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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.

RÉSUMÉ

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

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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.

1. Introduction

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 group of shoots at different stages of maturity that develop from a rhizome (Fig. 1). As the rhizome grows, each shoot

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