GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 13 (2012) 698–705

Basic and Applied Ecology

www.elsevier.com/locate/baae

An ant–plant mutualism induces shifts in the protist community structure of a tank-bromeliad

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Received 23 January 2012; accepted 8 October 2012

Abstract

Although ants may induce community-wide effects via changes in physical habitats in terrestrial environments, their influence on aquatic communities living in plant-held waters remains largely underexplored. The neotropical tank-bromeliad *Aechmea mertensii* (Bromeliaceae) occurs along forest edges in ant-gardens initiated by *Camponotus femoratus* or by *Pachycondyla goeldii*. Its leaves form wells that hold rainwater and provide suitable habitats for many aquatic organisms. We postulated that these ant–plant mutualisms indirectly affect the microbial community structure via changes in the environmental conditions experienced by the plants. To test this hypothesis, we analyzed the protist communities from 63 tank-bromeliads associated with either *C. femoratus* or *P. goeldii* (hereafter Cf-*Aechmea* and Pg-*Aechmea*) along a forest edge in French Guiana. For each plant, a large number of environmental variables (including habitat structure, food resources, incident radiation and the presence of aquatic invertebrates) were quantified to determine their relative importance in driving any observed differences across ant-associated plants. Pg-*Aechmea* are located in sun-exposed areas and hold low volumes of water and low amounts of detritus, whereas Cf-*Aechmea* are located in partially shaded areas and accumulate higher amounts of water and detritus. Protists (i.e., protozoa and algae) inhabiting Cf-*Aechmea* exhibit greater richness and abundances than those in Pg-*Aechmea*. Variations in detritus content, number of leaves, incident radiation, and the epiphyte richness of the ant-garden were the main factors explaining the variation in protist richness. A shift in the functional group composition of protists between bromeliads tended by different ant species suggested that mutualistic ants indirectly mediate changes in the microbial food web.

Zusammenfassung

Obgleich Ameisen gemeinschaftsübergreifende Effekte auslösen können, indem sie in terrestrischen Lebensräumen Änderungen des physikalischen Habitats bewirken, ist ihr Einfluss auf aquatische Gemeinschaften von Phytotelmata weitgehend

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1439-1791/$ – see front matter
http://dx.doi.org/10.1016/j.baae.2012.10.002

unerforscht. Die neotropische Trichterbromelie *Aechmea mertensii* (Bromeliaceae) kommt entlang von Waldrändern in Ameisengärten, die von *Camponotus femoratus* bzw. *Pachycondyla goeldii* angelegt werden, vor. Ihre Blätter bilden Trichter, die Regenwasser auffangen und ein Habitat für zahlreiche aquatische Organismen sind.

Wir postulierten, dass die mutualistischen Beziehungen zwischen der Pflanze und den Ameisenarten indirekt die Gemeinschaftsstruktur der Mikroorganismen beeinflussen - und zwar durch Änderungen der Umweltbedingungen, denen die Pflanzen ausgesetzt sind. Um diese Hypothese zu testen, analysierten wir entlang eines Waldrandes in Französisch-Guayana die Einzellergemeinschaften von 63 Trichterbromelien, die mit *C. femoratus* bzw. *P. goeldii* assoziiert waren (im Folgenden: Cf-*Aechmea* bzw. Pg-*Aechmea*). Für jede Pflanze wurde eine große Zahl von Umweltfaktoren (Habitatstruktur, Nahrungsressourcen, Strahlungsintensität, aquatische Wirbellose) untersucht, um deren relative Bedeutung für Unterschiede zwischen den mit Ameisen assoziierten Pflanzen zu bestimmen. Pg-*Aechmea* befinden sich an sonnenexponierten Stellen und enthalten geringe Mengen Wasser und Detritus, während Cf-*Aechmea* in partiell beschatteten Bereichen vorkommen und größere Mengen Wasser und Detritus speichern. Die Einzeller (d.h., Protozoen und Algen) von Cf-*Aechmea* zeigten größeren Formenreichtum und höhere Abundanzen als die in Pg-*Aechmea*. Detritusgehalt, Anzahl der Blätter, Einfallstrahlung und der Artenreichtum der Epiphyten im Ameisengarten waren die wichtigsten Erklärungsfaktoren für die Variation im Formenreichtum der Einzeller. Eine Verschiebung in der Zusammensetzung der funktionellen Gruppen der Einzeller zwischen Bromelien, die von verschiedenen Ameisenarten betreut wurden, legt nahe, dass die mutualistischen Ameisen indirekt Änderungen im mikrobiellen Nahrungsnetz vermitteln.

Keywords: *Aechmea mertensii*; Ant-garden; Protists; Biodiversity; *Camponotus femoratus*; *Pachycondyla goeldii*; Phytotelmata; French Guiana

Introduction

Ants are involved in an interlocking set of mutualisms (McKey et al. 2005) and ant-gardens are recognized as belonging to the most sophisticated of all symbioses between ants and flowering plants in lowland Amazonia (Orivel & Leroy 2011). Ant-gardens are initiated by a few species of ants whose founding queens and/or workers build arboreal carton nests. Ants collect and incorporate into the walls of their nests the seeds of selected epiphyte species which then germinate and grow (Orivel & Dejean 1999), so that the plant roots stabilize and anchor the entire structure in the supporting tree. The seeds of these epiphytes attract ants through nutritional rewards called elaiosomes, but even in their absence these seeds remain attractive to ant-garden-building ants thanks to compounds on the seed cuticle (Orivel & Dejean 1999; Youngsteadt, Nojima, Haberlein, Schulz, & Schal 2008). In turn, the plants benefit from seed dispersal and protection from defoliating insects (Orivel & Leroy 2011). Among the Neotropical epiphytes, the tank-bromeliad *Aechmea mertensii* Schult.f. (Bromeliaceae) only occurs (over its full range) in association with ant-gardens (Benzing 2000). In French Guiana, *A. mertensii* is found in pioneer growths in ant-gardens initiated either by *Camponotus femoratus* Fabr. or by *Pachycondyla goeldii* Forel (Corbara & Dejean 1996). The leaves of *A. mertensii* are tightly interlocking, forming several wells that collect water and organic detritus. These wells are characteristic of tank-forming bromeliads acting as phytotelmata. The aquatic communities inhabiting tank-bromeliads consist of micro- and macroinvertebrates, occasionally vertebrates (i.e., anurans) (Kitching 2000; Frank & Lounibos 2009), and diverse microorganisms (Brouard et al. 2012). Since *A. mertensii* is both a phytotelm- and an ant-garden bromeliad, it was deemed a relevant model for studying the role of interspecific mutualistic interactions in shaping aquatic communities in nature (Céréghino, Leroy, Dejean, & Corbara 2010; Céréghino et al. 2011).

We investigated the effect of these ant–plant mutualisms on aquatic microorganisms by analyzing protist (protozoa and algae) communities from 63 bromeliads associated with either *C. femoratus* or *P. goeldii*. In aquatic environments, protozoa control bacterial prey and release large amounts of dissolved inorganic nutrients (Sherr & Sherr 2002), while algae are frequently dominant primary producers and have recently been identified as a ubiquitous and relevant component of the aquatic communities of tank-bromeliads (Brouard et al. 2011, 2012). A previous study has shown that, as dispersal agents for *A. mertensii*, *P. goeldii* and *C. femoratus* indirectly influence the physical characteristics of the plant by determining the location of the seedling in areas ranging from sun-exposed to partially shaded (Leroy, Corbara, Dejean, & Céréghino 2009). We thus hypothesized that the density of algae would increase with the plant's exposure (i.e., from shaded to exposed areas), and thus would be more relevant to the microbial food web in Pg-*Aechmea* than in Cf-*Aechmea*. The latter constitute more complex and larger habitats and receive larger amounts of leaf litter from overhanging trees. Therefore, we expected larger densities and a greater richness of protists in Cf-*Aechmea* compared to Pg-*Aechmea.* Finally, we projected that ants would indirectly influence the microbial food web due to changes in the numerical importance of the functional groups of protists.