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Herpetofaunal community of a high canopy tank bromeliad (*Aechmea zebrina*) in the Yasuní Biosphere Reserve of Amazonian Ecuador, with comments on the use of "arboreal" in the herpetological literature

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***Abstract.*—Tank bromeliads provide microhabitat that supports a high diversity of organisms in the harsh environment of tropical forest canopies. Most studies of organisms occupying tank bromeliads have focused on invertebrates found within bromeliads near or at ground level. Few investigations of vertebrate communities utilizing this keystone resource are available. We describe the amphibian and reptile community occupying the high canopy tank bromeliad, *Aechmea zebrina*, in lowland rainforest of the Yasuní Biosphere Reserve in the Amazon Basin of Ecuador. We used single-rope climbing techniques to sample a total of 160 *A. zebrina* bromeliads from 32 trees, at heights of 18.3 to 45.5 m above ground. We collected 10 metamorphosed anuran species, one gecko, one snake, and observed two species of lizard within bromeliads. Summary statistics for a suite of environmental factors associated with herpetofauna in *A. zebrina* bromeliads are reported. We estimated the density of anurans occupying *A. zebrina* communities and contrast these estimates with anuran densities from tropical forest floor anuran studies. Finally, we discuss the use of the term "arboreal" within the herpetological literature, and make recommendations for terminology used to describe the vertical space occupied by a species or assemblage.**

Key words. Amphibian, anuran, epiphyte, forest, microhabitat, rainforest, reptile

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Introduction

Forest canopies provide habitat for approximately 50% of terrestrial species, yet there are few studies specific to canopy herpetofauna (Stewart 1985; Vitt and Zani 1996; Kays and Allison 2001; Guayasamin et al. 2006; McCracken and Forstner 2008; Lowman and Schowalter 2012; Scheffers et al. 2013; McCracken and Forstner 2014). Basic ecological knowledge of arboreality (tree-living) and utilization of high canopy microhabitats by amphibians and reptiles remain depauperate in the literature (Moffett 2000; Kays and Allison 2001; Lehr et al. 2007). A canopy microhabitat frequently used by herpetofauna in tropical forests are epiphytes, and in particular epiphytic tank bromeliads that are phytotelms capable of holding relatively large volumes of water (Lowman and Rinker 2004; McCracken and Forstner 2008). In lowland Neotropical rainforest, canopy tank bromeliads typically reside in the overstory and emergent canopy trees at vertical heights of 5–45+ meters with ~5 to >150 individuals on a single tree (McCracken and Forstner 2006). These arboreal bromeliad communities create a three-dimensional "wetland in the sky" that have been estimated to impound up to 50,000 liters of water per hectare (Kitching 2000; McCracken and Forstner 2006). Tank bromeliads function as a "keystone resource" in the harsh forest canopy environment where the atmosphere meets and interacts with 90% of Earth's terrestrial biomass; providing a climate-buffered refuge, water source, and food source for canopy herpetofauna (Nadkarni 1994; Ozanne et al. 2003; Cardelús and Chazdon 2005).

Kays and Allison (2001) found only 4% of 752 articles published between 1988 and 1998 on tropical forest arboreal vertebrates focused on reptiles and amphibians. Many species of herpetofauna are described as being arboreal regardless of whether they are restricted to the vertical stratum a few centimeters to a few meters above ground, or solely inhabit the high forest canopy at 20 or more meters vertical height (Chaparro et al. 2007; McCracken et al. 2007; Guayasamin and Funk 2009). Forest structure is associated with vertical partitioning or stratification of the component plant community (e.g., trees, shrubs, lianas) and accentuates vertical patterns followed by other organisms (Moffett 2000; Lowman and Rinker

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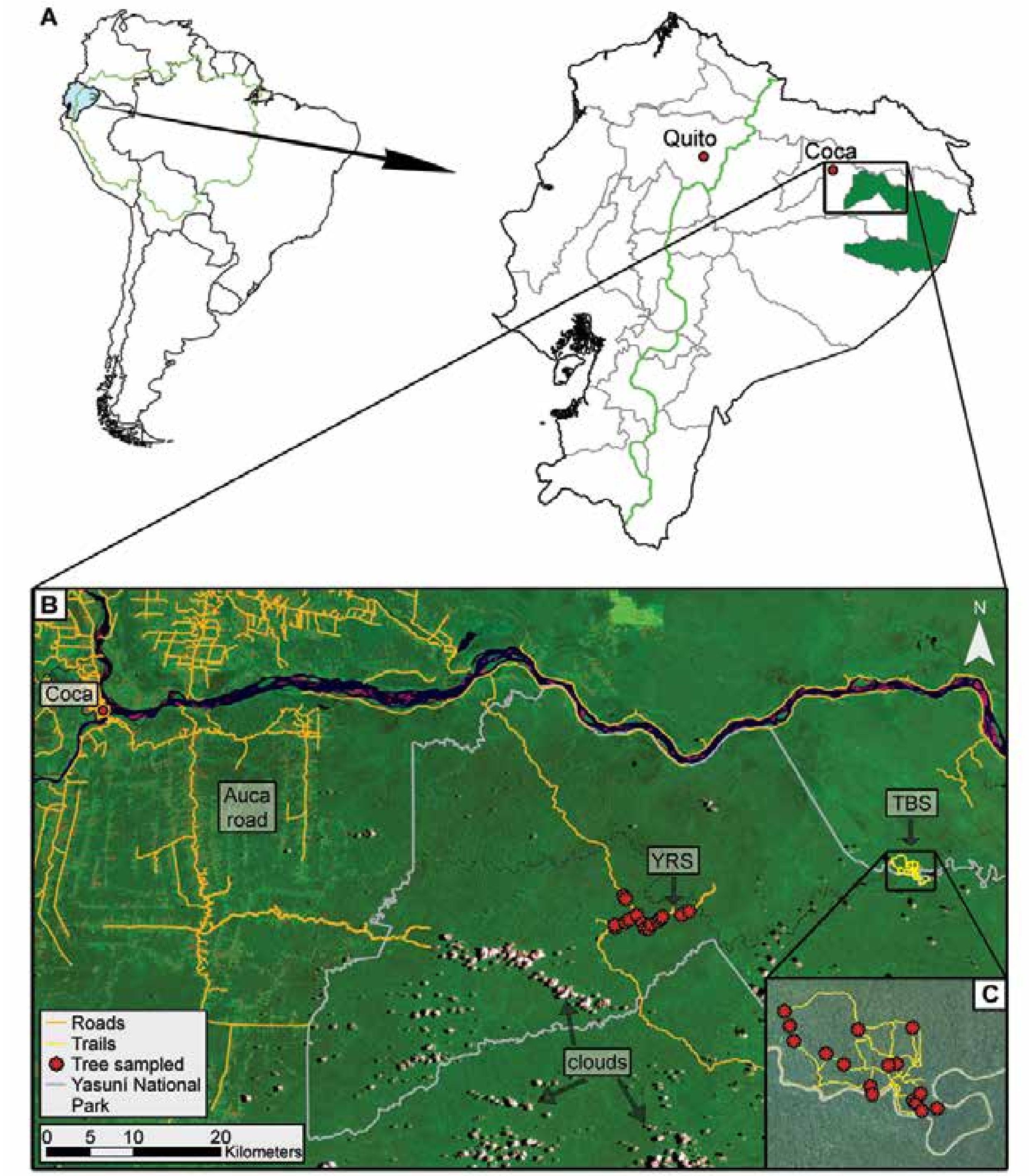


Fig. 1. (A) Map of South America with Ecuador (shaded light blue) and Yasuní National Park (solid dark green) highlighted. The Amazon ecoregion is outlined with light green line. (B) Northeastern section of Yasuní National Park (light gray line) and surrounding region where trees were sampled for *Aechmea zebrina* bromeliads within the vicinity of the Tiputini Biodiversity Station – Universidad San Francisco de Quito (TBS) and the Yasuní Research Station – Pontificia Universidad Católica del Ecuador (YRS). (C) Detail of TBS where trees were sampled for *A. zebrina* bromeliads. Note: Map is modified from Figure 2 in McCracken and Forstner (2014) and used under the Creative Commons Attribution license.

2004). Spatial patterns of forest cohabitants, such as tank bromeliads and their inhabitants, are likewise strongly influenced by forest structure as a result of the fundamental organization of resources and space (Lowman and Rinker 2004). Identifying the vertical space occupied by a particular amphibian or reptile species in its given habitat will allow greater insight to their ecological role in the system.

Herein, we describe amphibians and reptiles occupying the high canopy tank bromeliad, *Aechmea zebrina*, in lowland rainforest of the Yasuní Biosphere Reserve in the Amazon Basin of Ecuador. We report a suite of environ-

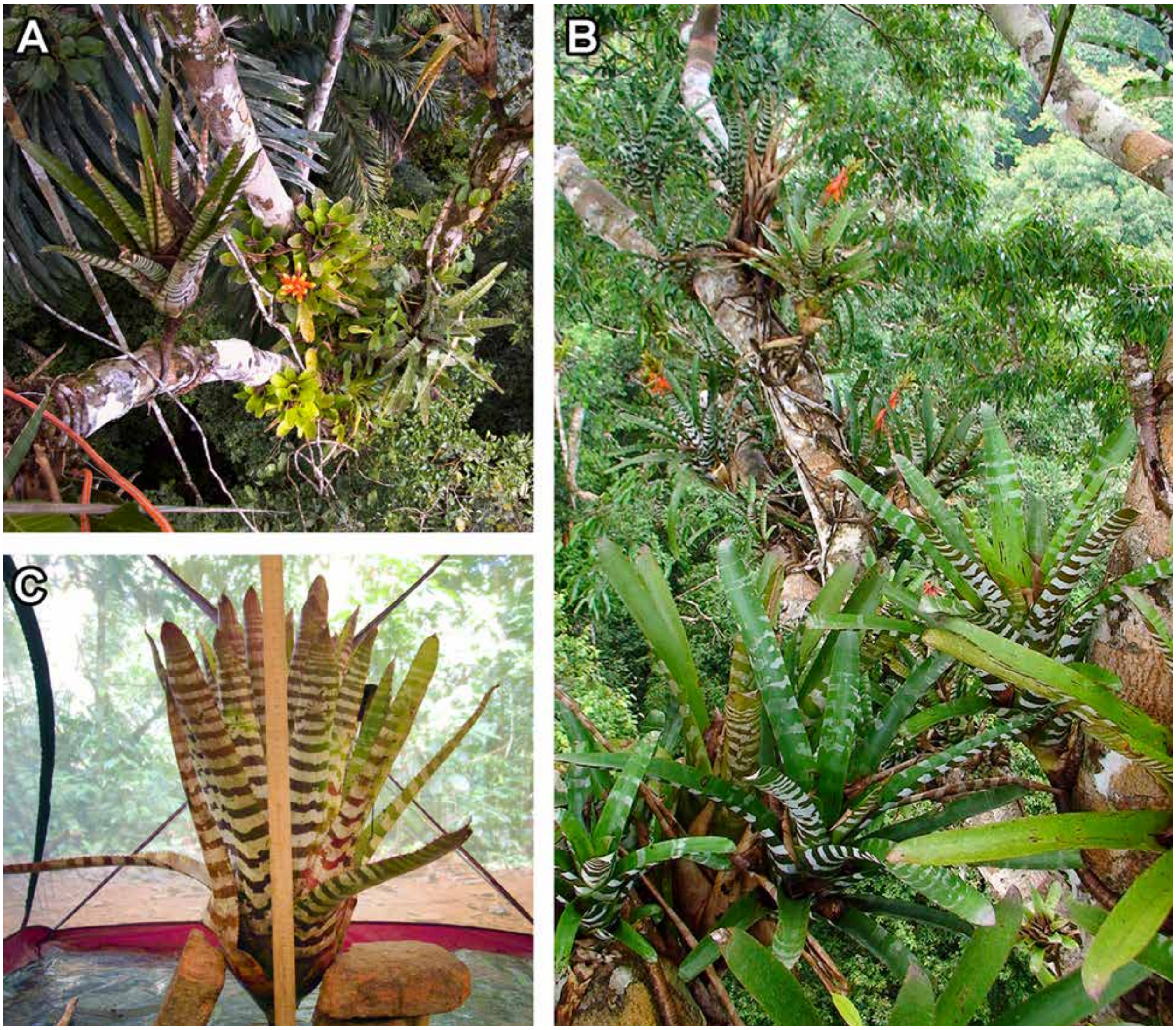


Fig. 2. (A) A downward vertical view (*in situ*) of *Aechmea zebrina* (foreground center left, and at lower elevation in upper right and center right) and a cluster of *Aechmea tessmannii* (center, with one in bloom) bromeliads in the tree canopy from ~34 m. (B) A community of *A. zebrina* bromeliads at ~38 m (*in situ*). (C) An *A. zebrina* bromeliad (*ex situ*) inside screen tent being measured and prepared for dismantling, collected from ~44 m in the canopy. Notice the more upright leaves and reddish color because of increased sun exposure due to high canopy location.

mental factors associated with herpetofauna in *A. zebrina* bromeliads. We estimate the density of anurans occupying mean *A. zebrina* community sizes in two tree size classes, representative of our shortest and tallest trees in the study. We then compared these with anuran densities from tropical forest floor anuran studies by calculating the two-dimensional area (m^2) of the tree crowns for the two tree size classes. In completing our review, we feel it is important to discuss the use of the term "arboreal" within the herpetological literature and make recommendations for the incorporation of additional terminology to provide a more informative description of the vertical space utilized by a species or assemblage.

Materials and Methods

The study was conducted in the northwestern portion of the Yasuní Biosphere Reserve (Yasuní) located in Orellana Province, Ecuador. The reserve includes Yasuní National Park, Waorani Ethnic Reserve, and their respective buffer and transition zones (Finer et al. 2009). Yasuní is part of the Napo Moist Forest terrestrial ecoregion covering approximately 1.7 million ha of the upper Amazon Basin (Finer et al. 2009; Bass et al. 2010). Yasuní has an elevation range of 190–400 m above sea level; the northwestern region averages 2,425–3,145 mm of rainfall per year with no less than 100 mm per month, temperature averages 25 °C (15 °–38 °C), and humidity averages 88% (Blandin 1976; Duellman 1978; Balslev et al. 1987; Bass et al. 2010). Yasuní holds world record species diversity for several taxa, including the highest documented landscape scale (lowland tropical rainforest) herpetofauna diversity with 150 species of amphibians and 121 species of reptiles (Bass et al. 2010). Collections were made in the vicinity of two research stations, the Tiputini Biodiversity Station (TBS) (0°38'14"S, 76°08'60"W) operated by

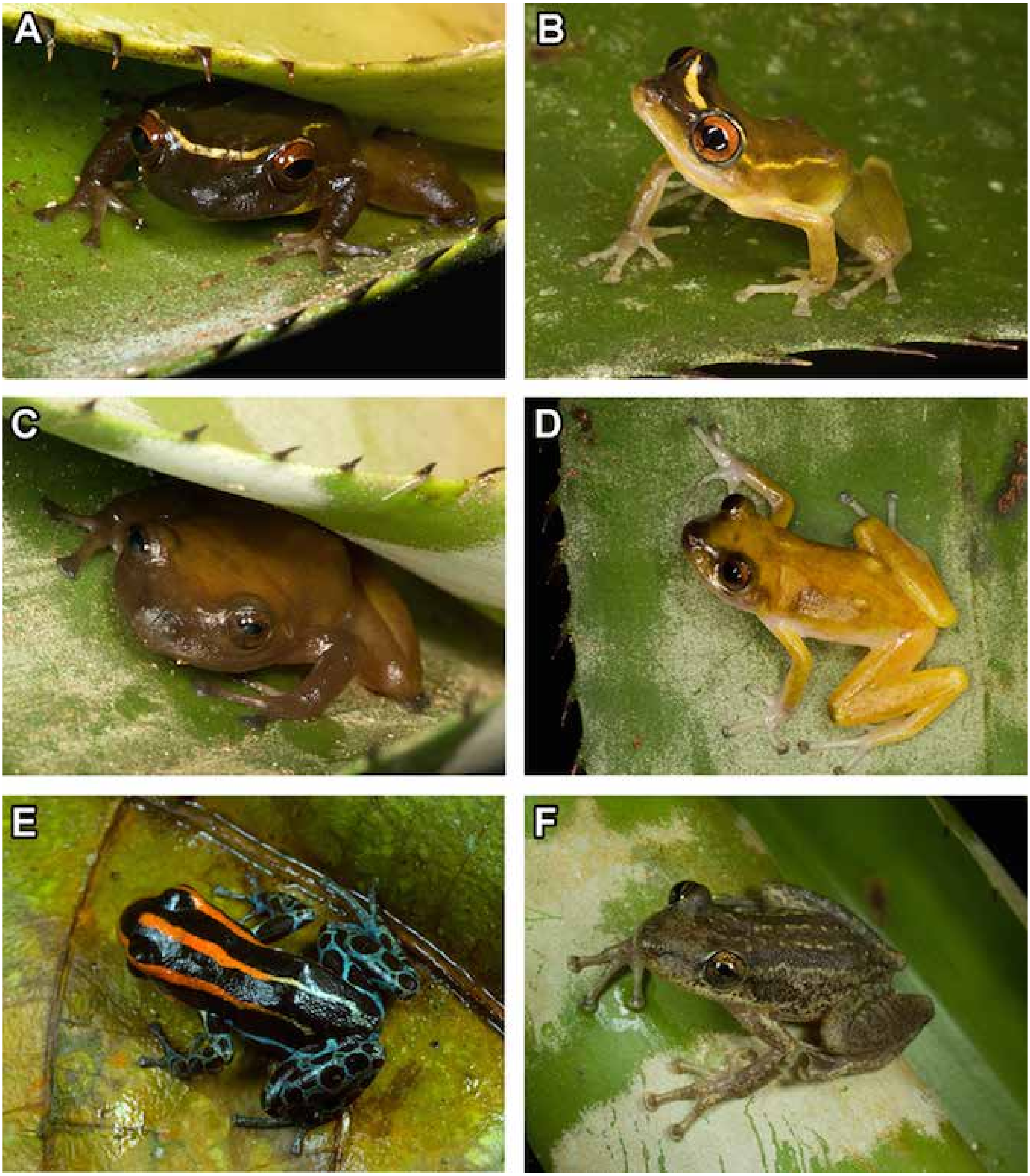


Fig. 3. A collection of anurans collected from *Aechmea zebrina* bromeliads. (A) *Pristimantis aureolineatus* hiding in leaf axil, and (B) on a leaf of *A. zebrina*. (C) *Pristimantis waoranii* emerging from leaf axil, and (D) on a leaf of *A. zebrina*. (E) *Ranitomeya ventrimaculata* and (F) *Scinax ruber* collected from *A. zebrina* bromeliads.

the Universidad San Francisco de Quito and the Yasuní Research Station (YRS) (0°40'27"S, 76°23'51"W) operated by the Pontificia Universidad Católica del Ecuador (Fig. 1). Tiputini Biodiversity Station is only accessible by river and surrounded by undisturbed primary lowland rainforest, and YRS is located approximately 27 km west on an oil pipeline road (Maxus road) that has been experiencing forest disturbance within its vicinity but is still surrounded by large tracts of undisturbed forest. Sampling of *A. zebrina* bromeliads took place between 0800 and 1800 hours from April to November of 2008.

We focused our sampling on a single large epiphytic tank bromeliad species, *Aechmea zebrina*, that is native to the Amazon regions of Ecuador and southeastern Colombia (Smith 1953). *Aechmea zebrina* occupy vertical heights of approximately 18–45+ m in the overstory and emergent canopy trees, and range between 1 to >150 individuals on a single host tree (SFM, unpublished data). The leaves are upright and arranged in a spiral with their leaf axils tightly overlapping to form water-holding reservoirs (Fig. 2). These cavities provide a critical refuge and food source for invertebrate and vertebrate species in the harsh canopy climate (Nadkarni 1994).

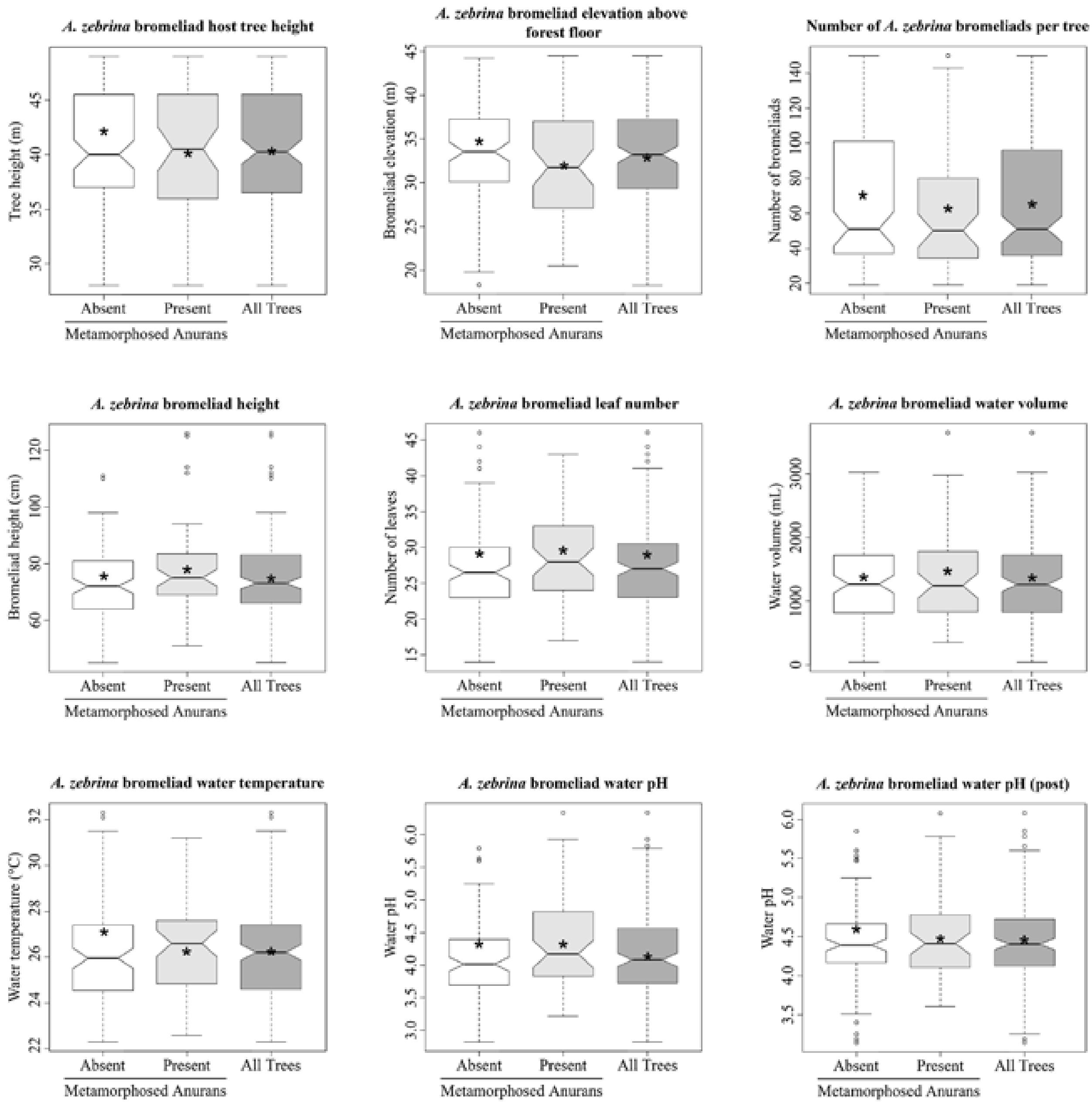
Sampling methodology for *A. zebrina* bromeliads followed our previously published methods (McCracken and Forstner 2008). Single-rope technique (SRT) was used to climb trees for canopy access, and five bromeliads were collected haphazardly from each tree at estimated even vertical intervals between one another (Perry 1978). Before each bromeliad removal, we checked for active amphibians or reptiles, we recorded the bromeliads elevation, measured the air temperature adjacent to the bromeliad, and the temperature and pH of water held in one of the outer leaf axils. Ideally, when the bromeliad is disturbed the response of most animals is a retreat into the bromeliads leaf bracts and thus prevents loss of specimens (McCracken and Forstner 2008). Bromeliads were removed and sealed in a 55-gallon (208 L) plastic bag and then lowered to the ground. After bromeliad collections we counted the number of *A. zebrina* inhabiting the tree and measured tree height. Bromeliads were transported back to camp where we processed them in a screened tent to prevent escape of animals. We first poured all water from the bromeliads through a 1 mm sieve to separate arthropods, leaf litter, and detritus. We then measured the water volume with a graduated cylinder and the pH of the homogenized solution. We counted the number of mature leaves (used as a size metric) and measured the height of bromeliads to nearest centimeter (from base of plant to highest vertical leaf tip). Bromeliads were then dismantled leaf-by-leaf to collect all herpetofauna.

We identified and counted all metamorphosed anurans and reptiles to species level for each bromeliad. Larval anurans were also collected and counted, with the majority identified to genus or species. In an attempt to better identify larval anurans we maintained individual tadpoles outdoors in 12 oz. plastic cups with water and detritus collected from bromeliads. Once tadpoles began to metamorphose the cups were covered with window screen to prevent escape. Upon sufficient development to allow identification the froglets were euthanized and preserved. All herpetofauna were handled and preserved following the guidelines compiled by the American Society of Ichthyologists and Herpetologists (ASIH), and in compliance to the rules overseen by the Texas State University Animal Care and Use Committee (Permit #: 0721-0530-7, 05-05C38ADFDB, and 06-01C694AF). Additionally, we report the herpetofauna species observed active amongst *A. zebrina* bromeliads but not collected. We calculated summary statistics of recorded habitat variables for each species and report raw data for

Fig. 4. The Banded cat-eyed snake, *Leptodeira annulata*, collected in an *Aechmea zebrina* bromeliad at 43.5 m above the forest floor.

singletons and doubletons. Summary statistics were calculated for recorded habitat variables across all bromeliads sampled, bromeliads occupied by ≥1 metamorphosed anurans, and bromeliads not occupied by anurans.

We then compared an estimated number of anuran individuals in *A. zebrina* bromeliads per 100 m^2 of tree crown area to other published work of tropical frog assemblages collected at or near ground level. No other studies were available to provide canopy estimates. Mean anuran abundance per tree was calculated by taking the mean number of metamorphosed anurans per *A. zebrina* bromeliad ($\overline{x} = 0.6$) and multiplying by the mean number of bromeliads per tree ($\overline{x} = 66$). Based on tree crown diameter measurements by Asner et al. (2002) in lowland rainforest of eastern Amazonia we calculated the number of anurans per 100 m^2 of a typical tree crown area for the two largest tree size classes. The two largest classes had mean tree heights of 25.3 m (Dominant) and 46.1 m (Super dominant) with a mean crown diameter of 11.6 m and 19.9 m, respectively. Mean tree crown diameters were used to calculate the area of a circle. These two tree size classes were used as we did not measure individual crown diameters and consider these two as representative of the shortest (28 m) and tallest (49 m) trees in our study. We then divided the mean number of anurans per tree



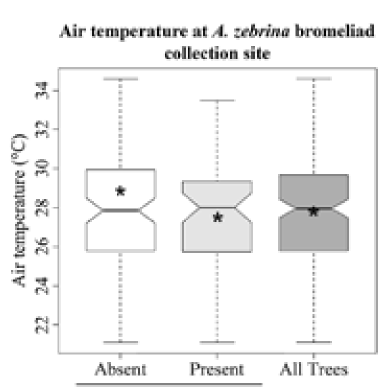


Fig. 5. Box plots of recorded habitat variables for *Aechmea zebrina* bromeliads collected from all trees, bromeliads with ≥1 metamorphosed anuran, and bromeliads absent of anurans. Asterisks represent the mean, open circles are outliers, horizontal line inside box is the median, top and bottom lines of the rectangle are the 3rd and 1st quartiles (Q3 and Q1), respectively, and the top and bottom whiskers are maximum and minimum values excluding outliers, respectfully.

in our study by the tree size class crown area calculated from Asner et al. (2002) and multiplied by 100 to generate an estimated density of individuals per 100 m^2.

All calculations and statistics based on counts of metamorphosed anurans collected (not larval anurans) and conducted in the R statistical software (version 3.0.1) (R Development Core Team 2013).

Results

We sampled five bromeliads from each of 32 trees for a total of 160 *A. zebrina* bromeliads sampled. We collected 10 metamorphosed anuran species (Fig. 3), one gecko, one snake (Fig. 4), and two species of lizard were observed amongst bromeliad leaves but not collected (Table 1). A total of 95 metamorphosed anurans ($\bar{x}$ = 0.6 per bromeliad) were collected from 56 of the 160 bromeliads (35%) sampled. Between one and five individuals ($\bar{x}$ = 1.7), and up to two species were observed in single *A. zebrina* bromeliads occupied by metamorphosed anurans. The species found together include (number of bromeliads with species together): *Pristimantis aureolineatus* and *P. waoranii* (7), *P. waoranii* and *P. acuminatus* (1), *P. waoranii* and *P. orphnolaimus* (1), *P. aureolineatus* and *Ranitomeya ventrimaculata* (1). We also collected a minimum of four larval amphibian species from the water-filled leaf axils of *A. zebrina* bromeliads including *Osteocephalus fuscifacies*, *O. planiceps*, *Ranitomeya variabilis*, and *R. ventrimaculatus*. A total of 271 larval anurans were collected from 35 of the 160 bromeliads (21.9%) sampled, with 14 of the 35 larval occupied bromeliads (40%) also occupied by ≥1 metamorphosed anurans. *Osteocephalus* spp. tadpoles account for 60.5% (*n* = 164) of confirmed species identifications for all larval anurans, and these were collected from five bromeliads. A single *O. fuscifacies* and a single *O. planiceps* (both adults) were each found in separate bromeliads with larvae of same species (identified after rearing). The gecko, *Thecadactylus solimoensis* (formerly *T. rapicauda*), was found in an *A. zebrina* bromeliad amongst the outer leaf axils at 31.5 m above the forest floor in a tree 46.0 m tall (Bergmann and Russell 2007). The Banded cat-eyed snake, *Leptodeira annulata*, was found in a central leaf axil of an *A. zebrina* bromeliad at 43.5 m above the forest floor in a tree 45.5 m tall (Fig. 4). *Anolis transversalis* was observed twice amongst the leaves of *A. zebrina* bromeliads during collections; once on a bromeliad at ~27 m above the forest floor (36 m tall tree) and in another tree at ~35 m above the forest floor (41 m tall tree). A single male *Anolis ortonii* was observed displaying his dewlap on an outer leaf of an *A. zebrina* bromeliad at ~20 m above the forest floor in a tree 28 m tall. Summary statistics for all species reported in Table 1.

Trees sampled for *A. zebrina* bromeliads were 28 to 49 m in height ($\bar{x}$ = 40.4 m ± 5.5, *n* = 32), and 28 to 49 m in height ($\bar{x}$ = 40.2 m ± 5.8, *n* = 27) for trees with ≥1 bromeliad occupied by metamorphosed anurans. *Aechmea zebrina* bromeliads were collected at above ground elevations of 18.3 to 44.5 m ($\bar{x}$ = 32.9 m ± 5.6, *n* = 160), and bromeliads occupied by ≥1 metamorphosed anurans occurred at elevations of 20.5 to 44.5 m ($\bar{x}$ = 32.1 m ± 6.3, *n* = 56). The number of *A. zebrina* bromeliads per host tree was 19 to 150 individuals ($\bar{x}$ = 66 ± 40, *n* = 32), and 19 to 150 individuals ($\bar{x}$ = 63 ± 38, n = 27) for trees with ≥1 bromeliads occupied by metamorphosed anurans. *Aechmea zebrina* bromeliads were 45 to 126 cm in height ($\bar{x}$ = 75 ± 14, *n* = 160), and 51 to 125 cm in height ($\bar{x}$ = 78 ± 15, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. The number of mature leaves per *A. zebrina* was 14 to 46 ($\bar{x}$ = 28 ± 6, *n* = 160), and 17 to 43 ($\bar{x}$ = 29 ± 6, *n* = 56) for bromeliads occupied

Table 1. Amphibians and reptiles collected or observed within *Aechmea zebrina* bromeliads. For each species the number observed, height range (bromeliad in tree), and mean height are provided. Only metamorphed anurans at time of collection included.

Species	Number observed	Height range (m)	Mean height (m)
Osteocephalus fuscifacies	3	24.3-28.1	25.6
Osteocephalus planiceps	1	31.5	–
Osteocephalus taurinus	1	30.6	–
Pristimantis acuminatus	1	40.4	–
Pristimantis aureolineatus	36	22-44.5	35.7
Pristimantis orphnolaimus	2	31.5-38.3	34.9
Pristimantis waoranii	35	21.2-43.9	31.9
Ranitomeya ventrimaculata	1	36.5	–
Ranitomeya variabilis	9	25.7-35.2	30.9
Scinax ruber	6	33.8-35	34.8
Anolis ortonii	1	20	–
Anolis transversalis	2	27-35	31
Thecadactylus solimoensis	1	31.5	–
Leptodeira annulata	1	43.5	–

by ≥1 metamorphosed anurans. The water volume of *A. zebrina* bromeliads was 42 to 3645 mL ($\bar{x}$ = 1343 ± 656, *n* = 160), and 355 to 3645 mL ($\bar{x}$ = 1428 ± 726, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. Water temperature within an outer leaf axil of *A. zebrina* bromeliads at time of collection was 22.3 to 32.3 °C ($\bar{x}$ = 26.2 ± 2.1, *n* = 160), and 22.6 to 31.2 °C ($\bar{x}$ = 26.2 ± 1.9, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. Water pH within an outer leaf axil of *A. zebrina* bromeliads at time of collection was 2.82 to 6.34 ($\bar{x}$ = 4.18 ± 0.66, *n* = 160), and 3.22 to 6.34 ($\bar{x}$ = 4.34 ± 0.73, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. Water pH of sieved homogenized water for each *A. zebrina* bromeliad was 3.14 to 6.08 ($\bar{x}$ = 4.44 ± 0.53, *n* = 160), and 3.60 to 6.08 ($\bar{x}$ = 4.48 ± 0.55, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. Air temperature adjacent to bromeliads at time of collection was 21.1 to 34.6 °C ($\bar{x}$ = 27.8 ± 2.8, *n* = 160), and 21.1 to 33.5 °C ($\bar{x}$ = 27.6 ± 2.7, *n* = 56) for bromeliads occupied by ≥1 metamorphosed anurans. Summary statistics for bromeliads absent of anurans are contrasted with those given above in Fig. 5.

By taking the mean number of metamorphosed anurans per bromeliad ($\bar{x}$ = 0.6) and multiplying by the mean number of *A. zebrina* bromeliads per tree ($\bar{x}$ = 66), we calculated an estimated mean of 39.6 metamorphosed anurans occupying the *A. zebrina* bromeliads of an average tree in our study. The Dominant class tree crown area from Asner et al. (2002) was 105.7 m^2 (25.3 m tall) with a calculated 37.5 anurans per 100 m^2, and the Super dominant class tree crown area was 311 m^2 (46.1 m tall) with a calculated 12.7 anurans per 100 m^2.

Discussion

Our study identified 14 species of herpetofauna (10 anurans and four reptiles) utilizing the tank bromeliad *Aechmea zebrina* as habitat in the high canopy environment of the northwestern Amazon Basin. A range of 1–5 metamorphosed anurans per bromeliad, with up to two species occupying a single bromeliad, were detected in over one-third of the bromeliads sampled. The observation of larval, metamorphs, and adults of *Osteocephalus fuscifacies* confirm that this species is a phytotelm breeder as proposed by Jungfer et al. (2013). The observation of larval, metamorphs, and an adult *Ranitomeya ventrimaculata* confirm that this species does deposit tadpoles in high canopy bromeliads as proposed by Brown et al. (2011). Our detection of the gecko *Thecadactylus solimoensis* at 31.5 m vertical height within the leaf axil of an *A. zebrina* bromeliad confirms this species use of bromeliads in the high canopy (Vitt and Zani 1997; Bergmann and Russell 2007). Our observation of the snake *Leptodeira annulata* within the leaf axils of an *A. zebrina* bromeliad at 43.5 m in the canopy is the highest recorded vertical height to our knowledge; *L. annulata* is described as terrestrial to semi-arboreal with a previous maximum observed vertical height of 6 m above ground (Duellman 1978; Vitt 1996; Kacoliris 2006; Ávila and Morais 2007).

In McCracken and Forstner (2014) we analyzed the habitat data for differences among forest disturbance treatments and found no differences in habitat variables between treatments and no relationships between habitat variables and anuran occupancy or abundance. Also, we found differences between forest disturbance treatments for anuran abundance and occupancy; but report the summary statistics of the habitat data here as a resource characterizing the habitat occupied by canopy tank bromeliad dwelling herpetofauna. Of particular interest in this study was the mildly acidic mean water pH (4.18 in situ in leaf axils, 4.34 in sieved homogenized water) in *A. zebrina* bromeliads; as this is within the range reported to affect development of embryonic and larval anurans (Beattie and Tyler-Jones 1992). However, bromeliads are a known breeding site for amphibians and we observed an abundance of aquatic invertebrates and larval anurans in our collections (Benzing 2000).

Using the two largest tree size classes of Amazonian trees from Asner et al. (2002) as representative crown area for the shortest (28 m) and tallest (49 m) trees in our study, we calculated an estimate of 12.7–37.5 anurans per 100 m^2 of crown area for an average tree in our study. We consider this estimated range of canopy anuran density to be conservative because 1) the height of trees for the tree size classes used from Asner et al. (2002) are shorter than our shortest and tallest trees; 2) it is calculated on the two-dimensional space of the tree crown and does not include the vertical space occupied by a tree; 3) anurans were only collected from *A. zebrina* bromeliads and not other available habitat; and 4) the mean anuran abundance per tree in our study was used for calculations of both tree size classes, not accounting for the range of tree heights and number of bromeliads per tree. Regardless of these constraints, the estimated high anuran density of 37.5 anurans/100 m^2 is the greatest of any reported density for tropical frog assemblages from comparable studies (e.g., 36.1 anurans/100 m2 at La Selva, Costa Rica [Lieberman 1986]; 15.5 anurans/100 m^2 at Rio Llullapichis, Peru [Toft 1980]; see also Allmon 1991 and Rocha et al. 2007 for compiled sites comparison). The low estimate of 12.7 anurans/100 m^2 is still amongst the highest densities of reported studies, particularly in South America (Allmon 1991; Rocha et al. 2007). A limitation of this comparison is that these studies rely on the method of quadrat surveys for density calculations, where the majority of observed anurans are going to be leaf-litter inhabitants or those that are within arms reach (~2 m vertical height). Achieving a more accurate canopy anuran density will require research sampling all available canopy microhabitats and recording crown measurements for all sampled trees.

Within the herpetological community the use of the term “arboreal” has deviated from its recognized definition of "inhabiting or frequenting trees" and taken on a broader meaning in reference to vertical habitat use by amphibians and reptiles to simply mean living above ground level (Merriam-Webster.com. 2014. Merriam-Webster Dictionary. Available from http://www.merriam-webster.com [Accessed 27 April 2014]). While this definition suffices to distinguish these species (arboreal) from those occupying fossorial and ground level habitat, it does not adequately clarify the above ground vertical space utilized by a particular species. As an example, Doan (2003) reports the visual encounter survey (VES) method as the best way to sample for arboreal herpetofauna in rainforests. The VES method only allows the researcher access to habitat within arms reach (~2 m vertical height) and fails entirely at observing animals within the other ~40+ m of vertical habitat above in many rainforests. Arboreal herpetofauna may occur at vertical heights between >0 m to 88 m on vegetation and/or trees; simply referring to a species as arboreal provides no information about its occupied vertical range (Spickler et al. 2006). To alleviate confusion and accurately represent the vertical space occupied by a species or assemblage we propose two alternatives to be used separately or preferably together. First, basic descriptors delineating vertical zones for a defined forest type could be used to accompany "arboreal" (e.g., "arboreal within the understory" where "understory" has been defined as "near-ground nondominant vegetation") (Dial et al. 2004). Second, authors should specify vertical height ranges when describing or discussing "arboreal" anurans (e.g., "the arboreal frog *Pristimantis waoranii* is found in the overstory at 20.5–44 m" where "overstory" has been defined as "high, dominant foliage") (Dial et al. 2004). Providing vertical range data or descriptions is critical to understanding the many aspects of natural history for a species.

Conclusion

The canopy of tropical forests are among the most species-rich terrestrial habitats on Earth, yet remain a relatively unexplored biotic frontier (Basset et al. 2003; Lowman and Schowalter 2012). Our research has shown the tank bromeliad *Aechmea zebrina* to support a diverse and abundant herpetofauna community in the harsh equatorial tree canopy environment of the Yasuní Biosphere Reserve in the Amazon Basin of Ecuador. Additionally, our canopy work has contributed to the description of two new species of bromeliad-inhabiting anurans (*Pristimantis aureolineatus* [Guayasamin et al. 2006] and *P. waoranii* [McCracken et al. 2007]), the detection of *Batrachochytrium dendrobatidis* (Chytrid fungus) on anurans from the forest floor to the canopy in Amazonia (McCracken et al. 2009), and identified the use of high canopy bromeliads by the anuran *Scinax ruber* (McCracken and Forstner 2014). While canopy surveys of tank bromeliads are labor intensive, they provide a very effective technique for collecting data on canopy inhabiting organisms and associated microhabitat factors.

Our estimates of canopy anuran densities, based on collections from a single species of bromeliad, demonstrate the potential ecological importance and current lack of knowledge on the canopy herpetofauna component in tropical systems. Typical inventories of herpetofauna in tropical forests are conducted at ground level (~2 m vertical height stratum) where microclimatic variables are more stable (Guayasamin et al. 2006). Sampling such shallow strata within the strongly vertical structure of these forests has likely served to bias metrics of herpetofauna assemblages by focusing on a narrow environmental space and neglecting the large available habitat above into the canopy (Guayasamin et al. 2006; Scheffers et al. 2014). Future inventory studies should routinely include canopy surveys to properly represent the herpetofauna of forested habitat.

Use of the term "arboreal" in the herpetofauna literature does not adequately define the vertical range of a species or assemblage. This serves to limit compilation and synthesis from the literature for the ecology of many of these tropical reptiles and amphibians. Our proposed amendments to accompany the description of arboreality in herpetofauna functionally serve to give scale and provide a better understanding of the vertical habitat utilized by a species or assemblage. As research on canopy herpetofauna continues to expand, knowledge of the vertical space occupied will be essential to answering hypothesis-driven research questions and enacting sufficient conservation measures to protect all species.

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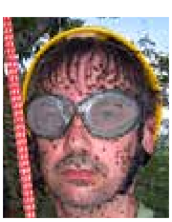

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