



Biodiversity/Biodiversité

Ants impact the composition of the aquatic macroinvertebrate communities of a myrmecophytic tank bromeliad

Impact des fourmis sur la composition des communautés aquatiques de macro-invertébrés d'une broméliacée myrmécophyte à réservoirs

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ABSTRACT

In an inundated Mexican forest, 89 out of 92 myrmecophytic tank bromeliads (*Aechmea bracteata*) housed an associated ant colony: 13 sheltered *Azteca serica*, 43 *Dolichoderus bispinosus*, and 33 *Neoponera villosa*. Ant presence has a positive impact on the diversity of the aquatic macroinvertebrate communities ($n=30$ bromeliads studied). A Principal Component Analysis (PCA) showed that the presence and the species of ant are not correlated to bromeliad size, quantity of water, number of wells, filtered organic matter or incident radiation. The PCA and a generalized linear model showed that the presence of *Azteca serica* differed from the presence of the other two ant species or no ants in its effects on the aquatic invertebrate community (more predators). Therefore, both ant presence and species of ant affect the composition of the aquatic macroinvertebrate communities in the tanks of *A. bracteata*, likely due to ant deposition of feces and other waste in these tanks. © 2018 Published by Elsevier Masson SAS on behalf of Académie des sciences. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

R É S U M É

Dans une forêt inondable du Mexique, sur 92 individus de la broméliacée myrmécophyte *Aechmea bracteata*, seuls trois étaient dépourvus d'une colonie de fourmis, 13 abritaient *Azteca serica*, 43 *Dolichoderus bispinosus* et 33 *Neoponera villosa*. La présence des fourmis favorise la diversité au sein des communautés aquatiques de macro-invertébrés (30 broméliacées étudiées, index de Shannon, profils de diversité). Une analyse en composantes principales (ACP) montre que la présence de fourmis n'est pas corrélée avec

1. Introduction

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la taille de la plante, la quantité d'eau, le nombre de puits, la quantité de matière organique et la radiation incidente. L'ACP et un modèle mixte généralisé montrent un impact d'*Azteca serica* (comparé aux autres cas) attribuable à une plus grande quantité de prédateurs (effet *top-down*). La présence et l'identité des fourmis jouent un rôle sur la composition des communautés de macro-invertébrés aquatiques à travers des interactions directes, les ouvrières évacuant fèces et déchets dans les réservoirs.

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Complex ecological networks result from direct, pairwise interactions (e.g., mutualisms, herbivory, predation and parasitism) and “indirect effects” (e.g., keystone predation, indirect mutualisms and trophic cascades) when intermediate species are present [1]. Among the indirect effects, trophically mediated interactions are the most cited, including trophic cascades that involve predators, prey, and plants, where the predators influence plant communities through their impact on prey abundance (prey killed) or behavior (“ecology of fear”: the prey avoid areas where there is a high probability of being captured). For example, two spider species, a stalker and an ambusher, have different impacts on meadow plants through the abundance or the reactions of their prey, an herbivorous grasshopper [2] (see also as an iconic example, the impact of the reintroduction of wolves into Yellowstone National Park [3]).

Mutualisms can also mediate “indirect effects” through the action of one partner on an intermediate species, which, in turn, impacts a recipient species or group of species. For example, the tank bromeliad *Aechmea mertensii* is an ant-garden epiphyte that depends on two ant species to develop. These ant species build arboreal carton nests within which the *A. mertensii* seeds then germinate and grow [4]. These ants directly influence the shape and size of their associated *A. mertensii* individuals, as one species installs its nests, and so its associated epiphytes, in sunny areas of tree crowns, and the other in shaded areas. These morphological changes indirectly affect the composition and biological traits of the aquatic macroinvertebrate communities in the tanks of the host bromeliads [5–7].

Most bromeliads are epiphytes that derive water and nutrients through absorbent leaf trichomes distributed on the surface of their leaves. Among them, tank bromeliads collect rainwater and debris thanks to a rosette of tightly interlocking leaves forming the tank or phytotelma (i.e. plant-held water) that represents a conspicuous adaptation to improving nutrient acquisition [8,9]. The debris that falls into the tanks constitutes the main source of nutrients for aquatic food webs that include bacteria, protists, algae, micro- and macroinvertebrates, and vertebrates [9–

12]. This incoming debris is shredded by invertebrates, so that small particles of organic matter are then washed into the tank, where they are further processed by invertebrate collectors and filterers. This comminution facilitates decomposition by bacteria and fungi, making nutrients available to the host bromeliad [13]. The macroinvertebrate communities of tank bromeliads are structured by the characteristics of the aquatic compartment (i.e. habitat size and complexity, food resources, presence of a top predator) [14–17]. Also, ants that abound in Neotropical rainforests can have opportunistic relationships with tank bromeliads [18–20], or narrow, mutualistic relationships as in the case of ant-garden bromeliads [4] and myrmecophytic bromeliads (myrmecophytes are plants housing a small number of ant species in hollow structures called domatia; in turn, their associated ants provide them with nutrients and/or with biotic protection) [21,22].

Here we focus on how associated ants can influence the nature of the interactions between a myrmecophytic bromeliad and the aquatic community in its tank, the focal taxon being *Aechmea bracteata* that, contrary to ant-garden epiphytes, does not depend on ants for its germination. Instead, this tank bromeliad shelters ant colonies in a central watertight cavity delimited by an amphora-shaped leaf situated around the base of the inflorescence in the heart of the rosette forming the tanks [22,23]. Because ants discard their waste and feces into the tanks of their host bromeliads and because each ant species has its own diet [8,14,22], we hypothesized that the species of the associated ants or their absence, by influencing the availability of organic matter, might impact the diversity, abundance, and community composition of aquatic macroinvertebrates in the tanks of *A. bracteata*.

2. Materials and methods

2.1. Study site and host plant species

This study was conducted in an inundated forest dominated by 10-m-tall *Metopium brownei* (Anacardiaceae) situated in southern Quintana Roo, Mexico (18.4267° N; 88.8043° W; 120 meters a.s.l). The mean temperature varies from 25.5 to 26.5 °C. The dry season lasts from February to May and the rainy season from June to January.

Aechmea bracteata is a large tank bromeliad (leaves ca. 1-m-long; inflorescences up to 1.7-m-long) found from Mexico to northern Colombia. Each plant is constituted of a

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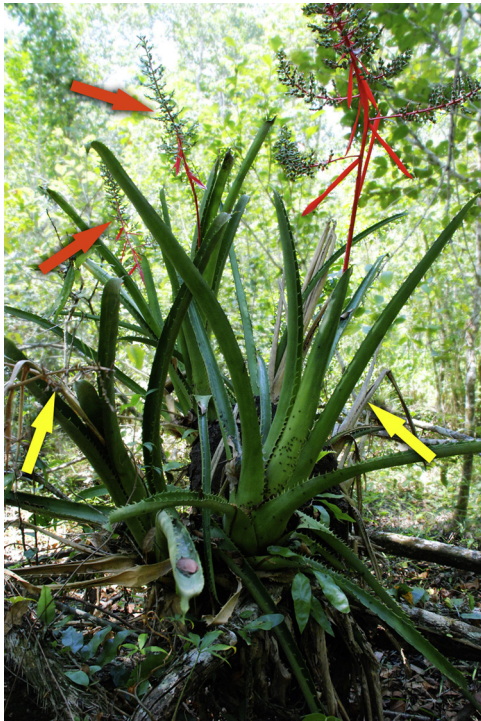


Fig. 1. An *Aechmea bracteata* individual. The oldest, dry shoots are in the background and at the base of the plant (yellow arrow at the right). At the left, a shoot with a dry inflorescence stands out from the group (yellow arrow at the left). Three mature shoots are recognizable as each bears a large inflorescence with pink bracts (red arrows for two of them, the third being in the foreground); *Dolichoderus bispinosus* workers are visible on the shoot situated in the foreground. All these shoots hide the younger ones devoid of any inflorescence.

group of shoots at different stages of maturity that develop from a rhizome (Fig. 1). As the rhizome grows, each shoot begins as a bud, which gives rise to a seedling, and then develops into a shoot whose leaves collect water until the inflorescence is formed, which is followed by the progressive drying out of the shoot before it begins to rot [8]. Each well-developed shoot forms a rosette with numerous reservoirs, where an abundant aquatic fauna develops. In the heart of the rosette, an amphora-shaped leaf grows around the inflorescence, creating a central watertight cavity suitable for housing ants [21,22].

Like most myrmecophytes, *A. bracteata* can be associated with several ant species, *Neoponera villosa* and *Dolichoderus bispinosus* being the most frequent [22]. The selection of host plants by arboreal ants depends on two factors: a “genetically determined attraction” toward a given plant species rather than another, and a kind of imprinting – due to the contact by individuals with their host plant during their larval life and the first days of their adult life – that supplants the genetically determined attraction (the contrary is true for species-specific associations) [24–26]. This process is at the origin of “regional traditions” for nest-site selection in certain arboreal ants and social wasps (*i.e.* they nest on the same plant species over very wide areas) [19,22,27]. When a given myrmecophyte can be associated with various species of ants, the first formed domatia and those

liberated after the death of an ant colony are colonized by winged queens swarming by chance at the right moment. One species of ant wins out through a “lottery competition”, the whole process resulting in a sequential partnering with different species of ants because the lifespan of myrmecophytes is longer than that of ant colonies [28,29].

Concerning the aquatic macroinvertebrate communities, much of the adult biomass of most taxa is obtained during the aquatic part of their life cycle as larvae, illustrating the importance of breeding- and oviposition-site selection. The principal parameters that favor oviposition by adult females followed by the adequate development of larvae are: (1) the size of the tank of the bromeliads [9,30–32], (2) their complexity (*i.e.* the number of wells corresponding to the number of leaves) [31–34], (3) their color [33,35], (4) the quantity of organic material [31–34], (5) the presence of competitors [9,33], and (6) for certain bromeliad specialists, an attractive odor emitted by the bromeliad or the water in their tanks [34,36].

2.2. Field sampling

We examined 92 *A. bracteata* individuals bearing inflorescences situated in the area studied. We determined the presence or absence of any ant colony in the central watertight cavity of shoots bearing an inflorescence and, when present, the species of ant.

We then examined 30 well-developed *Ae. bracteata* individuals including three devoid of any associated ant colony. They were selected based on the likelihood of obtaining an invertebrate sample without losing the contents of their tanks (details in Table 1 and Appendix S1). We detached from the rhizome a shoot bearing a mature inflorescence (*i.e.* with fruits and not yet dry) and noted which ant species it sheltered in the central cavity. We measured the height at which these shoots were located on their host tree and the percentage of incident radiation was quantified using hemispherical photography (see [37] for details). To characterize the habitat structure of the aquatic invertebrates, as per Céréghino *et al.* [5,6], we measured the water volume in the tanks and several plant parameters (see details in Appendix S1).

Each selected shoot was transported in a sealed plastic bag to the laboratory where it was dismantled in a large bucket and all the water, detritus and invertebrates were poured into wide-mouthed plastic bottles whose contents were preserved in 4% formalin (final concentration) until we were able to sort the macrofauna. Then, the leaves were placed in fine mesh sieves (100 μm) and rinsed to maximize the invertebrate and detritus sampling efficiency. After sorting the invertebrates (see paragraph below), the water was filtered through sieves of different mesh sizes (100 μm –1 mm; 1 mm–10 mm; and > 10 mm) to separate the detritus by size fractions (fine, mid-size, and coarse detritus, respectively). The detritus was then oven-dried (48 h at 60 °C) and weighed (grams; dry weight) (see details in Appendix S1).

Table 1

Comparison of diversity between the *Aechmea bracteata* sheltering colonies of three different ant species or not sheltering ants. Hill numbers (i.e. true diversities for orders 0, 1 and 2) are provided along with the rarefied number of species and the number of individuals recorded. Means and 95% confidence intervals are provided. FDR adjustment: *P*-value after FDR adjustment for simultaneous comparisons, BY correction [45].

	A – <i>Dolichoderus bispinosus</i> (13 cases)	B – <i>Neoponera villosa</i> (10 cases)	C – <i>Azteca serica</i> (4 cases)	D – No ants (3 cases)		
Observed richness (Mao–Tau)	18 ± 3.4	15 ± 3.3	14 ± 1.1	8 ± 2.2		
Chao1 (⁰ D)	20.2 ± 9.4	17 ± 4.8	14.5 ± 3.7	8.5 ± 2.4		
No. of individuals	2260	1660	1721	370		
Rarefied species richness (2000 individuals)	17.5 ± 3.4	15.7 ± 3.6	14.1 ± 1.1	9.5 ± 4.4		
Shannon exponential (¹ D)	5.5 ± 0.3	4.9 ± 0.3	5.0 ± 0.2	3.6 ± 0.3		
Simpson inverse mean (² D)	4.1 ± 0.2	3.5 ± 0.2	4.1 ± 0.1	2.6 ± 0.3		
	AxB	AxC	AxD	BxC	BxD	CxD
β diversity/Harrison 2	0	0.055	0	0.133	0	0.071
“Diversity t-tests” based on Shannon indices	<i>t</i> = 0.98 <i>df</i> = 334.2 <i>P</i> = 0.32	<i>t</i> = 1.17 <i>df</i> = 277.4 <i>P</i> = 0.24	<i>t</i> = 3.66 <i>df</i> = 274.3 <i>P</i> = 0.0003	<i>t</i> = 0.11 <i>df</i> = 245.7 <i>P</i> = 0.91	<i>t</i> = 2.55 <i>df</i> = 282.4 <i>P</i> = 0.011	<i>t</i> = 3.36 <i>df</i> = 182.5 <i>P</i> = 0.0009
After FDR adjustment	NS	NS	<i>P</i> < 0.05	NS	<i>P</i> < 0.05	<i>P</i> < 0.05

2.3. Sorting aquatic invertebrates

The aquatic invertebrates were sorted in the laboratory and preserved in 70% ethanol. They were mostly identified to species or morphospecies and enumerated. Professional taxonomists provided assistance for the identification of the Oligochaeta and other invertebrates (Prof. N. Giani and Dr. A.G.B. Thomas; University Toulouse, France).

2.4. Diversity of macrofauna communities

Species rarefaction and extrapolation curves were plotted on the abundance data matrices using EstimateS 9.1.0 software [38] with 100 randomizations of the sampling order without replacement. In order to standardize the comparisons between bromeliad categories (classified according to ant presence/absence and species of ant when present) and to estimate sampling completeness, these curves and the Chao1 non-parametric estimator of total species richness were calculated [39].

We calculated Hill numbers (i.e. “true diversities”) for three different orders (*q*) of diversity. True diversity indices obey the doubling property, preventing a mistaken interpretation of results [40]. Order *q* is related to the sensitivity of the index to the frequency of the species in the community: when *q* = 0, all species are given the same weight (rare species are thus favored); when *q* = 1, species are weighted for their frequency in the community (neither common nor rare species are favored); and when *q* = 2, more abundant species are favored. Accordingly, species richness is a measure of diversity of order zero (⁰D), the exponential of Shannon’s entropy index is the measure of diversity of order one (¹D), and the inverse of Simpson’s index is a measure of order two (²D) [40,41]. All three indices are in units of equivalent, equally abundant species and were calculated using Spade R online software [42]. Differences in species richness between habitats were assessed using the non-overlapping of 95% confidence intervals as a conservative criterion of statistical difference in species richness between habitats [38].

The global turnover between the different aquatic macroinvertebrate communities that depends on the

species of associated ant was analyzed using the second version of Harrison’s indices ($\beta_{H2} = [(S/\alpha_{\max}) - 1]/(N - 1)$), [43] as a beta-diversity index obtained using PAST 3 software. β_{H2} is an improvement over Whittaker’s index ($\beta_W = (S/\alpha) - 1$), which was modified to be effective in analyzing pairwise differentiation between sites; it is insensitive to species richness trends [44]. We also conducted pairwise comparisons of the diversity profiles of the four situations using “diversity t-tests” based on the Shannon index (PAST 3 software); multiple comparisons were adjusted using the false discovery rate (FDR) (see Table 1) [45].

2.5. Data analyses

The environmental parameters recorded allowed us to build a “17 (characteristics of the *A. bracteata* monitored plus abiotic parameters) × 30 shoots” matrix.

A first Principal Component Analysis (PCA) was conducted to ordinate the *A. bracteata* shoots based on the environmental variables (e.g., their structure, their height from the ground and the incident radiation; see Appendix S1) and the species of ant they sheltered (or absence of any associated ant colony). Another PCA was conducted to ordinate the *A. bracteata* shoots based on the aquatic macroinvertebrates sheltering in their tanks according to the species of associated ant (or absence of any associated ant colony). Also, three generalized linear model (GLM) analyses were conducted on the data corresponding to species richness, evenness, and the Shannon index. Another GLM analysis was conducted to determine the effects of ants (presence and species) on predators in the aquatic macroinvertebrate communities. In both cases, the fixed factors were the *A. bracteata* coordinates on Axes 1, 2 and 3 and the factor “Ant” (species of the associated ant colony or the absence of any associated ant colony), the *A. bracteata* shoots representing the random factor. These analyses were conducted with the ADE4, nlme and dplyr packages in R software [46].

3. Results and discussion

3.1. Ant species associated with *Aechmea bracteata*

Of the 92 *A. bracteata* studied, three individuals (3.26%) were devoid of associated ants, whereas all others sheltered an ant colony in the central, watertight amphora-shaped domatia of the mature shoots. Among these, 13 (14.13%) were associated with *Azteca serica*, 43 (46.74%) with *Dolichoderus bispinosus* (both Dolichoderinae) and 33 (35.87%) with *Neoponera villosa* (Ponerinae). These percentages are intermediary between those for the associations found in another low inundated forest and a semi-evergreen forest in northern Quintana Roo [22].

The low percentage of individuals devoid of any associated ant colony likely results from the much longer lifespan of the myrmecophytes compared to that of their associated ant colonies, so that myrmecophytes shelter several ant colonies successively throughout their life (see cases in [28,29]).

3.2. Diversity and composition of the aquatic macrofauna in the bromeliads' tanks according to ant presence and species

The global beta diversity (Harrison $\beta_{H2} = 0.018$; a very low value as this index varies between 0 and 1) denoted a large global species overlap (i.e. a small turnover) between the macrofauna in the tanks of the *A. bracteata* sheltering different species of ants or devoid of any associated ant colony; the same was true for pairwise comparisons between ant species (Table 1). Nevertheless, the multiple comparison of “diversity *t*-tests” based on the Shannon index showed significant differences for all comparisons involving *A. bracteata* devoid of any associated ant colony, whereas no significant differences were noted due to ant species (Table 1).

The same was true for the diversity profiles of the aquatic macroinvertebrate communities, those of bromeliads devoid of ants being significantly lower (Fig. 2a).

Because the rarefied species richness of macroinvertebrate communities was not affected by the species of ant (Table 1), we pooled the corresponding data showing that the rarefied species richness tended to an asymptote. Here,

too, the diversity profile of bromeliads devoid of ants was significantly lower than that of the individuals sheltering an ant colony (Fig. 2b). Note that the Chao1 estimators of species richness indicated a sampling completeness of 97% (19/19.3) and 94% (8/8.5) for bromeliads with or without ants, respectively (Table 1).

Therefore, these results, where the ant–plant relationships are narrow, complement those of the facultative relationships between ants and the tank bromeliad *Aechmea aquilega* [20], as, in both cases, the favorable impact of ant presence on the diversity of the aquatic macroinvertebrate communities developing in the tanks of their host plants was noted.

We previously noted that associated ants provide their tank bromeliads with discarded nitrogen-rich debris and feces [19,21]. Because we recorded numerous cocoons in the tanks of *A. bracteata* individuals sheltering a *N. villosa* colony, we deduced that the workers not only discarded these cocoons after the emergence of imagoes from the pupae (i.e. new workers), but, likely, also other waste (the two other associated ant species, of the Dolichoderinae subfamily, have naked pupae).

3.3. Impact of ant absence or species of ant on the aquatic macrofauna in the *Aechmea bracteata* tanks

In the PCA ordination of the *A. bracteata* shoots based on the species of ant they sheltered (or the absence of associated ants) according to the environmental variables selected, the first three components account for 60% of the variance (eigenvalues: Axes 1, 2 and 3 account for 30%, 17% and 13% of the variance, respectively). The parameters corresponding to the structure of the *A. bracteata* shoots (grouped along the right part of Axis 1) are separated from the parameters “height above ground” and “incident radiation”, which are related (grouped at the bottom of Axis 3) (Fig. 3a–b). Thus, these environmental variables did not influence the distribution of the ant species sheltered by these bromeliads (Fig. 3c–d). This result reflects the fact that the longevity of *A. bracteata* individuals is longer than that of the ant colonies they shelter (see above) and founding queens are guided to an available plant through a kind of imprinting to chemicals released by the host plant

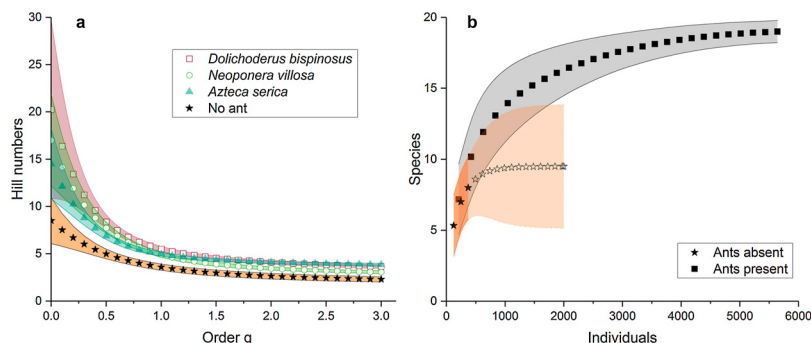


Fig. 2. a: diversity profiles and their 95% confidence intervals of the aquatic macrofauna found in the tanks of the four types of *Aechmea bracteata* according to ant presence and species; b: species richness (Mao-Tau and its 95% confidence intervals) of the aquatic macrofauna in the tanks of *Aechmea bracteata* with ($n=27$, data for the three ant species pooled) or without ants ($n=3$) extrapolated to 6000 and 2000 individuals, respectively (filled and empty stars represents real and extrapolated richness, respectively).

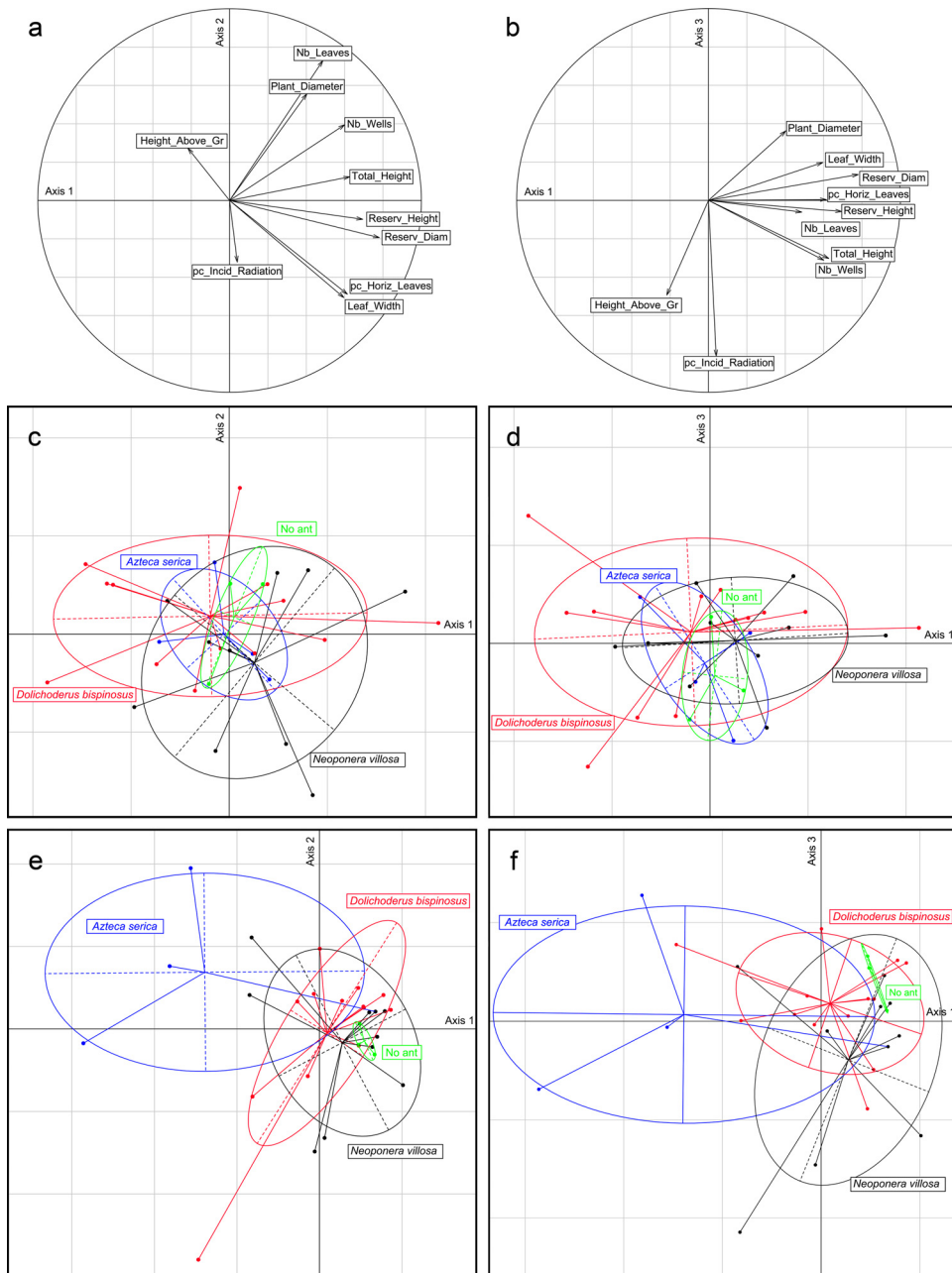


Fig. 3. PCA corresponding to the data recorded for the 30 *Aechmea bracteata* individuals studied. a–b: distribution of the environmental variables (variables corresponding to the structure of the bromeliads plus the height above ground and the incident radiation) on the PCA space; c–d: PCA ordination of the environmental variables based on the species of ant they sheltered or the absence of associated ants; e–f: PCA ordination of the aquatic macroinvertebrates in the tanks of the bromeliads studied based on the species of associated ant (or absence of associated ants).

on which they developed [24,25]. Note that these environmental variables can influence the aquatic macrofauna developing in the tanks of bromeliads ([6,7,31,47]; this study, see F1:F3, Table 2A).

In the PCA ordination of the *A. bracteata* shoots based on the distribution of the aquatic fauna found in their tanks according to the species of ant they sheltered (or absence of associated ants), the first three components account for 43.4% of the variance (eigenvalues: Axes 1, 2, and 3 account

for 17.8%, 15.0% and 10.6% of the variance, respectively) (Fig. 3e–f). The *A. bracteata* shoots sheltering an *A. sericea* colony are separated from the three other cases that overlap (i.e. shoots from individuals without associated ants and individuals sheltering a colony of *N. villosa* or of *D. bispinosus*) (Fig. 3e–f).

The GLM analysis conducted on the data corresponding to evenness and the Shannon index resulted in non-significant differences (results not shown), whereas

Table 2

Results of the GLM on species richness concerning the aquatic macroinvertebrates found in the tanks of *Aechmea bracteata* (A) and the numbers of aquatic predators (B). In both cases, fixed factors are represented by *A. bracteata* coordinates on Axes 1, 2 and 3 (F1, F2, F3, see Fig. 3a, b) and the species of the associated ants or the absence of an associated ant colony (factor “Ant”), the random factor corresponds to the *A. bracteata* individuals.

	Estimate	Standard error	t value	P-value
A (df= 25)				
Intercept	10.6455	1.1289	9.430	< 0.0001
F1	0.2926	0.2131	1.373	0.1820
F2	-0.5242	0.2805	-1.869	0.0735
F3	-0.3496	0.3243	-1.078	0.2913
Ant	-1.1023	0.4448	-2.478	0.0203
B (df= 25)				
Intercept	155.4459	34.0277	4.568	0.0001
F1	11.7749	6.4244	1.833	0.0787
F2	0.4214	8.4558	0.050	0.9606
F3	-4.5718	9.7755	-0.468	0.6440
Ant	-43.5886	13.4076	-3.251	0.0032

species richness was explained by the species of associated ant or the absence of associated ants (*i.e.* factor “Ant”; Table 2A). The same was true for the GLM analysis conducted on the data corresponding to the numbers of aquatic predators (Table 2B). The ant effect is at least partially due to the higher presence of predators (mostly *Bezzia*) in the *A. bracteata* sheltering an *A. serica* colony (see Appendix S1).

Therefore, in addition to the impact of ant presence compared to ant absence, the species of ant also plays a role in the composition of the macroinvertebrate communities developing in the tanks of *A. bracteata* shoots. Indeed, the tanks of *A. bracteata* associated with *A. serica* sheltered a community whose richness was different from those associated with *D. bispinosus*, *N. villosa* or in the absence of associated ants; the three latter categories did not differ from each other (see Fig. 3d, e). The aforementioned differences can be due to the various food regimes of these ants that, by discarding their feces and waste, fuel the aquatic food webs in the tanks, or may occur if workers of only certain species capture emerging adult insects and/or deter ovipositing females [37,48,49].

Nevertheless, an indirect effect of the ants on their host bromeliad morphology (*e.g.*, size and shape) via the intermediary of the aquatic macroinvertebrate community was not noted in this snapshot study. Indeed, only “height above ground” and “incident radiation”, which are related, can have a slight, indirect influence on the parameters corresponding to the structure of the *A. bracteata* individuals (Fig. 3a–b). Although this is in line with the results noted for the ant-garden bromeliad *A. mertensii*, the latter depends on ants for germination resulting in an indirect effect of ants on this plant’s size and shape [37]. This is not the case for *A. bracteata* whose seeds are disseminated by birds [8], so that further studies are needed to verify if there is an indirect ant effect on the fitness of the plant (*e.g.*, the number and/or size of the seeds; see [50]).

There is thus a kind of continuum in the relationships between ants and tank bromeliads as ant presence impacts

the aquatic macroinvertebrate diversity developing in the tanks of their host plants in both facultative relationships, the case of *A. aquilega* [20], and in narrow relationships with the myrmecophytic *A. bracteata* (this study; see Table 1; Fig. 1a, b). In the latter case, the species of ant also has an impact on the composition of the aquatic macroinvertebrate communities, in line with results noted for the ant-garden tank bromeliad *A. mertensii* [5,6].

In conclusion, both ant presence (*versus* absence) and the species of ant mediate the composition of the aquatic macroinvertebrate communities in the tanks of the myrmecophytic bromeliad *A. bracteata* through direct interactions (*i.e.* the ants discard their waste and feces into the tanks), whereas we did not note a perceptible indirect effect on the host bromeliad morphology.

Disclosure of interest

The authors declare that they have no competing interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crv.2018.02.003>.

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