species) of the two morphs with those from the herbarium holotype available at the Cayenne herbarium (*Institut de Recherche pour le Développement* in French Guiana) and found no morphological differences between specimens, supporting the assumption that the two morphs belong to the same species, despite important phenotypic variations. If we plot the percentage of vertical leaves (an indicator of plant shape) against incident radiation (Fig. 2), it clearly appears that (i) *A. mertensii* bromeliads show a phenotypic plasticity in relation to light environments and (ii) plants shift from a funnel-like, crateriform shape (with *C. femoratus*) to an amphora, bulbous shape (with *P. goeldii*) along a gradient of shaded to exposed areas.

Fig. 1. The tank bromeliad *Aechmea mertensii*, rooted on a *Pachycondyla goeldii* nest (left), and on a *Camponotus femoratus* nest (right).

Fig. 2. Relationship between the shape of the bromeliad *Aechmea mertensii* (% vertical leaves) and light environment (% incident radiation), in relation to the distribution of its ant partner (CF, *Camponotus femoratus*; PG, *Pachycondyla goeldii*).

ENVIRONMENTAL VARIABLES

All of the sampled bromeliads were at the flowering stage in the plant life cycle so that differences in plant size and/or shape would not be attributable to ontogeny (bromeliads do not grow further beyond this stage and the shoots die after fruit production). For each tank bromeliad, we recorded 15 variables. Plant height (cm) was measured as the distance from the bottom of the body to the top of the crown. Plant width (cm) was the maximum distance between the tips of the leaves (average of two measurements taken at 90°). After recording the total number of leaves and number of distinct wells constituting the reservoir, the leaf display was estimated as the proportion of horizontal and vertical leaves (%). The length and width of the longest leaf were also recorded, as well as the height and diameter (two random measurements taken at 90°) of the reservoir (cm). This first set of 10 variables described the vegetative traits of the bromeliads. We then recorded the elevation above the ground (m) and the number of epiphyte species (including *A. mertensii*) rooted on the AG. Percentages of total incident radiation above the bromeliads were calculated using hemispherical photographs and an image-processing software (Gap Light Analyzer 2.0) (Frazer, Canham & Lertzman 1999), as described by Leroy *et al.* (2009). This second set of three variables described the distribution of epiphytic bromeliads in the supporting AGs. Last, we emptied the wells in each plant by sucking the water out (see invertebrate sampling). The corresponding volume of water (mL) was recorded. The amount of fine particulate organic matter (FPOM; 1000–0·45 μm in size) was expressed as preserved volume (mm^3 after decantation in graduated test tubes; see also Paradise 2004). These two variables were chosen to describe the amount of water available to freshwater organisms and the amount of food resources at the base of the food webs.

AQUATIC INVERTEBRATES

As the *A. mertensii* roots are totally incorporated into the ant nest structure, we decided not to remove the plants in order to preserve the AGs. To sample the water retained in the tanks, we used 5- and 10-mL micropipettes with the end trimmed to widen the orifice (Jabiol *et al.* 2009; Jocque *et al.* 2010). We carefully emptied the wells in each plant by sucking the water out using pipettes of appropriate dimensions. The samples were preserved in the field in 4% formalin (final concentration). Aquatic invertebrates were sorted in the laboratory

and preserved in 70% ethanol. They were mostly identified to genus, species or morphospecies (Table 1) and enumerated. Professional taxonomists provided assistance for the identification of the Oligochaeta (Prof. N. Giani, Univ. Toulouse, France) and the Diptera (Dr A.G.B. Thomas; University Toulouse, France).

DATA ANALYSES

Community structure and environmental variables

The relationships between all of the environmental variables, bromeliads and invertebrate abundance data were examined using multivariate ordination. Invertebrate abundances were log $(n + 1)$ transformed prior to analyses. 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 = 2·46) along axis 1 (Lepš & Šmilauer 2003); thereafter, a redundancy analysis (RDA) was used to examine invertebrate relationships with bromeliads and with the 15 environmental variables. Forward selection was employed to test which of the 15 environmental variables explained a significant ($P < 0{\cdot}05$) proportion of the species variance. The significance of explanatory variables was tested against 500 Monte Carlo permutations.

Biological traits

The biological traits for each invertebrate taxon (Table 2) were obtained from the study of Merritt & Cummins (1996), Tachet *et al.* (2000) and the authors' observations of live and preserved specimens (e.g. locomotion, food acquisition, mouthparts). The biological traits examined were as follows: maximum body size (BS), aquatic developmental stage (AS), reproduction mode (RE), dispersal mode (DM), resistance forms (RF), food (FD), feeding group (FG), respiration mode (RM) and locomotion (LO). The categories for each trait were either ordinal or nominal. Information on the biological traits was then structured using a fuzzy-coding technique (Chevenet, Dolédec & Chessel 1994) derived from the fuzzy-set theory (Zadeh 1965): scores ranged from '0', indicating 'no affinity', to '3', indicating 'high affinity' for a given species traits category. This procedure allowed us to build the 'traits matrix'. This matrix was analysed using a 'fuzzy correspondence analysis' (FCA; Chevenet, Dolédec & Chessel 1994). Then, a principal component analysis (PCA) was used to obtain multivariate scores for invertebrate taxa (results not shown). Given our aim of analysing spatial trends in biological traits, the PCA was preferred to a correspondence analysis to obtain species scores because it tends to separate bromeliads by most abundant species. A simultaneous analysis of the invertebrate abundances and biological traits matrices was conducted using co-inertia analysis (CoA, Dolédec &

Table 1. List of the macroinvertebrate taxa occurring in the tank bromeliad *Aechmea mertensii* associated with ant gardens inhabited by the ants *Camponotus femoratus* (CF) and *Pachycondyla goeldii* (PG) in the Kaw and Petit-Saut areas (+ = presence)

Class	Order	Family	Sub-family	Tribe	Species	Taxa ID	Kaw		Petit-Saut	
							CF	PG	CF	PG
Insecta	Diptera	Culicidae	Culicinae	Culicini	***Culex* spp.**	1	+	+	+	+
				Toxorhynchitini	***Toxorhynchites* spp.**	2	+	+	+	+
				Sabethini	***Wyeomyia* spp.**	3	+	+	+	+
		Corethrellidae			***Corethrella* sp.**	4	+		+	+
		Ceratopogonidae	Ceratopogoninae		***Bezzia* sp.1**	5	+		+	+
					***Bezzia* sp.2**	6	+		+	+
			Forcipomyinae		**Forcipomyinae sp.1**	7	+	+	+	
					Forcipomyinae sp.2	8		+		+
		Chironomidae		**Chironomini**		9	+	+	+	+
			Tanypodinae			10	+		+	+
				Tanytarsinii		11			+	
		Cecidomyiidae			***Cecidomyiidae* sp.1**	12		+		+
		Psychodidae			***Telmatoscopus* sp.**	13	+		+	
		Limoniidae	**Limoniinae**			14			+	
		Tabanidae				15		+		+
		Syrphidae				16			+	
	Hemiptera	Veliidae			***Microvelia* sp.**	17	+			
	Coleoptera	Scirtidae	Scirtinae		***Cyphon* sp.**	18	+	+	+	+
			Sphaeridiinae		**Sphaeridiinae sp.1**	19	+			
					Sphaeridiinae sp.2	20			+	
		Dytiscidae			***Copelatus* sp.**	21	+			
		Hydrophilidae				22				
	Odonata	Coenagrionidae			**Coenagrionidae sp.1**	23			+	
Acari	[1]**Hydracarina**					24	+		+	+
Oligochaeta		Naididae			***Aulophorus superterrenus***	25	+	+	+	+
					Pristina menoni*, *P. notopora*, *P. osborni	26	+	+	+	+
		Aelosomatidae			***Aelosoma* sp.**	27			+	+

Bold characters indicate the level of taxonomic resolution for this study. Culicidae and Chironomidae were found both as larvae and pupae, and all other insects were only found as larvae. [1]Sub-order. *Taxa ID as in Table 2 and Fig. 1.

Table 2. Summary of the biological traits under consideration and their categories. Scores range from '0' (no affinity) to '3' (high affinity)

Traits	Modality	Abbreviation	Taxa ID*																										
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
BS	≤0·25 cm	BS1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	3	0	0	1	0	0	0	0	3	0	3	3
	>0·25–0·5 cm	BS2	1	0	1	3	3	3	3	3	0	3	3	3	0	0	3	0	3	0	3	3	0	3	2	3	0	0	0
	>0·5–1 cm	BS3	3	0	3	0	0	0	0	0	1	0	0	0	2	2	0	0	0	2	0	1	3	1	3	0	0	0	0
	>1–2 cm	BS4	0	3	0	0	0	0	0	0	3	0	0	0	3	3	0	0	0	3	0	0	0	0	0	0	3	0	0
	>2–4 cm	BS5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
AS	Egg	AS1	1	1	1	1	1	1	0	0	0	0	0	1	2	2	1	0	0	3	3	3	3	3	2	1	3	3	3
	Larva	AS2	3	3	3	3	2	2	2	2	3	3	3	3	2	2	2	2	3	3	3	3	3	3	3	2	3	3	3
	Nymph	AS3	3	3	3	3	2	2	2	2	3	3	3	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	Adult	AS4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	2	2	2	0	2	3	3	3
RE	Ovoviviparity	RE1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Isolated eggs, free	RE2	1	1	1	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2	2
	Isolated eggs, cemented	RE3	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1
	Clutches, cemented or fixed	RE4	0	0	0	0	3	3	3	3	1	1	1	1	3	1	3	0	3	0	3	3	0	3	0	3	0	0	0
	Clutches, free	RE5	3	3	3	0	0	0	0	0	3	3	3	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0
	Clutches in vegetation	RE6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
	Clutches, terrestrial	RE7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	3	2	3	1	1	3	1	0	0	0	0	0
	Asexual reproduction	RE8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3
DM	Aerial passive	DM1	2	2	2	2	0	0	0	0	3	3	3	3	1	3	0	1	1	0	0	0	0	0	0	3	3	3	3
	Aerial active	DM2	3	3	3	3	2	2	2	2	1	1	1	1	3	1	3	3	3	3	3	3	3	3	3	0	0	0	0
RF	Eggs, statoblasts	RF1	3	3	3	3	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
	Cocoons	RF2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3
	Diapause or dormancy	RF3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	3	0	0	0
	None	RF4	0	0	0	0	3	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3	3	3	3	0	0	0	0
RM	Tegument	RM1	0	0	0	0	1	1	1	1	3	3	3	1	0	1	0	0	0	1	1	1	1	1	1	3	3	3	3
	Gill	RM2	0	0	0	0	3	3	3	3	1	1	1	0	0	3	0	0	0	3	0	0	0	0	3	0	3	0	0
	Plastron	RM3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
	Siphon/spiracle	RM4	3	3	3	3	0	0	0	0	0	0	0	3	3	3	3	3	3	0	3	3	3	3	0	0	0	0	0
	Hydrostatic vesicle	RM5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
LO	Flier	LO1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0
	Surface swimmer	LO2	3	3	3	3	1	1	0	0	0	0	0	0	1	0	1	1	3	0	0	0	1	0	0	2	0	0	0
	Full water swimmer	LO3	2	2	2	2	3	3	0	0	1	3	2	0	0	0	0	0	0	0	3	3	3	3	1	3	2	2	2
	Crawler	LO4	0	0	0	0	1	1	3	3	3	2	3	3	2	3	3	3	0	3	3	3	1	3	3	3	0	0	0
	Burrower	LO5	0	0	0	0	1	1	0	0	2	1	0	2	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
	Interstitial	LO6	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
FD	Microorganisms	FD1	3	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3
	Detritus (< 1 mm)	FD2	2	1	2	0	1	1	0	0	3	0	3	0	2	0	1	1	0	3	0	0	0	0	0	3	2	2	3
	Dead plant (litter)	FD3	0	0	0	0	0	0	1	1	2	1	1	0	3	3	1	2	0	1	0	0	0	0	0	0	0	0	0
	Living microphytes	FD4	3	0	3	0	2	2	3	3	1	1	1	0	2	0	0	1	0	1	3	3	0	3	0	0	2	2	0
	Living leaf tissue	FD5	0	0	0	0	0	0	1	1	1	0	0	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Dead animal (≥1 mm)	FD6	0	0	0	0	1	1	0	0	0	1	0	0	2	0	0	2	1	0	0	0	0	0	0	0	0	0	0
	Living microinvertebrates	FD7	0	1	0	0	3	3	0	0	1	2	0	0	0	0	0	0	3	0	3	3	2	3	2	0	0	0	0
	Living macroinvertebrates	FD8	0	3	0	3	2	2	0	0	0	3	0	0	0	0	3	0	1	0	1	1	3	1	3	0	0	0	0
FG	Deposit feeder	FG1	2	1	2	0	1	1	3	3	3	0	3	0	2	1	1	3	0	0	0	0	0	0	0	3	3	3	3
	Shredder	FG2	0	0	0	0	1	1	0	0	2	0	2	0	3	3	0	1	0	2	1	1	0	1	0	0	0	0	0
	Scraper	FG3	0	0	0	0	0	0	1	1	1	0	2	0	1	0	0	0	0	3	0	0	0	0	0	0	1	0	0
	Filter-feeder	FG4	3	0	3	0	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Piercer	FG5	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0
	Predator	FG6	0	3	0	3	3	3	0	0	1	3	0	0	0	0	0	0	1	0	3	3	3	3	3	0	0	0	0
	Parasite	FG7	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

*Taxa ID as in Table 1 and Fig. 1. BS, body size; AS, aquatic stage; RE, reproduction mode; DM, dispersal mode; RF, resistance form; RM, respiration mode; LO, locomotion; FD, food; FG, feeding group.

Chessel 1994). This analysis studies co-structure by maximizing covariance between faunistic and biological traits ordination scores in the FCA and PCA (Dray, Chessel & Thioulouse 2003). The aim of the CoA is to schematize spatial variations in the combinations of the biological traits of tank bromeliad invertebrates. A permutation test (Dolédec & Chessel 1994) was used to check the significance of the resulting correlation between the two sets of data resulting from the two kinds of analysis (FCA and PCA). We carried out 500 co-inertia analyses of the taxonomic and biological traits data sets after the random permutation of their rows. We measured the correlation between the two tables using the *RV* coefficient, a multidimensional equivalent of the ordinary correlation coefficient between two variables (Robert & Escoufier 1976; Dolédec *et al.* 2006). The test was significant when the observed value was in a class containing only a few random values among the 500 possible. The objective was to determine the common structure between the two sets of data and then to interpret differences

in bromeliad ecosystems in terms of the combinations of the biological traits of their aquatic communities. Mann–Whitney tests were used to test significant differences in bromeliad distribution in the CoA according to sites and to ant species using the coordinates of samples on the most significant axis. These analyses were conducted with R software (R Development Core Team 2010).

Results

COMMUNITY STRUCTURE

Axes 1 and 2 of the RDA accounted for 25·8% of the total species variance and 67·7% of the species–environment relationship (Fig. 3). Eigenvalues for axes 1 and 2 were 0·18 and 0·07, respectively. Species–environment correlations were 0·838 for axis 1 and 0·683 for axis 2. Forward selection identified eight variables as explaining a significant amount of the species variance (bold arrows in Fig. 3): water volume (WV), FPOM (OM), number of epiphyte species (NE), reservoir height (RH) and number of wells (NW) (P = 0·002), incident radiation (IR) (P = 0·004), number of leaves (NL) and elevation above ground (EG) (P = 0·03). Water volume accounted for the greatest proportion of the total canonical eigenvalues (14%; F = 17·93; P = 0·002). The scatterplot of the RDA allowed us to distinguish two main subsets along axis 2 when the bromeliads were more specifically grouped according to sampling areas (Fig. 3a); i.e. the Petit-Saut area (bottom part of the scatterplot), and the Kaw area (top area). Bromeliads from Petit-Saut showed higher abundances for the dipterans *Culex* spp., *Bezzia*, *Corethrella* sp., *Telmatoscopus* sp.1, Chironominii and Tanypodinae, Coenagrionidae sp.1, and the Oligochaeta *Aoelosoma* sp. and *Pristina* spp. (Fig. 3b). Bromeliads from Kaw were characterized by higher abundances for some taxa such as the Oligochaeta *Aulophorus superterrenus*, the dipterans Forcipomyinae sp.1 and *Wyeomyia* spp., and the coleopteran *Cyphon* sp. The remaining taxa were common to both sampling areas and did not show clear spatial patterns. Axis 1 displayed a clear gradient of phytotelm habitat conditions. First, invertebrate taxa found in *P. goeldii*-associated bromeliads were mostly a nested subset of the pool of potential species for this type of phytotelmata (Fig 1b). Secondly, there was a gradient of habitat size (i.e. water volume, number of reservoirs) and amount of FPOM made available to the aquatic fauna from low (left side of the scatterplot) to high (right), and a gradient of incident radiation ranging from low (right) to high (left). Within these gradients, *P. goeldii*-associated bromeliads were found in exposed areas. They were smaller and contained less water and detritus than the *C. femoratus*-associated bromeliads, which rather occurred in shady areas. Finally, it appeared that the Petit-Saut AGs bore a higher diversity of epiphyte species (NE) than those from Kaw. Therefore, the gradient analysis conducted through the RDA basically portrayed the spatial changes in the compositional structure of invertebrate communities, with respect to factors acting over broad scales (site effect, axis 2) and local scales (ant-garden effect, axis 1).

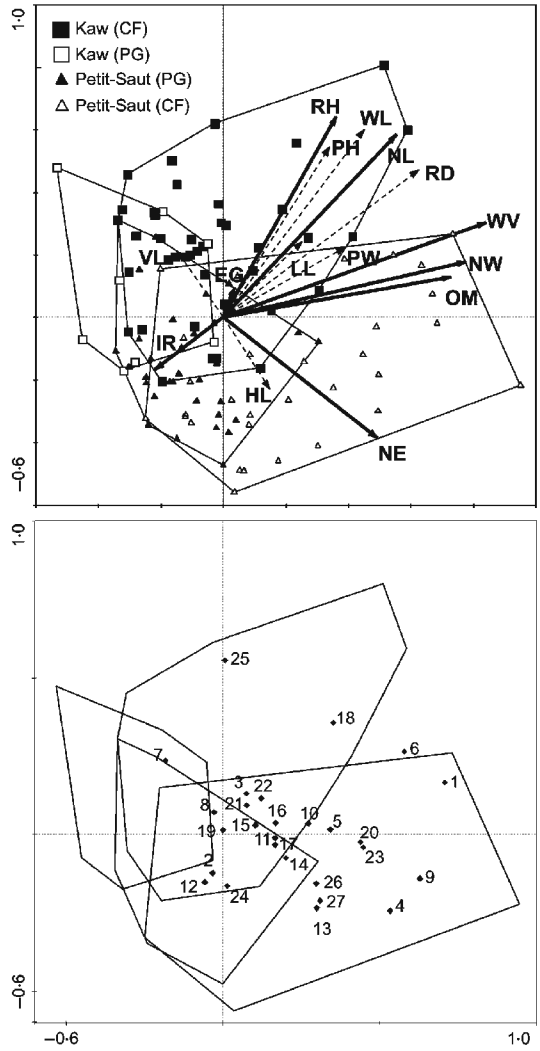

Fig. 3. Redundancy analysis (RDA) biplots. (top panel) Bromeliads and environmental variables. Environmental variables are represented as vectors; directions show the gradients, arrow length represents the strengths of the variables on the ordination space. Different markers were used to identify the corresponding sites (squares, Kaw vs. triangles, Petit-Saut) and the associated ant species. CF, *Camponotus femoratus*; PG, *Pachycondyla goeldii*; (bottom panel) distribution of invertebrate taxa in the ordination space. Invertebrates are identified by numbers, as in Tables 1 and 2. Associated ant species × site clusters as in Fig. 3a. Abbreviations for environmental variables are: PH, Plant height (cm); PW, Plant width (cm); NL, total number of leaves; NW, number of distinct wells constituting the reservoir; HL, proportion of horizontal leaves (%); VL, proportion of vertical leaves (%); LL, length of the longest leaf (cm); WL, width of the longest leaf (cm); RH, reservoir height (cm); RD, diameter of the reservoir (cm); EG, elevation above ground (m); NE, number of epiphyte species rooted on the AG; IR, percentage of total incident radiation above the bromeliads; WV, water volume (mL); OM, amount of fine particulate organic matter (mL). Variables explaining a significant (P < 0.05) proportion of the species variance are represented by bold arrows; other variables are represented by dotted arrows.

BIOLOGICAL TRAITS OF INVERTEBRATES IN RELATIONSHIP TO TANK BROMELIADS

A permutation test indicated that the co-inertia between taxa distributions and biological traits matrices was significant

(RV = 0·23; P < 0·05). Axes 1 and 2 expressed 56·5 and 16·6% of the overall variance, respectively. The grouping of bromeliads according to sampling sites (Fig. 4a) did not separate bromeliads into distinct groups along axis 1 (the most significant CoA axis, see above) on the basis of invertebrate traits (Mann–Whitney test using the coordinates of the samples, P > 0·05). However, the grouping of bromeliads according to the identity of the ant partner separated the samples' centroids along axis 1 (Fig. 4b), and there was a significant difference in sample coordinates along this axis (P < 0·01).

Camponotus femoratus-associated bromeliads were characterized by higher proportions of large-bodied invertebrates (> 0·5 cm) and passive dispersers (e.g. phoretic Oligochaeta, small insects with 'flying' adults mostly dispersed by the wind). Most aquatic taxa found in these bromeliads were interstitial (in the detrital material, between cracks in the leaves) or surface and open-water swimmers. Their diet was mostly based on micro-organisms (including microscopic algae) and small detritus < 1 mm in size. Deposit feeders, scrapers and collector filterers were numerically dominant.

Fig. 4. Co-inertia analysis results: (a) ordination of the 111 bromeliads on the first two axes of the co-inertia analysis (axes 1 and 2 contributed to 56.5 and 16.6% of the overall variance, respectively); left panel: grouping of bromeliads according to sites (Kaw vs. Petit-Saut); right panel: grouping of bromeliads according to their associated ant species (*Camponotus femoratus* vs. *Pachycondyla goeldii*). (b) Distribution of categories of species traits on the first two axes (see Table 2 for category codes). Categories are positioned at the weighted average of their species.

Reproduction was mostly sexual, although the Oligochaeta (particularly abundant in these bromeliads) also reproduce asexually. Eggs were laid either as clutches or isolated, cemented or free. Eggs and cocoons were the commonest resistance forms.

Pachycondyla goeldii-associated bromeliads showed higher proportions of small-bodied invertebrates (< 0·5 cm) and of active dispersers (e.g. flying adults) than those associated with *C. femoratus*. Most invertebrates were crawlers (on the inner side of the bromeliad leaves), but there were also higher proportions of aquatic winged adults, notably coleopterans. Consequently, plastron and hydrostatic vesicles were common respiratory structures. Overall, diet was based either on litter and dead invertebrates, or live micro- and macroinvertebrates. Shredders, piercers and predators were numerically dominant. Eggs were mostly laid as clutches, cemented or fixed on the bromeliad leaves at the aquatic–aerial interface. Lastly, the majority of the invertebrates found in these bromeliads did not show particular resistance forms.

Discussion

Habitat theory (Southwood 1977; Block & Brennan 1993) provides a broadly relevant framework for analysing the physical and biological settings that underlie community functions when species create habitats for other species either through their activity (ants) or presence/physical structure (bromeliads). Biological assemblages are believed to integrate the variability of their habitat, so that taxa with certain adaptations should be those selected by the dynamics of local physical and biological conditions. The persistence or elimination of a species thus depends on appropriate morphological, physiological and behavioural attributes, and on habitat characteristics, respectively. This suggests that the dominance of certain traits may be more predictable than the abundance of individual taxa, but also that the functioning of any community in relation to environmental variables can be inferred from its combination of biological traits (Reiss *et al.* 2009).

In this context, and owing to their characteristic ecological settings and small size, tank bromeliads have often been used as model systems for studying many basic ecosystem processes (Srivastava 2006), from community assembly rules (Jabiol *et al.* 2009) to diversity–ecosystem functional relationships (Leroy *et al.* 2009; Romero & Srivastava 2010). However, the *indirect* (plant-mediated) influence of terrestrial animals on the functioning of the aquatic portion of the bromeliad microcosm has not been considered so far. Regardless of possible interactions with terrestrial animals, the influence of tank bromeliads on phytotelm communities is related to their morphology (e.g. large central pools vs. many small separate pools) that determines the amount of water (available habitat) and detritus (a good indicator of available resources at the lower end of the food chain) that enter the reservoirs (Armbruster, Hutchinson & Cotgreave 2002). The morphology of bromeliads is strongly influenced by the amount of transmitted light that penetrates under tree canopies (Montero, Feruglio & Barberis 2010). In the bromeliad

A. mertensii, the phenotypic plasticity of the plant has resulted from seed dispersion by the ants *C. femoratus* and *P. goeldii* along a gradient of local conditions (e.g. incident radiation, incoming litter and rainwater). Our field observations suggest that *C. femoratus* selects bromeliad seeds from its own gardens, while *P. goeldii* collects seeds on the ground, but we found no significant difference in seed size between *C. femoratus* and *P. goeldii*-associated bromeliads (C. Leroy, unpublished data). However, Leroy *et al.* (2009) reported differences in leaf anatomy (i.e. leaf thickness, number of cell layers, water and chlorophyll parenchyma) in relation to ant species. Based on these observations, we assume that changes in phytotelm invertebrate communities are not only attributable to the ant but attributable to the interaction between the ant and the plant. The *A. mertensii* rosettes were either very wide (*C. femoratus* AGs) or were small and amphora shaped (*P. goeldii* AGs) (Leroy *et al.* 2009). Importantly, patterns of plant phenotypes in relation to ant species with different habitat preferences were consistent between sites (this study). A related result is that the influence of ant–plant mutualisms may overcome geographical effects on the physical characteristics of the container habitat. As ant–plant interactions impact the vegetative traits of the bromeliad, one may expect functional shifts as sets of phytotelm invertebrate species with particular traits are eliminated or replaced by other sets with different traits when shifting from one ant partner to the other.

For a given ant partner, some aquatic taxa only occurred at one of the two sites (e.g. *Aeolosoma* sp. and Sphaeridinae sp.2 at Petit-Saut; *Microvelia* sp. and Sphaeridinae sp.1 at Kaw) or were numerically dominant at a site but rare at the other site (e.g. the abundances of *Aulophorus superterrenus* and *Cyphon* sp. were on average threefold higher at Kaw than at Petit-Saut). This suggests that the site had an effect on the taxonomic structure (composition and abundance patterns) of phytotelm communities, but also that the distance between our sampling areas (125 km) allowed us to properly assess the relative influence of geography and ant–plant interactions upon phytotelm invertebrate diversity. At a given site, the invertebrate taxa found in *P. goeldii*-associated bromeliads were a subset of the taxa occurring in the larger *C. femoratus*-associated bromeliads. Because the latter also hosted more individuals per plant, we assume that larger habitats were more easily colonized by immigrants, which resulted in positive species–area relationships (Srivastava & Lawton 1998; Jabiol *et al.* 2009). Finally, AGs that had the highest epiphyte richness (4–5 species) were all associated with *C. femoratus*, and their invertebrate phytotelm communities were amongst the richest. It is worth noting that such AGs were found at both sites (even if they were more frequent at Petit-Saut) and that the variable 'number of epiphyte species' did not covary with any other significant variables such as plant descriptors or water volume (see Fig. 3). It is thus likely that, in addition to phytotelm habitat features, some AGs as a whole (in relation to the identity of the ant partner) are more attractive to immigrants than others, which could partly account for the observed diversity patterns. Overall, these results also show that the alternative association of *A. mertensii* with two ant species having different ecological requirements increases the bromeliads' local range and subsequently promotes the diversity of the associated invertebrates.

Regardless of ant species, and despite changes in the taxonomic composition from one sampling area to the other, similar trait profiles were found for the phytotelm communities sampled at Kaw and Petit-Saut. Assuming that ecological strategies reflect how species cope with the temporal and spatial variability of their environment (Statzner, Dolédec & Hugueny 2004), the composition of the biological traits and subsequently the functioning of the invertebrate phytotelm communities were rather influenced by plant phenotype and local environments in relation to the identity of the ant partner.

The traits of phytotelm invertebrates in *C. femoratus*-associated bromeliads suggest that habitat occupancy and resource use are favoured by larger body size and a higher diversity of feeding groups. Those populations are likely to be selected by more stable (i.e. higher moisture and supply of organic matter in shaded areas) and/or structured habitats (i.e. greater number of wells) resulting in interspecific competition and/or resource partitioning through the spatial segregation of species (Céréghino *et al.* 2008). The dominant functional feeding groups in *C. femoratus*-associated invertebrates were collector gatherers and collector filterers. These communities thus strongly relied on litter supply and the decay of particulate organic matter by micro-organisms, something which suggests a bottom-up influence on community structure (Kitching 2001). Overall, *C. femoratus*-associated communities showed the highest diversity of trait modalities (strategies). In addition to larger amounts of water and FPOM captured by larger reservoirs, *C. femoratus*-associated bromeliads had more habitat subunits (more leaves forming more wells). The increase in habitat complexity from *P. goeldii*- to *C. femoratus* AGs could thus promote trait diversity by creating new niches (Montero, Feruglio & Barberis 2010) and/or by reducing the likelihood of an encounter between potential competitors (Young 2001). Larger reservoirs and a more diverse range of microhabitats could allow for a higher diversity of locomotion modes. Open-water and surface swimmers, burrowers and interstitial species were more frequently observed in plants associated with *C. femoratus*. The higher proportions of passive dispersers (notably annelids) in *C. femoratus*-associated bromeliads suggest that more stable conditions fostered associations between phoretic invertebrates and dispersal agents. We observed many poison frogs (*Dendrobates ventrimaculatus*) when sampling large *A. mertensii* bromeliads, and these amphibians are known to act as dispersal agents for bromeliad annelids (Serramo-Lopez, Pena-Rodrigues & Iglesias-Rios 1999).

The biological traits of *P. goeldii*-associated invertebrates suggested that species allocated more energy to reproduction (asexual reproduction was dominant: eggs clutches, cemented or fixed eggs) compared with *C. femoratus*-associated invertebrates. These characteristics and others such as small body size or the dominance of active dispersers suggest that

populations are selected because of unstable habitats or by habitats fluctuating in an unpredictable way. *Pachycondyla goeldii*-associated bromeliads experienced water- and nutrient-stressed conditions, and, because the plants were located in exposed areas, they mostly obtained windborne nutrients and their water-to-FPOM volume ratio was on average two times lower than in the *C. femoratus*-associated bromeliads. In these conditions, *P. goeldii*-associated communities contained higher proportions of predators, something which suggests a greater role for predators in controlling community structure.

In summary, biogeography and mutualistic interactions successively act as a coarse-to-fine filter for phytotelm communities in the AG-bromeliad *Aechmea mertensii*. First, the geographical site determines the potential species pool for this type of phytotelm. Then, the identity of the ant partner indirectly selects sets of invertebrates with traits that are best adapted to the bromeliads' morphology and local environments, and species trait combinations have a direct influence upon community functioning. Ant-garden ants can be seen as allogenic engineers (Jones, Lawton & et Shachak 1994), because they build and shape habitats for species (e.g. epiphytes including tank bromeliads, phytotelm invertebrates, amphibians, but also spiders and cockroaches that were not considered in this study) that otherwise would not be present. Among these species, tank bromeliads are autogenic engineers that provide habitat through their presence. As the outcome of the ant–bromeliad interaction depends on the ant species, and because the alternating association of a given bromeliad species with two ants generates a broader habitat gradient than the association with one species only would, the ant–plant mutualism acts as a top-down influence on the invertebrate community functions and food webs within the tanks. Previous studies showed that mutualistic interactions can modify some of the biological traits of the partners (e.g. physiology, morphology, behaviour, ontogeny) and may consequently mediate the influence that some species have on other components of ecological communities (Wood *et al.* 2007). However, biological diversity is not only a sum of coexisting species; it also includes the complexity of the 'web of life' that links these species (Bascompte 2009). To the best of our knowledge, this is the first report of shifts in community functioning as a result of alternating mutualistic interactions (e.g. a greater structuring role for allochtonous inputs vs. predators in *C. femoratus* and *P. goeldii* AGs, respectively). Ant-gardens hosting *Aechmea* or *Neoregelia* tank bromeliads (as well as other epiphytes) occur frequently throughout the Neotropics (Orivel & Leroy 2011). In a context of biodiversity loss, ecologists seek to understand how species turnover affects ecosystem functions and more specifically the stability of food webs. We know that species identity/turnover can be very important in determining ecosystem functions on a local-regional basis (e.g. through cross-scale interactions, this study), but we do not know whether large-scale changes in partners/community composition affect ecosystem function. We also know little of the community-wide implications of human-induced perturbations. Partly, this is owing to the fact that most studies on global change have focused on population abundance or distribution shifts (Tylianakis *et al.* 2008). Most biological systems form complex networks, but little is known of the effect of species turnover (or loss) on networks of antagonistic and mutualistic interactions. Therefore, our study provides perspectives for replicated observations and/or experiments over broad geographical and anthropogenic gradients to decipher the role that ecological and co-evolutionary processes play in the assembling of ecological networks at the man–forest interface.

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