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Arboreal frogs, tank bromeliads and disturbed seasonal tropical forest

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Abstract: We investigated the relationship between arboreal frogs, tank bromeliads and landscape transformation in tropical forests of southeastern Campeche, Mexico. We surveyed frogs in six distinct habitats: slash and burn agriculture, seasonally flooded forest (bajo), aquatic habitats (lagoons and small ponds), second growth upland forest, primary forest and creek habitat using both systematic and non-systematic surveys. The highest species richness of frogs was documented in primary forest and small ponds. In contrast, no frogs were recorded in second growth forest. Similarly, tank bromeliads (Aechmea bracteata) were completely absent from early successional stages and were almost twice as abundant in seasonally flooded forest as in upland forest. The vertical distribution of A. bracteata differed between forest types, and they significantly more abundant in larger diameter trees. We examined 60 tank bromeliads during the peak of the dry season to test their use as refugia by frogs. Approximately 27% of tank bromeliads sampled had arboreal frogs belonging to three species, but 9 species have been recorded as occasional users of bromeliads in the region. There were significantly more frogs on large than on medium-sized bromeliads, and frogs were more abundant on bromeliads higher on host trees, particularly those above 3 m in height. Our results suggest that the loss of tank bromeliads from drier and less structurally complex habitats created by slash and burn agriculture and selective logging results in loss of refugia for arboreal frogs in this seasonal tropical forest. We suggest that Aechmea bracteata be a keystone species in seasonal tropical forest.

Ranas arbóreas, bromelias de tanque y la perturbación en selvas tropicales estacionales
Resumen: Investigamos la relación entre las ranas arbóreas, las bromelias de tanque y la transformación del paisaje en la selva tropical del sureste de Campeche, México. Hicimos muestreos de ranas en seis hábitats distintos: agricultura de roza, tumba y quema, selvas inundables (bajos), hábitats acuáticos (laguna, estanque pequeño), selva perturbada, selva primaria y hábitat ribereño utilizando métodos sistemáticos y no sistemáticos. Encontramos la mayor riqueza de especies de ranas en bosque primario y en el pequeño estanque. Por el contrario, no registramos ranas en selva secundaria. De igual manera, no registramos ninguna bromelia de tanque (Aechmea bracteata) en etapas sucesionales tempranas. Hubo casi el doble de bromelias en selvas inundables que en selvas no inundables. La distribución vertical de A. bracteata cambia en diferentes tipos de selvas y son más abundantes en árboles con diámetros mayores. Examinamos 60 bromelias de tanque para probar su utilización como refugio de ranas. Durante la época mas seca 27% de las bromelias de tanque muestreadas tuvieron ranas arbóreas. En este estudio registramos tres especies de ranas en las bromelias, pero se han registrado 9 especies que usan bromelias de en la región. Encontramos más ranas en las bromelias de mayor tamaño y en las que se encuentran en posiciones más altas en los árboles, particularmente por encima de los 3 metros de altura. Nuestros resultados indican que la pérdida de bromelias de tanque de hábitats más secos y menos complejos estructuralmente creados por las prácticas de roza, tumba y quema, y por la explotación selectiva, tiene como consecuencia la pérdida de refugios para las ranas arbóreas en estas selvas tropicales estacionales. Sugerimos que las bromelias de tanque funcionan como especies clave en las selvas tropicales estacionales.

INTRODUCTION

Worldwide declines in amphibian populations have been explained by a variety of factors including habitat loss and fragmentation, introduced species, increased ultraviolet radiation (UV-B), contaminants, acidic precipitation, diseases and overharvesting (Barinaga 1990; Blaustein & Wake 1990; Wyman 1990; Wake 1991; Pearman et al. 1995; Reaser 1996; Duellman 1999), and global warming (Pounds et al. 1999). Because a large proportion of amphibian species in tropical forests are adapted to arboreal life, microhabitat loss and fragmentation are important factors in their conservation. Arboreal amphibians (some frogs and salamanders) may be affected by dramatic changes in forest cover and also by more subtle removal of critical habitat, which provides refugia from weather and predators, as well as sites for breeding and foraging.

In tropical forests, large epiphytes (bromeliads), crevices, hollow trees, stumps, termite mounds, and logs provide critical habitat for wildlife. Large "tank" bromeliads (Bromeliaceae) in particular, accumulate rain water and debris from the host tree, providing foraging sites, protection and a moist environment ideal as habitat for many invertebrates and some vertebrates (Benzing 1980; Dejean et al. 1995; Frank 1996). Arboreal frogs use bromeliads for oviposition, tadpole development (Scott and Limerick 1983; Lee 1996; Campbell 1998; Schiesari et al. 1996; Lannoo et al. 1987), to complete metamorphosis (Donnelly 1989), and as daily or seasonal refugia (Lee 1996; Campbell 1998). Bromeliads may be particularly important refugia for amphibians in strongly seasonal forests, where their tanks are one of the few places that retain water throughout the dry season.

Like other epiphytes, bromeliads have strong microhabitat associations (Hietz-Seifert et al. 1996). Many bromeliads are old-growth forest specialists (Benzing 1980) that are affected by human activities that progressively eliminate forest structures. Selective logging targets large diameter trees, which provide crevices and holes and support large epiphytes. Slash and burn agriculture completely removes forest cover and critical structures. Regenerating forests need many years to produce these structures after the sites are abandoned, and therefore may be unsuitable for arboreal frogs that use bromelias and tree cavities.

Southeastern Campeche contains the largest continuous forest in tropical Mexico. Since the beginning of the last century, the region has been subjected to widespread selective logging for species such as mahogany (Swietenia macrophylla) and cedar (Cedrela odorata). Microclimate changes induced by logging favored a different tree species composition (Martinez & Galindo-Leal 2002). More recently, human settlements rapidly changed landscape composition and structure through slash and burn agriculture (Carranza et al. 1996; Sandler et al. 1998). Because of low soil productivity, agricultural fields were abandoned after one or two years. Although some studies have looked at the effects of forest structure and logging on amphibians (Pearman 1997, Tocher et al. 1997, Lemckert 1999), little is known about how forest changes affect the distribution and abundance of bromeliads and frogs (Hietz-Seifert et al. 1996, Dejean & Olmsted 1997).

The objectives of this study were threefold. First, we examined the distribution of frogs in a slash and burn landscape mosaic. The local frog assemblage uses a variety of habitats (Table 1); therefore we hypothesized that greater frog species richness would be related to structural habitat diversity and water availability. The seasonally flooded forest would contain the most frog species because it provides both cover and temporary ponds (Lee 1993). We expected the less structurally complex agricultural fields to have the lowest diversity of anurans.

Second, we hypothesized that tank bromeliads may be lost from structurally simplified forest. While bromeliads are not restricted to particular tree species, they may be influenced by host tree diameter (Zimmerman & Olmsted 1992) and bark texture (Dejean et al. 1995). We therefore determined the distribution and abundance of bromeliads in different habitats and successional stages.

Third, we investigated whether arboreal frogs used tank bromeliads (Aechmea bracteata) as refugia in the dry season when they are not breeding. While none of the frog species in the study area have been recorded using bromeliads for breeding (Lee 1996; Campbell 1998), the region is extremely dry during part of the year and half of the species are arboreal. We hypothesized that tank bromeliads were important refugia for several frog species.

Study areas

The study area was around the town of Zoh-Laguna in southeastern Campeche (Lat. N. 18° 35' Long. W 89° 26'), Mexico on the eastern side adjacent to Calakmul Biosphere Reserve (Galindo-Leal et al. 2000). The rainy season occurred from June – October, with precipitation ranging from 100 – 200 mm/mo. During the dry season, precipitation was only 20 – 50 mm/mo (INEGI 1996). Mean annual temperature was 24.6° C (Zoh-Laguna weather station 1953-1997). There were very few permanent streams in the area and little surface water.

The main economic activities of Zoh-Laguna (1056 inhabitants; INEGI 1994) and the nearby communities included extensive and intensive agriculture, apiculture, and forestry (i.e. lumber and chicle extraction). Zoh-Laguna was a good representative of a landscape mosaic that had been converted from forest to agriculture and fallow fields. Additional data were obtained in two other study areas: the upland forest of Calakmul Reserve (one night), and near the town of Cristobal Colon (two nights). Calakmul Reserve contained a substantial area of relatively undisturbed forest (7000 km2). Cristobal Colon was similar to Zoh-Laguna and had a mosaic of slash and burn agriculture and second growth forest surrounding it.

Five broad habitat types were identified in the region of Zoh-Laguna: upland forest, second growth forest, seasonally flooded forest, agricultural fields, and strictly aquatic habitats (lagoons, ponds, and creeks). All were disturbed in some way. Creeks were not present near Zoh-Laguna. Upland forests, although seemingly undisturbed, had a long history of mahogany and cedar extraction that caused shifts in species composition (Martinez & Galindo-Leal 2002). Canopy tree height ranged from 15 – 30 m and diameter at breast height (dbh) was usually greater than 30 cm.

Second growth forest resulted mostly from abandoned agricultural fields or runaway burns (Martinez & Galindo-Leal 2002). Seasonally flooded forest (known locally as "bajos") had smaller trees ranging from 2 – 7 m in height and 2 – 20 cm in diameter (Miranda 1958, Martinez & Galindo-Leal 2002). Epiphytes were more abundant and diverse in this seasonally flooded forest habitat (Dejean et al. 1995), and seasonally flooded for ests are considered important breeding habitats for amphibians (Lee 1996).

Agricultural fields were the dominant habitat created by humans. They consisted of 1 - 2 ha sections of either primary or second growth forest cleared and burned for corn, bean and squash agriculture.

Aquatic habitats were rare in the study area. Like seasonally flooded forests, they represent important breeding habitat for frogs and some species rarely venture far from their vicinity (Lee 1996). Strictly aquatic habitats included lagoons, small ponds, and creeks.

METHODS

We assessed the spatial distribution of frogs in the middle of the rainy season (July and August, 1996). Systematic frog surveys were conducted only in four distinct habitats near Zoh-Laguna: agricultural fields, seasonally flooded forest, second growth forest (< 10 y old forest), and aquatic habitats (a small pond and a lagoon). The land use mosaic is representative of areas around settlements and therefore useful to assess the impact of human activities on frogs. Sites were interspersed around Zoh-Laguna in agricultural fields (n=3), second growth forest (n=3), and in seasonally flooded forest (n=2). Every site had two parallel 150 m transects separated by 25 m. Each transect was visited a total of eight times (four from 07:00 to 11:00 and four from 20:30 to 1:30) in July and August 1996. We searched for frogs in a 4 m wide area including the ground and up to 2 m high in trees while slowly walking along the transects for approximately 45 min (Crump and Scott 1994). In each transect we recorded the number of individuals, species, time, and place of observation for each visual encounter. The order of visits to transects was randomized.

Because some frog species congregate near bodies of water, a large lagoon (2 hectares) and a small pond (0.25 ha) were also sampled in Zoh-Laguna. These sites were located approximately 0.8 kilometers apart. Four nocturnal and four diurnal surveys (same hours as for the transects) were conducted in July and August. The observations involved walking around the pond perimeter of the water for approximately 45 – 60 min, identifying any frogs observed within a 4 meter wide area. Because no individuals were recorded during the day in visual encounter surveys, relative abundance is reported as the mean number of individuals per night-transect or night search for all surveys.

In addition, we also obtained information on frog abundance through non-systematic observations and conversations with local people. Non-systematic observations took place in Zoh-Laguna during the day and night and in two sites south of Zoh-Laguna during the night: Calakmul Archaeological Site in the Reserve (75 km SW) and in the surroundings of Cristobal Colon (50 km S). In Calakmul, a survey was conducted by walking an unused road surrounded by primary forest for three hours (20:00 to 23:00) on the night of July 6th. In Cristobal Colon surveys took place during two nights (July 11 th and 13th), walking for three hours (20:00 to 23:00) alongside a creek with running water surrounded by second growth forest.

Voucher specimens of each species were collected and deposited in the Vertebrate Museum of El Colegio de la Frontera Sur (ECOSUR) in Chetumal, Quintana Roo, Mexico. Species identifications relied on appropriate keys (Behler 1979; Savage 1980).

Tank bromeliad (Aechmea bracteata) surveys were conducted from June – August 1998. We did not restrict our sampling to the surroundings of Zoh-Laguna but sampled a larger region to include less disturbed habitats. We used 19 transects in five habitat types: second growth forest < 10 years old (n=3), second growth forest > 10 years old (n=2), low primary forest (n=5), tall primary forest (n=3) and seasonally flooded forest (n=6). Transects varied in length from 100 – 500 m. We recorded the distance from the transect to the host tree, bromeliad leaf size (in three categories: small <20 cm; medium 21 to 100 cm; large > 100 cm, position, and estimated height in the host tree. In addition, in 135 circular plots (10 m2) we recorded tree diameter classes (< l0, 11-20, 21-30, 31-40, > 40 cm). Plots were sampled over the transects every 50 m. To compare the distribution of bromeliads among host tree diameter classes we used log-likelihood tests (Sokal and Rohlf 1981).

We sampled bromeliads for frogs at the end of the dry season, 21 – 24 April 1999. We collected 60 individual tank bromeliads (Aechmea bracteata) from a range of heights (0 – 5 m) and substrates (ground, tree branches and trunks). Aechmea bracteata is the largest species of this Neotropical family in the region (Figure 1), with leaves and red inflorescenses sometimes exceeding one meter in length. Species within Aechmea are classified as “phytotelm tank” bromeliads because of their capacity to hold water (Dejean et al. 1995; Dejean & Olmsted 1997). They are pollinated and dispersed by birds (Benzing 1980). Plants take from 2 – 5 years to mature and flower. After flowering the individual plant dies slowly, but vegetative reproduction is common and Aechmea are often found in clusters. Mature plants have four types of cavities: 1) wide open cavities delimited by the external whorl of leaves; 2) interfoliar cavities; 3) inter-leaf cavities and 4) a watertight cavity in the center of the plant. Interfoliar cavities are deep and narrow and accumulate rainwater, which remains well into the dry season because of low evaporation.

Our sampling method was destructive since the frogs cannot be sampled without removing and opening the bromeliad to search in interfoliar cavities. We gathered bromeliads in four areas near Zoh-Laguna in which human activities were common, and the forest was likely to be transformed or removed. Almost half of the bromeliads were collected in seasonally flooded forest (n=34). The rest were collected from riparian forest (n=10), disturbed forest (n=10), and near ponds (n=6). We reached bromeliads by climbing trees and isolated individual plants from clusters using a machete. They were immediately lowered and placed in large fastened transparent plastic bags. We characterized bromeliads as large (> 70 cm) or medium-sized (< 70 cm) by their length from the bottom of the tank to the tip of the leaves. We transported plants to the camp laboratory where we submerged the bromeliads in a large bucket filled with water. Three observers carefully searched for frogs in the interfoliar cavities while removing individual leaves. Frogs were immediately identified and returned to the sites from which the bromeliads were collected. We used log-likelihood tests to compare the distribution of frogs among habitats, height, and bromeliad size categories (Sokal & Rohlf 1981).

RESULTS

Frogs in a slash and burn landscape mosaic

Habitat use and abundance. A total of 135 frogs belonging to eleven species was recorded in transect surveys and non-systematic surveys (Figure 2). The number of species per habitat was low (< 5) and there was little overlap in habitat use among species. Seven species were commonly recorded (> 7 records): Bufo valliceps, Hyla loquax, H. microcephala, Hypopachus variolosus, Leptodactylus labialis, Rana berlandieri, and Smilisca baudinii. Four species were rare (< 4 records): Bufo marinus, Hyla picta, Phrynohyas venulosa, and Triprion petasatus.

Within the transect surveys, the largest number of species (3) was recorded at the small pond (Rana berlandieri, Hyla loquax, and Bufo valliceps) (Figure 2a). In contrast, only Rana berlandieri was recorded in the lagoon. We recorded two species (Leptodactylus labialis and Bufo valliceps) in agricultural fields, one (Hyla microcephala) in the seasonally flooded forest and no species in the second growth forest (Figure 2a). Despite substantially lower sampling effort in the non-systematic surveys, we recorded the greatest species richness and abundance in the primary upland forest (Hypopachus variolosus, Smilisca baudini, Phrynohyas venulosa, Bufo valliceps and Rana berlandieri). Hypopachus variolosus was recorded only from this site. Four species were recorded along the creek: Bufo marinus, B. valliceps, Rana berlandieri, and Smilisca baudini (Figure 2b). Finally, three species were found near human habitation. Hyla picta was recorded in the grass near a house, Phrynohyas venulosa was recorded in a water tank and in a tree next to a house, and Smilisca baudinii was observed inside houses or in small trees nearby.

Distribution of tank bromeliads

Bromeliads were completely absent from early successional stages (both second growth less than 10 y old and between 20 and 40 y old); (Figure 3). In late successional forest, we sampled a total of 179 tank bromeliads, which were almost twice as abundant in seasonally flooded forest (=66.9 individuals/ha) as in upland forest (=26.65 individuals/ha), (Figure 3); ($t=-3.055$, $df=13$, $p<0.005$). Tank bromeliads were significantly more common on large diameter trees (> 20 cm) than in small diameter trees both in upland forest ($G=202.66$, $df=3$, $p<0.001$) and in seasonally flooded forest ($G=48.001$, $df=3$, $p<0.001$), (Figure 4).

The vertical distribution of Aechmea differed among forest types. In seasonally flooded forest, they were similarly abundant at different heights below 7 m of height. In upland forest, they were more abundant between 4 and 8 meters, and less abundant at higher and lower heights (Figure 5).

Tree frogs and tank bromeliads

We found 23 hylid frogs of three species (Hyla microcephala (n=2), H. picta (n=1) and Scinax staufferi (n=20)) in a sample of 60 individual bromeliads. Frogs were present in 16 of 60 plants (27%): 11 bromeliads had one frog, three had two frogs, and two bromeliads had three and four frogs respectively. Frog distributions were not significantly associated with forest types ($G=6.542$, $df=3$, $p>0.05$)

Significantly more frogs were found on large than on medium-sized bromeliads ($G=6.478$, $df=1$, $p<0.025$). Frogs were not distributed randomly across the vertical strata. More frogs than expected were in bromeliads located higher in the host tree, particularly above 3 m ($G=13.972$, $df=4$, $p<0.01$), (Figure 6).

DISCUSSION

Our results suggest that loss of habitat structures such as tank bromeliads from managed forests or agricultural fallows results in microhabitat loss for arboreal frogs. We found many arboreal frogs using tank bromeliads, possibly as refugia (Table 1). However, both tank bromeliads and arboreal frogs were absent from second growth forests, which lacked suitable microhabitat conditions (i.e. humidity, structural complexity) for successful establishment of tank bromeliads.

Frog habitat use and abundance

We did not expect second growth forest to be of great importance, but were surprised at the complete absence of frogs in this habitat. It is alarming that no frogs were recorded in three sites (six transects) during eight visits. Second growth forests were common near towns, and will most likely continue to expand because slash and burn agriculture has a very short cycle in the region. After two or three years fields were abandoned for seven to ten years. Almost half of the species present in the area (Hyla loquax, H. microcephala, H. picta, Scinax staufferi, Agalychnis callidryas, Phrynohyas venulosa, Smilisca baudinii, and Triprion petasatus) were arboreal, and may need arboreal refugia such as bromeliads and tree cavities, which were not available in second growth forests.

Few anurans co-occurred; there were only two or three species per habitat. Three species were widespread: Bufo valliceps, Rana berlandieri and Smilisca baudinii. In the aquatic habitat where three species were recorded, two were exclusively found in either the lagoon or the small pond, whereas a single species was found at both places. The remaining eight species were almost exclusively recorded in one habitat. These patterns may change as longer studies are conducted. Although our study sampled during the rainy season when frog activity was highest, we only sampled during a two-month period. At present, we are monitoring amphibian spatial distribution and abundance at a wider spatial scale and longer time frame.

Frog habits corresponded with available habitat structure. Terrestrial species were recorded in agricultural fields; aquatic species in the lagoon; arboreal species in the seasonally flooded forest; and both terrestrial and arboreal species in the small pond. Many species were recorded in the non-systematic surveys. Some of the species were highly restricted in their distributions. Of the five species found in primary upland forest in Calakmul, only one, Hypopachus variolosus was found exclusively in that habitat (Figure 2). Similarly, Bufo marinus was only recorded along the creek in Cristobal Colon (Figure 2b). These two sites were visited only once, and further sampling is required to confirm the habitat use by these frogs. Information gathered from local residents and non-systematic surveys revealed that certain man-made structures, like household water tanks, could serve as refugia.

Succession, bromeliads and frogs

Our results indicate that tank bromeliads (Aechema bracteata), like other vascular canopy dwellers (Benzing 1980) were restricted to older forest stages and completely absent from younger forests. They were particularly abundant in seasonally flooded forest where humidity was higher. Changes in forest structure and composition due to human activities affected bromeliads in several ways. First, removal of larger diameter trees decreased adequate substrate availability ((Zimmerman & Olmsted 1992, this study). Second, some of the common tree species in disturbed forest, such as chaka (Bursera simaruba) and tzalam (Lysiloma satisiliqua), have an extremely smooth bark that does not offer support to bromeliads (Dejean et al. 1995). Finally, canopy reduction produces drier microclimates that may affect colonization and survival of small seeds.

Tank bromeliads (Aechmea bracteata) were a critical habitat for arboreal frogs during the dry season. In our study, frogs occupied approximately one third of the sampled plants. This likely was an underestimation due to sampling problems. Frogs were likely to escape from bromeliads during sampling and transportation. Most frogs we recorded were very small (less than 2 cm snout-vent length) and cryptic. While searching for frogs in the lab, we had instances of frogs leaping out of bromeliads, despite having three people search every plant. Other frogs might have escaped unnoticed in the field. Other studies in nearby sites documented lower occupancy rates (9% Dejean et al. 1995; 17 % Mendez et al. 1999; Castañeda-Moya & Mendez 1999) in Aechmea bracteata and Aechmea nudicaulis, respectively. Their lower success was probably due to more abrupt handling of sampled bromeliads. We enclosed the bromeliads in plastic bags and examined them in the lab.

The rate of bromeliad occupancy by frogs increased with height. However, in this study we only sampled frog occupancy up to 5 m. Tank bromeliads were more abundant between 0 and 8 m in seasonally flooded forest and between 4 and 8 m in upland forest (this study, Dejean et al. 1995). In our study area, we observed Mexican tree frogs (Smilisca baudini) as high as 10-12 m. To obtain more accurate information on occupancy, future studies should encompass the full vertical range of tank bromeliads.

Frogs were disproportionately encountered in large bromeliads, which have higher tank capacity and slower water loss rates than smaller bromeliads (Zotz & Vera 1999). While we recorded only three frog species inside bromeliads, casual encounters during the last three years yielded almost every other species of hylid using large native bromeliads (Aechmea bracteata, Tillandsia stretophylla) and an introduced bromeliad (Bromelia penguin) planted as a living-fence of some human settlements (Table 1). Salamanders (i.e. Bolitoglossa rufescens, B. mulleri, B. mexicana, B. subpalmata) have also been recorded using tank bromeliads as refugia (Scott & Limerick 1983; Lee 1996; Campbell 1998). During this study we also documented for the first time the presence of the rare, endemic Yucatan salamander (Bolitoglosssa yucatana) inside a large tank bromeliad located 4 m above the ground (Calderon, Cedeño and Pozo 2003).

In Costa Rica, experimental addition of bromeliads (Vriesia spp.) increased the density of territorial strawberry poison frogs (Dendrobates pumilio) (Donnelly 1989), which defend bromeliads as tadpole-rearing sites. None of the species in our study area used bromeliads as breeding sites; all the species laid eggs in permanent or ephemeral ponds, or in overhanging vegetation. However, we suggest that because of the extreme seasonality of the area, tank bromeliads provide one of the few moist environments for frogs, especially in the dry season.

Aechmea as a keystone species

Many species of bromeliads inhabit the highly seasonal tropical forests of the Yucatan Peninsula. In our study area most bromeliads were small (genus Tillandsia) and not used by amphibians. However, at least three species of tank bromeliads (Aechmea bracteata, A. bromeliifolia, and A. tillandsioides; E. Martinez, pers. com) were large, and their leaves collected water, intercepted debris, and housed diverse invertebrates (Benzing 1980; Dejean et al., 1995). They also had a peripheral reservoir and a waterproof central cavity. Aechmea bracteata, for example, shelters a higher species richness and abundance of invertebrates than smaller bromeliad species (i.e. Tillandsia spp.) (Dejean et al. 1995).

A large variety of invertebrates, including detritivores (mites, isopods, collembolans, termites) and predators (scorpions, dermaptera, ants, giant dragonfly larvae), live in tank bromeliads (Benzing 1980; Dejean et al. 1995; Gonzalez 1997; Moron & Blackaller 1997). Up to 35 taxa of invertebrates and vertebrates and 21 species of ants live in Aechmea bracteata (Dejean et al. 1995), which has a waterproof cavity commonly occupied by ants or termites. Ants protect the bromeliad's host tree against herbivores. Defoliation by insects and leaf cutter ants (Atta cephalotes) seems lower in trees with Aechmea (Dejean et al., 1995). Frogs, salamanders, lizards, snakes, and small mammals also use this epiphyte (Dejean et al., 1995).

Because of the highly seasonal nature of the area, tank bromeliads are one of the few places that provide a protected moist environment for many species. Their absence may have strong consequences for the overall community. We hypothesize that tank bromeliads in seasonal tropical forests function as keystone species since a large number of other species in the ecosystem depend on them.

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