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Ants mediate the structure of phytotelm communities in an ant-garden bromeliad

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Abstract. The main theories explaining the biological diversity of rain forests often confer a limited understanding of the contribution of interspecific interactions to the observed patterns. We show how two-species mutualisms can affect much larger segments of the invertebrate community in tropical rain forests. *Aechmea mertensii* (Bromeliaceae) is both a phytotelm (plant-held water) and an ant-garden epiphyte. We studied the influence of its associated ant species (*Pachycondyla goeldii* and *Camponotus femoratus*) on the physical characteristics of the plants, and, subsequently, on the diversity of the invertebrate communities that inhabit their tanks. As dispersal agents for the bromeliads, *P. goeldii* and *C. femoratus* influence the shape and size of the bromeliad by determining the location of the seedling, from exposed to partially shaded areas. By coexisting on a local scale, the two ant species generate a gradient of habitat conditions in terms of available resources (space and food) for aquatic invertebrates, the diversity of the invertebrate communities increasing with greater volumes of water and fine detritus. Two-species mutualisms are widespread in nature, but their influence on the diversity of entire communities remains largely unexplored. Because macroinvertebrates constitute an important part of animal production in all ecosystem types, further investigations should address the functional implications of such indirect effects.

Key words: Aechmea mertensii; *ant-gardens; biodiversity; bromeliads;* Camponotus femoratus; Crematogaster levior; *macroinvertebrates; mutualism;* Pachycondyla goeldii; *phytotelmata; secondary forest, Sinnamary, French Guiana; species interactions.*

Introduction

Although the concept of "biodiversity" encompasses all living forms on earth and their interactions, the main theories explaining biological diversity (Hutchinson 1959, Hubbell 2001) often confer a limited understanding of the contribution of interspecific interactions to the observed patterns. While they only represent 6–7% of the continental surface, tropical rain forests shelter more than half of Earth's species (Wilson 1988). Among plant species, epiphytes represent a keystone resource in tropical forests because of their important role in shaping the biodiversity (e.g., frog, bird, or invertebrate diversity; nutrient cycling) of these ecosystems (Nadkarni 1994); for instance, the interlocking leaves of epiphytic tank-bromeliads (Bromeliaceae) form wells, or phytotelmata (reviewed in Kitching [2000]), that collect rainwater and leaf litter and provide a habitat for aquatic organisms ranging from prokaryotes to vertebrates. The detritus provides a source of nutrients for the aquatic food web, as well as for the bromeliad itself (Ngai and Srivastava 2006). Because many aquatic invertebrates complete their development in tank-bromeliads, differences in plant species, morphology, and/or location may play an important role in habitat selection by colonizers (Jabiol et al. 2009).

Some epiphyte species, including tank-bromeliads, are involved in complex associations with arboreal ants, associations called "ant-gardens" (AGs) (Benzing 2000). AGs are initiated by a few species of ants whose founding queens and/or workers build fragile, rough carton nests containing organic material. Ants collect and incorporate the seeds or fruits of selected epiphyte

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species that then germinate and grow on the nest (Orivel et al. 1998, Orivel and Dejean 1999), so that the plant roots stabilize the carton walls of the nest and anchor the entire structure. The full-grown epiphyte often provides food rewards to the ants (Kaufmann and Maschwitz 2006). In turn, the plants mainly benefit from seed dispersal and protection from defoliating insects. Among the AG epiphytes, we focused on *Aechmea mertensii*, which is both a phytotelm- and an AG-bromeliad. The published literature suggests that *A. mertensii* always occurs in association with AGs (Benzing 2000). In French Guiana, it only occurs in AGs initiated by either the ant *Camponotus femoratus* Fabr. or the ant *Pachycondyla goeldii* Forel (Corbara and Dejean 1996, Vantaux et al. 2007). Such an association (obligatory for the bromeliad) is one of the most complex and sophisticated of all mutualisms between ants and flowering plants (Benzing 2000). Thus, *A. mertensii* AGs are relevant natural microcosms for studying the influence of biological interactions on epiphytes and on the biodiversity of their associated biota in tropical areas. We addressed the role of species-specific interactions in determining the biodiversity patterns of a broader range of organisms by using *A. mertensii* as a model system. We hypothesized that (1) as dispersal agents of the bromeliads, ants determine the location of the seedling, and (2) if different ant species have different habitat preferences, this will affect the physical characteristics of the bromeliad tanks. Subsequently, we predicted that the structure of the aquatic communities that inhabit the tanks would be indirectly affected by the associated ant species.

METHODS

Study area and ant-gardens

The study was conducted in French Guiana in January 2007 in a secondary forest (pioneer growths) near the Petit Saut dam, Sinnamary (latitude, 5°03′43″ N; longitude, 53°02′46″ W). The climate is tropical moist, with 3400 mm of yearly precipitation distributed over 280 days. 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 monthly temperature averages around 33.5°C, and the monthly minimum around 20.3°C. All samples were taken along an 11-km-long dirt road from well-developed ant-gardens (AGs) inhabited by either the ants *Camponotus femoratus* and *Crematogaster levior* ($n = 42$ bromeliads), or *Pachycondyla goeldii* ($n = 30$ bromeliads; see Plate 1) (hereafter "*C. femoratus* samples" and "*P. goeldii* samples"). Ant-gardens occurred from 0.4 m to 12 m above the ground in the supporting trees (i.e., from the foot of the tree to its canopy). *C. femoratus* is a polygynous (multiple queens), arboreal formicine species living in a parabiotic association with the myrmicine species *C. levior*; that is to say, they share the same nests and trails, but shelter in different cavities of the nests (Orivel et al. 1997, Longino 2003, Vantaux et al. 2007). 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) ponerine arboreal species with comparatively smaller populations, although the colonies may be polydomous (Corbara and Dejean 1996).

Transmitted light

All sampled bromeliads were in the flowering stage of the plant life cycle, so we were confident that differences in plant size and/or shape were not due to ontogeny (bromeliads do not grow anymore at this stage and the shoots die after fruit production). However, the morphology of the plants is strongly influenced by the amount of transmitted light that penetrates under tree canopies (Kawamura and Takeda 2002). We used hemispherical photographs to estimate the percentage of transmitted light above 40 randomly selected AGs (20 *C. femoratus* AGs and 20 *P. goeldii* AGs). Photographs were taken with a digital Nikon Coolpix 4600 camera with a Nikon Fisheye converter FC-E8 0.21X lens (Nikon, Tokyo, Japan) positioned on an adjustable tripod. Pictures were taken near dusk to avoid direct sunlight. We used an image-processing software (Gap Light Analyzer 2.0) to calculate the percentages of total incident radiation (Frazer et al. 1999). Significant differences in transmitted light values were tested using F and t tests.

Habitat variables and aquatic invertebrates

As *A. mertensii* roots were totally incorporated into the ant nest structure, we decided not to remove the plants in order to preserve the AGs. For each bromeliad, we recorded the elevation aboveground (in meters), and the height and diameter of the plant (in centimeters). To sample the water retained in the tanks, we used flexible plastic tubes (length, 10–30 cm; diameter, 2–5 mm) connected to 50-mL syringes (see Jabiol et al. 2009). We emptied the wells in each plant by sucking the water out using several tubes of appropriate dimensions. The water volume extracted (in milliliters) was recorded for each plant. The amount of fine particulate organic matter (FPOM; 1000 μm to 0.45 μm in size) was expressed as preserved volume (in cubic millimeters after decantation in graduated test tubes; see also Paradise 2004). The samples were preserved in the field in 70% ethanol. Aquatic invertebrates were sorted in the laboratory, mostly identified to species or morphospecies by professional taxonomists (Oligochaeta: Prof. N. Giani, University of Toulouse, France; Diptera Culicidae: Dr. R. Girod, Institut Pasteur, French Guiana; other invertebrates: Dr. A. G. B. Thomas; University of

Toulouse, France), and enumerated. Culicidae and Chironomidae were found both as larvae and pupae; all other insects were only found as larvae. The use and limitations of morphospecies identification for some taxa (e.g., "Forcipomyinae sp. 1") have been discussed in Armbruster et al. (2002); however, this approach, which is a common and often inevitable practice in ecological studies on tropical invertebrates, remains appropriate when local systems are compared.

Modeling procedure

Ecological data such as organism counts and environmental variables often vary and co-vary in a nonlinear fashion. Therefore, nonlinear modeling methods such as artificial neural networks (ANNs) should theoretically be preferred for dealing with such data. Combining ordination, clustering, and gradient-analysis functions, the self-organizing map algorithm (SOM; see Kohonen [2001] for details) is relevant for analyzing nonlinear data and/or variables that have skewed distributions, without an a priori transformation. Additionally, the SOM algorithm averages the input data set using weight vectors, and thus removes noise. These features were needed in our study because we analyzed organism counts with distributions so strongly skewed (many zeroes) that no transformation could normalize them.

The SOM consists of two layers: the input and the output. The data set presented to the network consisted here of 72 independent samples (72 bromeliads) characterized by p descriptors (28 invertebrate species or morphospecies). Each sample is represented by a vector that includes all p descriptors, and there are as many sample vectors as samples. The input layer is comprised of p nodes, or neurons. The output layer forms a rectangular two-dimensional grid (map) with C neurons laid out over a hexagonal lattice. Each neuron c_j of the output layer is also called a "cell" (visualized as a hexagon), and is linked to the neurons $i = 1, 2, \ldots, p$ of the input layer by connections that have weights w_{ij} associated with them, forming a vector $\mathbf{w}_{ij}$. These weights represent the virtual values for each descriptor in each output neuron such that each cell in the output layer c_j stores a "virtual vector" of connection weights $\mathbf{w}_{ij}$. These virtual vectors represent the co-ordinates of centers of groups of similar input vectors, where similarity is measured in terms of Euclidean distance $D(\mathbf{x}, \mathbf{w}_j) = [\Sigma(i = 1, \ldots, p)\ (x_i - w_{ij})2\ ]^{1/2}$ for all neurons c_j. The aim of the SOM is to organize the distribution of sample vectors in a two-dimensional space using their relationship to the virtual-vector distribution, thus preserving the similarities and the differences between the input vectors. Similar input vectors are allocated to the same virtual vector and the virtual vector changes with the addition of new input vectors. The virtual vectors that are neighbors on the map (neighboring neurons) are expected to represent neighboring groups of sample vectors; consequently, sample vectors that are dissimilar are expected to be distant from each other on the map.

The process of organization involves the random selection of a sample vector that is presented as input in the SOM. Using a distance measure, the sample vector is compared to each virtual vector that has been randomly assigned to the output neurons at the beginning of the algorithm. The output neuron for which the virtual vector is closest to the sample vector is selected and called the "best matching unit" (BMU), or "winner." The virtual vectors of the BMU and of its neighbors are then moved slightly (connection weights are adjusted) towards the sample vector using a Gaussian function. The process is repeated for all of the samples until a total of 10 000 iterations is completed. At the end of the training, a BMU is determined for each sample vector such that each sample (bromeliad) is assigned to a neuron on the map, and the virtual values of the descriptors (invertebrate abundances) are known for each neuron on the map. In other words, the bromeliads that are in the same cell are very similar in terms of invertebrate community, and the bromeliads that are distant in the modeling space represent larger expected differences in their invertebrate communities. A k-means algorithm was applied to cluster the trained map. The SOM units (hexagons) were divided into clusters according to the weight vectors of the neurons, and clusters were justified according to the lowest Davis Bouldin index, i.e., for a solution with low variance within clusters and high variance between clusters (Céréghino et al. 2003).

Significant differences in invertebrate taxa richness among SOM clusters were then tested using a one-way ANOVA followed by post hoc tests (Tukey hsd tests). Finally, in order to bring out relationships between physical and biological variables, we introduced the five physical variables into an SOM previously trained with the abundance data for the 28 invertebrate taxa. During the training, we used a mask function to give a null weight to the five physical variables, whereas biological variables were given a weight of 1 so that the ordination process was based on the 28 invertebrate taxa only (Compin and Céréghino 2007). Setting mask value to 0 for a given component removes the effect of that component on organization (Sirola et al. 2004).

RESULTS

Pachycondyla goeldii colonized small trees in exposed environments, whereas *Camponotus femoratus* rather colonized larger trees in partially-shaded areas. Therefore, *P. goeldii* ant-gardens (AGs) received significantly more light (range = 32–70%; mean ± SE = 54.58% ± 2.50%) than *C. femoratus* AGs (16–47%; 35.52% ± 1.44%) (t test, $t = 6.577$, $P < 0.0001$).

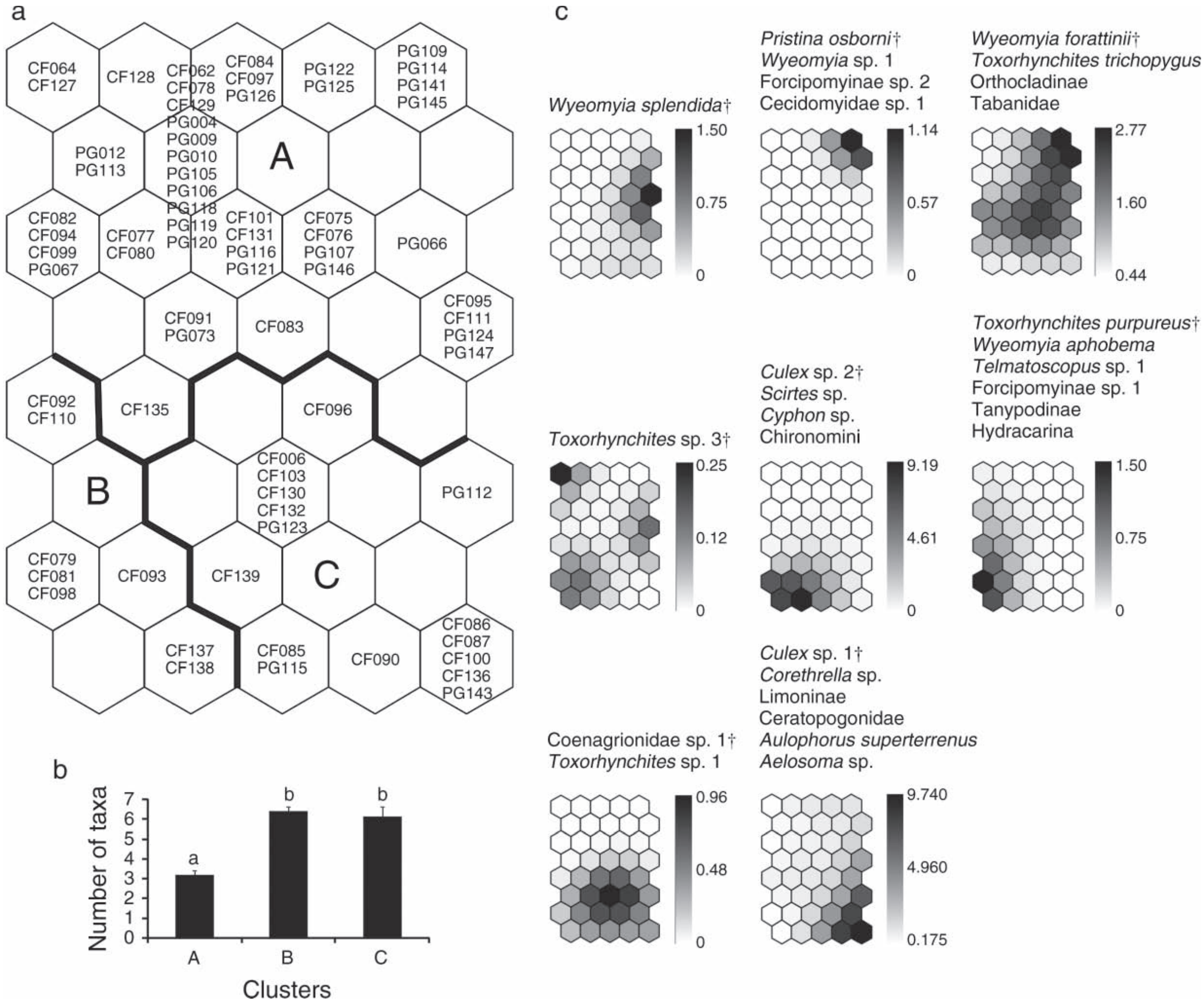

FIG. 1. (a) Distribution and clustering of bromeliads on the self-organizing map (SOM) according to the abundance of 20 macroinvertebrate taxa. Codes within each hexagon (e.g., CF103, PG112) correspond to individual plants (sampling units); CF = *Aechmea mertensii* associated with *Camponotus femoratus*, PG = *A. mertensii* associated with *Pachycondyla goeldii*. Clusters A–C (separated by a wide black line) were derived from the *k*-means algorithm applied to the weights of the 20 variables in the 40 output neurons of the SOM. (b) Number of macroinvertebrate taxa (mean + SE) per SOM cluster (A–C). Significant differences in terms of taxonomic richness between clusters were tested with one-way ANOVA and Tukey post hoc tests; error bars with different lowercase letters above indicate significant differences in taxonomic richness at $P < 0.01$. (c) Gradient analysis of the abundance (number of individuals per plant) for each taxon on the trained SOM represented by a shaded scale (dark = high abundance, light = low abundance). Each small map representing taxa that follow similar patterns (†, example shown) can be compared to (or superimposed on) the map representing the distribution of bromeliads presented in panel (a), thus showing the distribution patterns of the various taxa (in shades of gray) within each sub-area of the SOM.

The invertebrate assemblages associated with *C. femoratus* and *P. goeldii* AGs were rather distinct (see Appendix), with only 15 out of 28 taxa (i.e., 53.5%) shared by both AGs. Nine out of the 24 taxa recorded in *C. femoratus* samples (37.5%) were exclusive to these bromeliads. There was greater taxa richness for Diptera in *C. femoratus* AGs than in *P. goeldii* AGs. On the other hand, the list of invertebrates derived from *P. goeldii* samples comprised 19 taxa, among which 4 taxa (21%) were exclusive to these bromeliads.

After training the self-organizing map (SOM) with the invertebrate abundances in 72 tank-bromeliads, the bromeliads were classified into three subsets (clusters A–C) according to the quantitative structure of their macroinvertebrate assemblages (Fig. 1a). Cluster A showed a mixture of *C. femoratus* (46%) and *P. goeldii* samples (54%). Clusters B and C were exclusively or mainly composed of *C. femoratus* samples (100% and 75%, respectively). When the distribution of each invertebrate taxon was visualized on the trained SOM

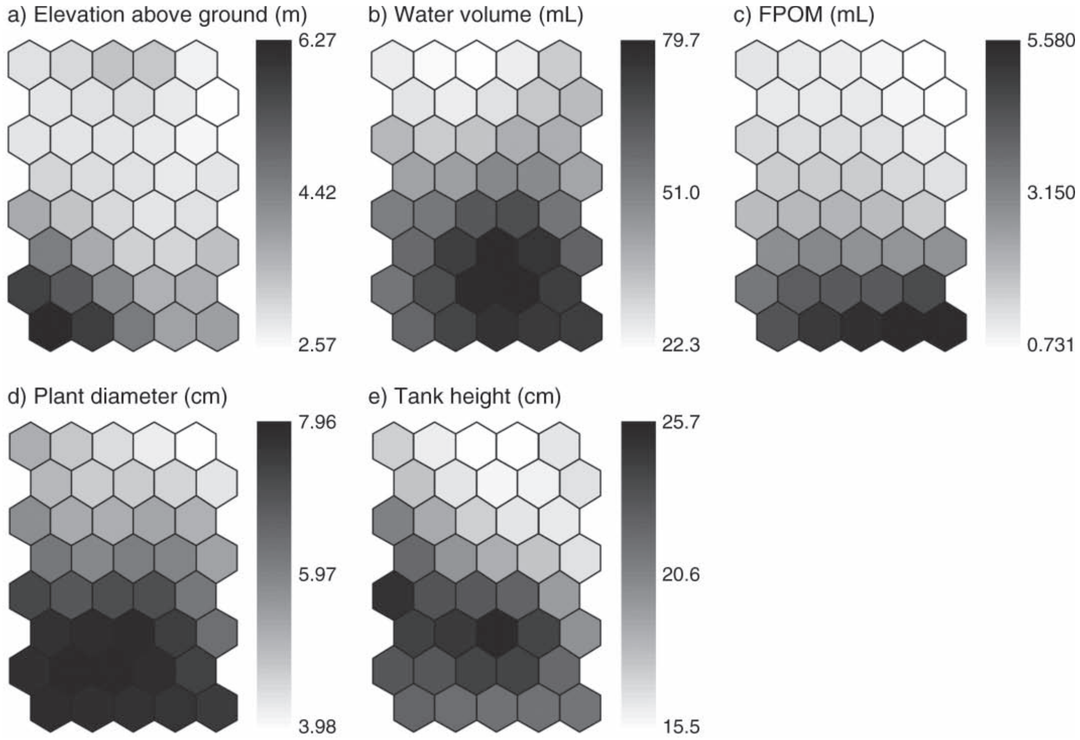

FIG. 2. Visualization of the five physical variables that characterize the bromeliads, in shades of gray. The interlocking leaf bases form the rainwater-holding reservoir or "tank." The mean value for each variable was calculated in each output neuron of the SOM previously trained with macroinvertebrate data. Dark represents a high value, while light is a low value. FPOM stands for fine particulate organic matter.

using a shaded scale, cluster A had the lowest taxon richness, compared to clusters B and C (Fig. 1b, c; see figure legend for the statistical tests). Cluster B was characterized by high abundances of *Culex* sp. 2, *Toxorhynchites purpureus*, *Wyeomyia aphobema*, *Telmatoscopus* sp. 1, Forcipomyinae sp. 1, Tanypodinae, *Scirtes* sp., *Cyphon* sp., and Hydracarina. Cluster C was associated with high abundances of *Culex* sp. 1, *Toxorhynchites* sp. 1, *Corethrella* sp., Ceratopogoninae, Limoniinae, Coenagrionidae sp. 1, *Aulophorus superterrenus*, and *Aelosoma* sp. Cluster A was characterized by low numbers of individuals for taxa that were not found in other clusters (e.g., *Wyeomyia splendida*, *Pristina osborni*), or that were not found in any particular cluster (e.g., *Wyeomyia forattinii*, *Toxorhynchites* sp. 3).

When physical variables were introduced into the SOM previously trained with invertebrate taxa (Fig. 2), the ordinate on the SOM showed a gradient of (b) water volume and (c) amount of FPOM (from the top to the bottom of the map), whereas the abscissa of the map chiefly represented (a) elevation above the ground, (d) plant diameter, and (e) tank height (from right to left). Cluster A appeared to group the smallest bromeliads. The corresponding plants were located at the lowest elevation in the supporting tress (<4 m), and clearly showed the lowest volumes of water and amounts of FPOM. Bromeliads in Clusters B and C were the largest, and held the most water. All plants in cluster B were associated with *C. femoratus* AGs located at higher elevations in trees (>4 m). Bromeliads in cluster C were characterized by the highest amounts of FPOM.

DISCUSSION

Most of our current understanding of plant-mediated impacts upon biodiversity has come from studies of herbivory. Modifications in vegetative traits resulting from herbivory are common in terrestrial plants, and, subsequently, this can indirectly affect the diversity of other organisms that utilize the same host plant (Ohgushi 2005). However, to the best of our knowledge, there has been no previous evidence of indirect plant-mediated impact upon the structure of entire animal communities as a result of mutualistic interactions. Assuming that "mutualisms between plants and animals pervade nature" (Vázquez et al. 2009:1445), addressing this question is highly relevant to broadening our understanding of the mechanisms underlying community organization and the maintenance of biodiversity in nature, especially in the species-rich tropical areas where the importance of nontrophic links cannot be ignored (Ohgushi et al. 2007).

Because they span a broad range of ecological gradients in terms of habitat structure, amount of

PLATE 1. The tank-bromeliad *Aechmea mertensii*, rooted on a *Pachycondyla goeldii* ant-garden covered with moss. Photo credit: A. Dejean.

resources, surrounding landscape, etc., tank-bromeliads have proven to be relevant model systems for studying the associations between the biodiversity of phytotelm communities (including biological interactions and functional processes) and these gradients in tropical environments (Richardson et al. 2000, Armbruster et al. 2002). Previous studies have highlighted the role of the container's characteristics (complexity, age) and direct biological interactions (food webs) in shaping invertebrate communities (reviewed in Kitching [2001]). While these studies focused on the diversity of aquatic communities, the indirect role of the terrestrial animals associated with the bromeliads in mediating phytotelm biodiversity has not been considered so far. Hence, our findings shed new light on how a two-species mutualism can affect much larger segments of the invertebrate community in tropical rain forests. Interestingly, the freshwater invertebrate communities that depend on ant-associated bromeliads are sensitive to environmental gradients, as they are "captive" within small and discrete pools that form aquatic islands within a terrestrial matrix. For the bromeliad *Aechmea mertensii* and its aquatic communities, the outcome of the ant–plant interaction is spatially conditioned, and the environment-dependent outcome in the mutualism is linked to the identity of the ant partner. The ants did not have a direct influence upon the aquatic communities; i.e., there was no direct ant–invertebrate interaction. However, differences in the habitat preferences of ant-garden (AG) ants has induced a phenotypic variability in individual plants (plant size and leaf display; see Leroy et al. 2009) that was echoed at the phytotelm community level. Indeed, *Pachycondyla goeldii* selected sunny areas, while *Camponotus femoratus* preferred partially shaded environments that are also characterized by higher humidity and leaf litter from the canopy. Because many aquatic invertebrates complete their larval development in tank-bromeliads, such differences in plant phenotype and local environment are likely to play an important role in habitat selection by colonizers and ovipositing adults.

The distribution of bromeliads in the self-organizing map (SOM) showed that invertebrate communities primarily responded to a gradient related to plant size (i.e., diameter and height), which determined a gradient in water volume and amount of fine particulate organic matter (FPOM). Nevertheless, with a greater average size for those *A. mertensii* associated with *C. femoratus*, the volumes of water and detritus available in the tank were greater compared to the ones in *P. goeldii* AGs (clusters B and C in our analyses). In other words, by coexisting on a local scale, the two ant species generated a gradient of habitat conditions in terms of available resources (including space and food resources). Water volume is an indicator of the aquatic habitat available. Larger habitats are more easily colonized by immigrants, resulting in positive species–area relationships (Drakare et al. 2006). The number of taxa and individuals per plant thus increases with greater water volume (see also Srivastava et al. 2008). Bromeliads with wider canopies (*C. femoratus* AGs) can also collect greater amounts of leaf litter.

The amount of FPOM can be considered as a good indicator of available resources at the lower end of the food chain in phytotelmata (Frank 1983), and nutrient-rich habitats are expected to sustain more species than nutrient-poor habitats (Paradise 2004). Detritivores can be divided into shredders, feeding on coarse particulate organic matter (CPOM; >1000 μm in size), and collectors (filter feeders and gatherers) feeding on FPOM. In *A. mertensii*, the partition of the non-predatory taxa into functional feeding groups (sensu Merritt and Cummins 1996) shows that all of the taxa at the bottom of the invertebrate food web are collectors (e.g., Oligochaeta, *Telmatoscopus* sp. 1, *Culex* spp.), and that their abundance tended to increase with increasing amounts of FPOM. Thus, the relationship between community structure and the volume of FPOM could be also generated through bottom-up effects (Kitching 2001). It is likely that large predators can only occur in a larger habitat once a sufficient set of saprophages is present (Kitching 2000); e.g., the predatory taxa *Corethrella* sp. and Coenagrionidae sp. 1 were characteristic of cluster C in our analysis. Finally, it should be noted that cluster B grouped those bromeliads located higher than 4 m above the ground in the host trees. The corresponding *A. mertensii* were all associated with *C. femoratus* AGs, and their aquatic biota was distinct (e.g., *Toxorhynchites purpureus*, *Wyeomyia aphobema*, *Telmatoscopus* sp. 1). It is thus likely that cluster B corresponded mostly to the vertical stratification of the invertebrate communities (in relation to the distribution of *C. femoratus* AGs), rather than to the influence of water volume or tank size.

Further investigations should now address the functional implications of such indirect effects. Indeed, macroinvertebrates constitute an important part of animal diversity within all ecosystem types, and are tightly integrated into the structure and functioning of their habitats (e.g., organic-matter processing, nutrient retention, food resources for vertebrates). For instance, because nutrient assimilation by tank-bromeliads relies heavily on invertebrate feces, one could postulate that the structural and/or functional diversity of invertebrates in the tanks influence nutrient assimilation by *A. mertensii* leaves, and thus plant fitness, in a kind of plant–invertebrates–plant feedback loop. Although such an assumption cannot be verified from our data, further experimental studies addressing this type of hypothesis might help to disentangle the processes underlying the relationships between biological interactions, biodiversity patterns, and ecosystem functioning. Lastly, it is clear that either mutualistic or antagonistic interactions often play an important role in modifying some of the biological traits of the partners (e.g., physiology, morphology, behavior) and may, consequently, mediate the influence hosts have on other components of an ecological community (Wood et al. 2007). Although two-species mutualisms (and not only those between plants and insects) are widespread and are found in all ecosystem types, the study of their ecological influences on other community members has mostly been limited to third species (Schmitt and Holbrook 2003, Savage and Peterson 2007), while their influence on the diversity of entire communities (this study) remains largely unexplored.

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Literature Cited

Armbruster, P., R. A. Hutchinson, and P. Cotgreave. 2002. Factors influencing community structure in a South American tank bromeliad fauna. Oikos 96:225–234.

Benzing, D. H. 2000. Bromeliaceae: profile of an adaptative radiation. Cambridge University Press, Cambridge, UK.

Céréghino, R., Y. S. Park, A. Compin, and S. Lek. 2003. Predicting the species richness of aquatic insects in streams using a limited number of environmental variables. Journal of the North American Benthological Society 22:442–456.

Compin, A., and R. Céréghino. 2007. Spatial patterns of macroinvertebrate functional feeding groups in streams in relation to physical variables and land-cover in Southwestern France. Landscape Ecology 22:1215–1225.

Corbara, B., and A. Dejean. 1996. Arboreal nest building and ant-garden initiation in a ponerine ant. Naturwissenschaften 83:227–230.

Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. Ecology Letters 9:215–227.

Frank, J. H. 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. Pages 101–128 *in* J. H. Frank and L. P. Lounibos, editors. Phytotelmata: terrestrial plants as host for aquatic insect communities. Plexus Publishing, Medford, New Jersey, USA.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap light analyzer (GLA) 2.0. Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs: users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, Canada, and the Institute of Ecosystems Studies, Millbrook, New York, USA.

Hubbell, S. P. 2001. The Unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:245–249.

Jabiol, J., B. Corbara, A. Dejean, and R. Céréghino. 2009. Structure of aquatic insect communities in tank-bromeliads in an East-Amazonian rainforest in French Guiana. Forest Ecology and Management 257:351–360.

Kaufmann, E., and U. Maschwitz. 2006. Ant-gardens of tropical Asian rainforests. Naturwissenschaften 93:216–227.

Kawamura, K., and H. Takeda. 2002. Light environment and crown architecture of two temperate *Vaccinium* species: inherent growth rules degree of plasticity in light response. Canadian Journal of Botany 80:1063–1077.

Kitching, R. L. 2000. Food webs and container habitats: the natural history and ecology of phytotelmata. Cambridge University Press, Cambridge, UK.

Kitching, R. L. 2001. Foodwebs in phytotelmata: "bottom-up" and "top-down" explanations for community structure. Annual Review of Entomology 46:729–760.

Kohonen, T. 2001. Self-organizing maps. Third edition. Springer-Verlag, Berlin, Germany.

Leroy, C., B. Corbara, A. Dejean, and R. Céréghino. 2009. Ants mediate foliar structure and nitrogen acquisition in a tank-bromeliad. New Phytologist 183:1124–1133.

Longino, J. T. 2003. The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. Zootaxa 151:1–150.

Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Third edition. Kendall/Hunt, Dubuque, Iowa, USA.

Nadkarni, N. 1994. Diversity of species and interaction in the upper tree canopy of forest ecosystems. American Zoologist 34:70–78.

Ngai, J., and D. Srivastava. 2006. Predators accelerate nutrient cycling in a bromeliad ecosystem. Science 314:963.

Ohgushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. Annual Review of Ecology Evolution and Systematics 36:81–105.

Ohgushi, T., T. P. Craig, and P. W. Price. 2007. Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, Cambridge, UK.

Orivel, J., and A. Dejean. 1999. Selection of epiphyte seeds by ant-garden ants. Ecoscience 6:51–55.

Orivel, J., A. Dejean, and C. Errard. 1998. Active role of two ponerine ants in the elaboration of ant-gardens. Biotropica 30:487–491.

Orivel, J., C. Errard, and A. Dejean. 1997. Ant gardens: interspecific recognition in parabiotic ant species. Behavioral Ecology and Sociobiology 40:87–93.

Paradise, C. J. 2004. Relationship of water and leaf-litter variability to insects inhabiting treeholes. Journal of the North American Benthological Society 23:793–805.

Richardson, B. A., C. Rogers, and M. J. Richardson. 2000. Nutrients, diversity, and community structure of two phytotelm systems in a lower montane forest, Puerto Rico. Ecological Entomology 25:348–356.

Savage, A., and M. Peterson. 2007. Mutualism in a community context: the positive feedback between an ant–aphid mutualism and a gall-making midge. Oecologia 151:280–291.

Schmitt, R. J., and S. J. Holbrook. 2003. Mutualism can mediate competition and promote coexistence. Ecology Letters 6:898–902.

Sirola, M., G. Lampi, and J. Parviainen. 2004. Using self-organizing map in a computerized decision support system. Pages 136–141 *in* N. Pal, N. Kasabov, R. Mudi, S. Pal, and S. Parui, editors. Neural information processing. Springer-Verlag, Berlin, Germany.

Srivastava, D. S., M. K. Trzcinski, B. A. Richardson, and B. Gilbert. 2008. Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. American Naturalist 172:761–771.

Vantaux, A., A. Dejean, A. Dor, and J. Orivel. 2007. Parasitism versus mutualism in the ant-garden parabiosis between *Camponotus femoratus* and *Crematogaster levior*. Insectes Sociaux 54:95–99.

Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting pattern and process in plant–animal mutualistic networks: a review. Annals of Botany 103:1445–1457.

Wilson, E. O. 1988. The current state of biological diversity. Pages 3–18 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

Wood, C. L., J. E. Byers, K. L. Cottingham, I. Altman, M. J. Donahue, and A. M. H. Blakeslee. 2007. Parasites alter community structure. Proceedings of the National Academy of Sciences (USA) 104:9335–9339.

APPENDIX

A table listing the macroinvertebrate taxa occurring in the tank-bromeliad *Aechmea mertensii* associated with ant-gardens inhabited by the ants *Camponotus femoratus* and *Pachychondyla goeldii* (*Ecological Archives* E091-107-A1).