

## LOW ABUNDANCE AND DIVERSITY OF CANOPY AMPHIBIANS IN AN ANDEAN CHOCO FOREST OF ECUADOR

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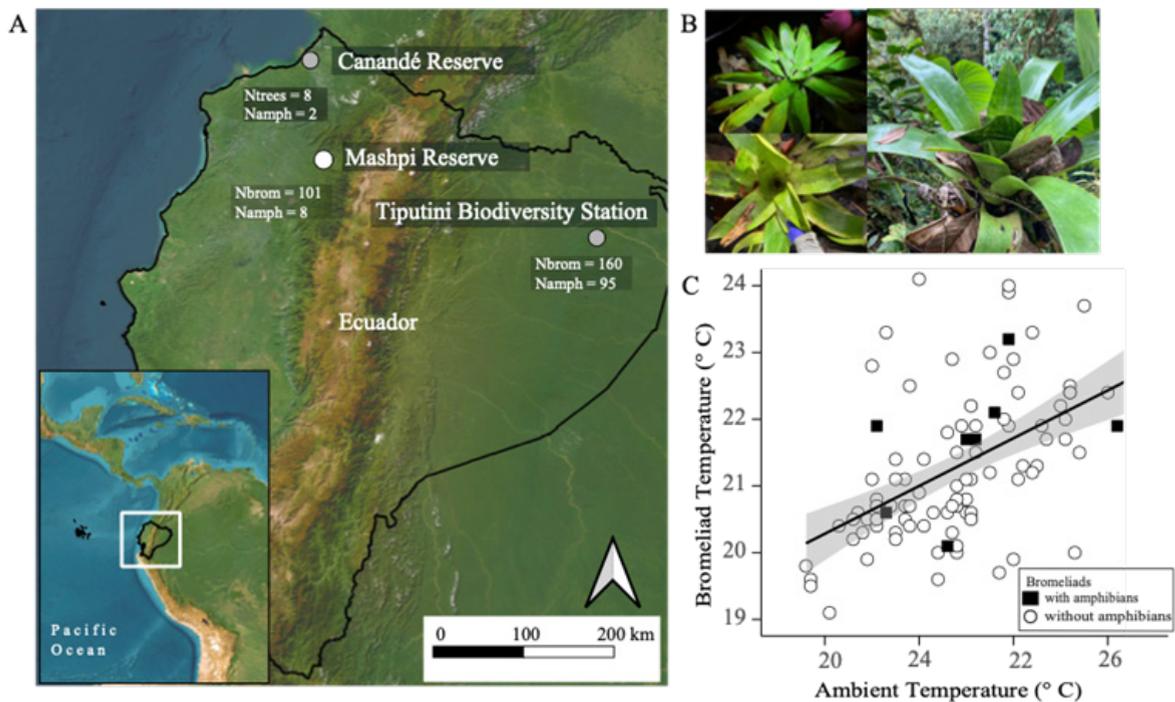
**Abstract.**—The Andes Mountain range, home to the Tropical Andes biodiversity hotspot, harbors extraordinary amphibian diversity, particularly in Ecuador. Despite significant threats such as habitat destruction, infectious diseases, and climate change, the region remains underexplored, especially its canopy fauna. We investigated the amphibian community inhabiting canopy bromeliads in Mashpi Reserve, an ecological preserve located in the Andean Choco bioregion of Ecuador (about 900 m elevation). We employed single rope-climbing techniques to systematically survey 101 bromeliads from 20 trees at heights ranging from 16.3 to 35.6 m. We found amphibians in only 7.9% of bromeliads: two adult Salidero Robber Frogs (*Pristimantis subsigillatus*), five juvenile *Pristimantis* sp., and one clutch of eight *Pristimantis* sp. eggs between 20.0 and 33.1 m above ground. We measured bromeliad morphology (height, width, and width of the base) and environmental conditions at the time of collection (pH and temperature of the water inside the bromeliads, and ambient temperature). None of the environmental variables significantly predicted amphibian presence in bromeliads. The low amphibian abundance and diversity observed in the canopy of Mashpi Reserve contrasts with findings from the lowland Amazon of Ecuador, suggesting that the relatively constant subcanopy humidity and water availability at Mashpi may help explain the lesser use of bromeliads as amphibian refuges. Our findings highlight the need for more surveys of canopy-dwelling amphibian communities across elevations, forest types, and seasons, as canopy occupancy appears highly variable between locations.

**Key Words.**—canopy ecology; herpetofauna; natural reserve; tropical Andes; tropical forests

### INTRODUCTION

The Andes Mountain range spans seven South American countries and hosts the Tropical Andes biodiversity hotspot, identified as the most species-rich place on Earth (Myers et al. 2000). This area boasts twice the amphibian diversity compared to the entire Amazonian lowland rain forest (Hyatt et al. 2007; Hutter et al. 2017), with approximately 70% (about 1,120) of its species considered endemic (Zador et al. 2015). Simultaneously, the Andes is home to one of the greatest concentrations of threatened amphibian species (Luedtke et al. 2023), many of which are found in Ecuador, a country that is longitudinally bisected by the Andes mountains. Of 679 amphibian species that are known to occur

in Ecuador (Frost 2024), 22.9% are considered Threatened, 13.2% are Critically Endangered, and 3.9% are Data Deficient (Ortega-Andrade et al. 2021). The most significant threats to Ecuadorian amphibian diversity are habitat destruction, habitat fragmentation, infectious diseases, and climate change (Ortega-Andrade et al. 2021; Luedtke et al. 2023). Amphibian species inhabiting montane forests and paramo ecosystems are particularly threatened, and nearly 10% of amphibians inhabiting those ecosystems are not legally protected and lie outside of the Ecuadorian System of Protected Areas (Ortega-Andrade et al. 2021). Because governmental resource constraints are often a significant barrier to the protection of threatened amphibian populations,



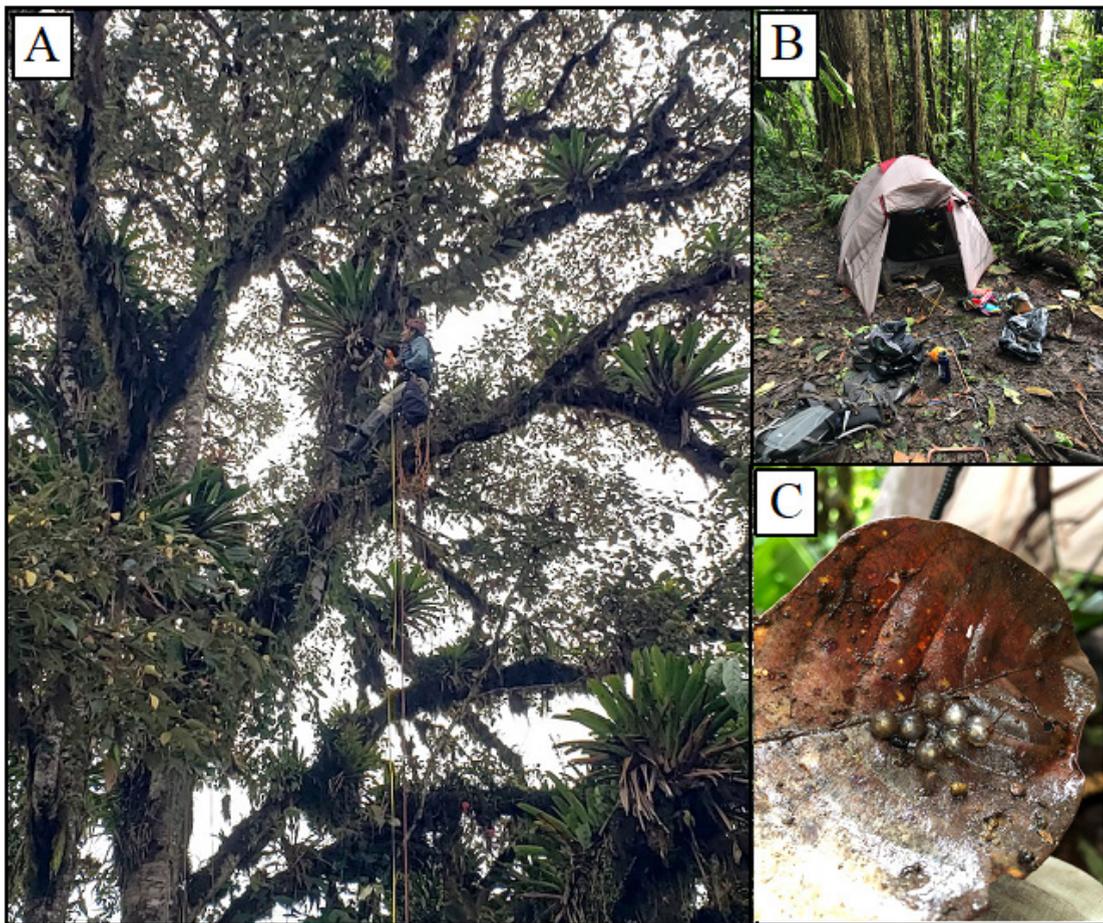
**FIGURE 1.** (A) Locations of the three herpetofauna canopy explorations in Ecuador to date: Mashpi Reserve (this study), Fundación Jocotoco’s Canandé Reserve (Thomas et al. 2023), and Tiputini Biodiversity Station (McCracken and Forstner 2008). Nbrom represents the number of bromeliads sampled, Ntree represents the number of trees explored, and Namph represents the number of anurans found, including juveniles and adults, in the canopy of each sampling site. An egg clutch was considered as one anuran at Mashpi Reserve. (B) Example bromeliads (*Guzmania* spp.) in the canopy of Mashpi Reserve, Ecuador. (C) Relationship between ambient air temperature and interior bromeliad water temperature, and presence/absence of anurans, for 101 bromeliads in the canopy of Mashpi Reserve, Ecuador. The solid line represents a Linear Regression model, indicating a significant positive relationship between the two variables. The gray band represents the 95% confidence interval of the regression. (Photographs in B by Moises Tenorio).

non-governmental nature reserves can play an important role in safeguarding existing diversity (Guayasamin et al. 2022).

Mashpi Reserve (0°9′50.98″N, 78°52′46.07″W) is one such private ecological preserve located in the Andean Choco bioregion at 500–1,200 m elevation and comprises a total of 2,900 ha (Fig. 1). This reserve was established in 2001 and is currently composed of about 70% primary forest, about 25% secondary forest, and about 5% ongoing natural forest regeneration (Salazar et al. 2023). The main threats to most amphibians inhabiting the Mashpi Reserve include adjacent habitat loss, chemical contamination from peripheral agriculture activities, mining operations, and cattle ranching (Guayasamin et al. 2022). In 2022, Guayasamin et al. (2022) recorded 21 amphibian species from the reserve, six of which are considered endemic to the Tropical Andes.

Most herpetological inventories are typically conducted at ground level, based on opportunistic and visual encounters (Cruz-García et al. 2023; Coloma and Duellman 2025), which inevitably biases data

toward ground-dwelling taxa (<2 m above the ground; Basham et al. 2023). Considering that the canopy and understory differ in resource availability and abiotic conditions (Yanoviak and Kaspari 2000), some amphibians may use canopy habitats as an alternative or complementary spaces within the forest (Basham et al. 2023). These vertical ecosystems remain severely understudied, however, despite growing evidence of their ecological importance and potential to support a variety of amphibian species (Basham et al. 2023). For instance, tropical epiphytes, such as bromeliads, are abundant throughout the canopy and are known to provide habitat for multiple frog species (Guayasamin et al. 2006; McCracken and Forstner 2014; Basham et al. 2019). Canopy bromeliads help buffer the effects of harsh environmental conditions by maintaining stable microclimates (McCracken et al. 2007; Basham et al. 2019) and can act as physical barriers to terrestrial predators (McKeon and Summers 2013). Nonetheless, vertical stratification of amphibians remains poorly understood (Guayasamin et al. 2006; Basham et al. 2023).



**FIGURE 2.** Canopy sampling in Mashpi Reserve, Ecuador. (A) Climber next to a bromeliad using single rope-climbing techniques. (B) Screen tent used to process bromeliads. (C) *Pristimantis* sp. eggs found between leaves of a bromeliad at 26 m above ground. (A photographed by Moises Tenorio, B by Mar Moretta-Urdiales, and C by Francisco Velasquez-Espin).

In Ecuador, two studies have explored amphibian diversity patterns in forest canopies. The first study was conducted in the lowlands of the Amazon region at Tiputini Biodiversity Station ( $0^{\circ}38'15.1''\text{S}$ ,  $76^{\circ}08'58.6''\text{W}$ ; about 250 m elevation; Fig. 1) by McCracken and Forstner (2014), and the second and most recent study was conducted in the coastal forests of Ecuador at Fundación Jocotoco's Canandé Reserve ( $0^{\circ}31'08.0''\text{N}$ ,  $79^{\circ}12'55.0''\text{W}$ ; about 300 m elevation; Fig. 1) by Thomas et al. (2023). Although these were seminal studies, more thorough and systematic surveys of amphibian diversity in forest canopy habitats are still needed, especially at higher elevations. Here, we determined the occurrence of amphibians in bromeliads from the forest canopy of Mashpi Reserve through systematic surveys and we assessed if their presence was associated with bromeliad distance to the ground, bromeliad morphology, ambient temperature, and the pH and

temperature of bromeliad water.

#### MATERIALS AND METHODS

We employed single rope-climbing techniques, following the methodology of McCracken and Forstner (2008) to survey canopy amphibians in Mashpi Reserve (Fig. 2). This technique involves accessing the forest canopy using a single-rope ascent system, allowing researchers to reach and sample microhabitats at varying heights. We used a slingshot to position a leader line in the trees, allowing the climber to ascend with specialized harnesses and mechanical knee and foot ascenders. Once we reached the canopy, we removed bromeliads by cutting the base support stem using a retractable saw while preventing specimen escape. We then placed bromeliads in industrial 189 L (50-gallon) plastic bags and lowered them to the ground with

a rope through a carabiner on the harness of the climber. We categorized amphibians as adults or juveniles based on their estimated snout-vent length (SVL), using published size ranges for the Salidero Robber Frog (*Pristimantis subsigillatus*; Coloma and Duellman 2025).

We conducted sampling during the daytime between 0945 and 1700 for 15 d in June 2022, which corresponds to the dry season in this region. Each sampling crew consisted of two climbers and one ground technician. We selected 20 trees based on accessibility and presence of bromeliads, ensuring a diverse range of canopy heights. We only selected trees if they hosted at least 15 bromeliads of any species to be sampled to ensure continued persistence of the bromeliad community as recommended by McCracken and Forstner (2008). For each tree, we selected five bromeliads by sampling the lowest and highest bromeliads first, then selecting the remaining three at approximately even height intervals between them and prioritizing those large enough to hold water and support amphibian life. We sampled five bromeliads per tree, except for one where we sampled six bromeliads, for a total of 101 sample units. The distance between sampled trees ranged from 42 to 2,377 m.

Before removing each bromeliad, we measured pH and temperature of the water inside the bromeliad using a pH meter (model HI98128; Hanna Instruments, Inc., Woonsocket, Rhode Island, USA) and ambient temperature using the same device. We processed the bromeliads by removing all leaves inside a screen tent to exhaustively catalog any bromeligenous fauna and to prevent underestimation owing to escapes (Fig. 2). We measured the following variables using a long measuring tape (model 34-760; Stanley Black & Decker, New Britain, Connecticut, USA) for each bromeliad: (1) height (m) above ground level; (2) bromeliad height (cm) from the base to the highest standing leaf; (3) bromeliad width (cm) from outer-to-outer leaf; and (4) bromeliad base width (cm). We collected and preserved all vertebrates and invertebrates in 95% ethanol and deposited them at the Museum of Zoology at Universidad San Francisco de Quito (USFQ), along with an herbarium sample from each bromeliad for later identification.

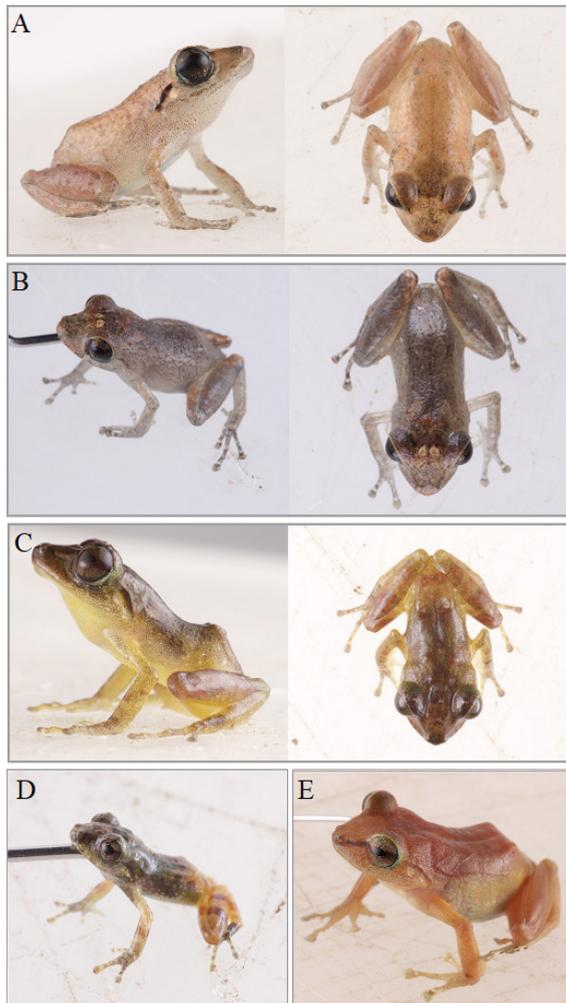
To assess whether all numerical variables were accurate predictors of bromeligenous amphibian presence, we standardized all continuous predictors by centering and scaling (mean = 0, standard deviation = 1) to ensure comparability. We used a Generalized Linear Model (GLM) with a binomial family and a

logit link function, implemented using the *binom* package in R (R Development Core Team 2018). The response variable was binomial: 1 = amphibian presence in the bromeliad or 0 = amphibian absence. Predictors were bromeliad morphological features (height from the ground, bromeliad height, and bromeliad width and base width) and environmental variables (bromeliad water pH, temperature of the water inside the bromeliad, and ambient temperature at the time of collection). To ensure model stability and identify potential multicollinearity, we calculated the Variance Inflation Factor (VIF) for each predictor using the *vif* function from the *car* package in R. We used a VIF threshold of five as a guideline for identifying predictors with moderate to high multicollinearity, but no predictors exceeded this threshold.

We ensured independence by systematically sampling different trees and different bromeliads. Additionally, we assessed overdispersion in the binomial model by calculating the dispersion parameter as the ratio of the residual deviance to the residual degrees of freedom (residual deviance/df = 1.04). Because this value was close to 1, we found no evidence of overdispersion in our data, indicating that the binomial model assumptions were met. To explore the relationship between ambient temperature and bromeliad water temperature, we used a linear model (*lm* function in R). We visually inspected residual plots to assess model assumptions and confirmed that linearity, homoscedasticity, and normality were met.

## RESULTS

We sampled 101 bromeliads at elevations ranging from 760 to 1,295 m elevation, positioned between 16.3 and 35.6 m above ground (mean  $\pm$  standard deviation =  $25.3 \pm 4.1$  m). Although we were unable to identify all bromeliads at the species level, they all belonged to the genus *Guzmania* (Tillandsioideae; Fig. 1). The mean width of the bromeliads was 84.7 cm ( $\pm 32.8$  cm), the mean height was 40.5 cm ( $\pm 27.8$  cm), and the mean width of the base was 8.0 cm ( $\pm 5.6$  cm). The linear regression between ambient temperature and bromeliad water temperature revealed a significant positive association ( $\beta = 0.357$ ,  $F_{1,92} = 33.11$ ,  $P < 0.001$ ), indicating that for an increase of 1° C in ambient temperature, bromeliad temperature increased by approximately 0.357° C (Fig. 1).



**FIGURE 3.** Photographs of anurans collected in the canopy of Mashpi Reserve. (A–C) Two views each (lateral and dorsal) of three different *Pristimantis* sp. juveniles (of five collected), each found in a separate bromeliad. (D) A fourth *Pristimantis* sp. juvenile. (E) One of the two adult Salidero Robber Frogs (*Pristimantis subsigillatus*), each collected from a different bromeliad. (A, C, and D photographed by Amanda Quezada; B and D by Francisco Velasquez-Espin).

We found eight anurans inhabiting the 101 sampled bromeliads (7.9%), each in a separate bromeliad and tree: two *Pristimantis subsigillatus* (family Strabomantidae) adults, five *Pristimantis* sp. juveniles, and one clutch of eight *Pristimantis* sp. eggs between 20.0 and 33.1 m above ground (mean  $\pm$  standard deviation =  $26.0 \pm 4.3$  m; Figs. 2 and 3). The eight bromeliads hosting anurans were all located  $> 20$  m above ground (mean =  $25.07 \pm 3.46$  m; range of values, 20.8–30.9 m). These bromeliads occurred at elevations ranging from 741 to 984 m (mean =  $832.8 \pm 88.1$  m), with a height range of 20.8 to 125 cm (mean =  $45.8 \pm 36.1$  cm), a width range of 58 to 210 cm (mean =  $99.4 \pm 48.1$  cm), and a base width

range of 10 to 20.8 cm (mean =  $12.48 \pm 3.51$  cm). Environmental conditions within these bromeliads varied, with ambient temperature ranging from  $21.3^\circ$  to  $26.2^\circ$  C (mean =  $23.4^\circ \pm 1.3^\circ$  C), bromeliad water temperature from  $20.1^\circ$  to  $23.2^\circ$  C (mean =  $21.6^\circ \pm 1.1^\circ$  C), and water pH from 4.2 to 5.1 (mean =  $4.61 \pm 0.32$ ). No environmental variables significantly predicted amphibian occurrence in the canopy of Mashpi Reserve based on our GLM analysis.

## DISCUSSION

Over 168 Neotropical anuran species from 10 families are known to inhabit bromeliads, with Dendrobatidae and Hylidae being the most abundant (Zocca et al. 2024). Bromeligenous frogs have been found in 18 countries, but among Strabomantidae, only the Canelos Robber Frog (*Pristimantis acuminatus*), Cutín de Banda Dorada (*Pristimantis aureolineatus*), and the Waorani Robber Frog (*Pristimantis waorani*) have been recorded in bromeliads from Ecuador. Notably, *Pristimantis subsigillatus* has not been reported as bromeligenous, despite being the sole species identified in bromeliads within the canopy of Mashpi Reserve in our study.

Our findings indicate a relatively low abundance of bromeliad-dwelling amphibians in the canopy of Mashpi Reserve, particularly when compared to McCracken and Forstner (2014), the only study in Ecuador to investigate amphibian presence using bromeliad-focused sampling techniques. McCracken and Forstner (2014) surveyed 160 bromeliads across 32 trees (five bromeliads per tree, as in our study) in the northwestern portion of the Yasuní Biosphere Reserve (about 250 m elevation), finding 95 metamorphosed anurans, averaging three anurans per tree and 0.6 anurans per bromeliad. In contrast, we found only seven amphibians across 101 bromeliads from 20 trees (0.35 anurans per tree; 0.07 per bromeliad), despite replicating the same bromeliad-focused canopy survey protocol used by McCracken and Forstner.

While Thomas et al. (2023) documented an even lower average (0.25 anurans per tree) in the canopy of Fundación Jocotoco's Canandé Reserve ( $< 500$  m elevation), their methodology relied on visual and acoustic encounter and did not prioritize bromeliads as microhabitat. As a result, their findings may underestimate true amphibian richness and diversity, particularly of bromeligenous or cryptic species that require intensive microhabitat surveys to detect. It is possible that more intensive protocols, such as

those used in our study, could result in different outcomes. This underscores the importance of standardized, habitat-targeted methods for accurately assessing amphibian presence in complex canopy environments.

Given our comprehensive assessment of each bromeliad, our results suggest relatively low amphibian abundance in the canopy of Mashpi Reserve. The lower abundance of amphibians in bromeliads could potentially be a result of the high levels of humidity and constant availability of water in the subcanopy. Throughout the sampling year of 2022, Mashpi Reserve had a mean monthly precipitation of 620.6 mm, with no month experiencing precipitation below 90.9 mm, and monthly average temperatures ranging from 19°–21° C (meteorological data was collected by Mashpi Lodge from January to November 2022). Although amphibian abundance was also low in the coastal lowland forests studied by Thomas et al. (2023), the subcanopy at Mashpi Reserve presents a different set of environmental conditions. The consistently high humidity and abundant water availability throughout the year may provide ample alternative microhabitats in the subcanopy (e.g., moss, leaf litter, or other epiphytes), potentially reducing the reliance on canopy tank bromeliads. In contrast, in drier lowland forests, even modestly humid canopy refuges may hold more ecological importance. For instance, Basham and Scheffers (2020) detected drastic changes in temperature along vertical stratification at the Esteban Alphonso Lee Natural Reserve in central Panama, where thermal variance over 24 h averaged 5° C in the canopy, 3° C in the understory, and 1° C in the soil. These temperature changes may drive amphibians to inhabit a lower, and more stable stratum. In our study, bromeliad water temperature increased significantly with ambient temperature, yet the slope of the relationship was shallow ( $\beta = 0.357$ ), suggesting a low magnitude response of water temperature to changes in ambient temperature. This supports the idea that bromeliads offer some degree of thermal buffering. Because we did not measure diurnal or nocturnal temperature fluctuations, however, we cannot fully assess short-term thermal variability within bromeliads. More stable conditions in the subcanopy could also explain why, in general, there is a unidirectional pattern of abundance of amphibians and mammals across forest layers, with greater abundance found in lower strata (Basham et al. 2023).

We found only one amphibian genus (*Pristimantis*) inhabiting the 101 sampled bromeliads in the canopy of Mashpi Reserve, with all individuals likely being the same species, suggesting a markedly low species richness. In contrast, McCracken and Forstner (2014) documented 10 species and 95 anuran individuals in 160 bromeliads at a lowland site in Yasuni Biosphere Reserve (about 250 m elevation), despite using the same sampling protocol. This apparent difference in diversity seems to contradict the mid-elevation bulge hypothesis (Smith et al. 2007), which proposes that biodiversity peaks at mid-elevations due to a combination of environmental gradients and ecological processes. Although more studies across elevational gradients are needed to fully assess these patterns in Ecuador, the lower species richness observed at Mashpi (about 900 m elevation) provides an interesting counterpoint to the expected trend. Additionally, the arboreality hypothesis by Scheffers et al. (2013) suggests that, as elevation increases, amphibian species may shift upward into arboreal habitats due to favorable microclimatic conditions in the canopy and inhospitable conditions at ground level. Given that only two published studies have investigated amphibian distribution in the canopy of Ecuador (McCracken and Forstner 2014; Thomas et al. 2023), both conducted at low elevations, we cannot rule out the possibility that higher canopy diversity may be present at elevations above 1,000 m.

Furthermore, the low abundance and diversity of amphibians observed in the canopy of Mashpi Reserve could possibly be attributed to the deadly Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*; *Bd*). For example, McCracken et al. (2009) reported 33% of 21 amphibians they captured were infected with the parasitic fungus in the canopy of a lowland Amazonian site in Ecuador. Additionally, Cossel and Lindquist (2009) found *Bd* in five of nine water samples collected from bromeliads in the canopy of Los Quetzales Preserve in Panama (8°52'30.5" N, 82°31'54.0" W). Given that we did not test amphibians found in the canopy during our study for *Bd* infection, the possibility of its presence cannot be discounted, especially because *Bd* has been detected on amphibians sampled from the ground in this area (Brunner 2022; unpubl. data). Further, the optimal temperature for *Bd* ranges between 17°–25° C (Piotrowski et al. 2004; Kriger et al. 2007; Turner et al. 2021), which is consistent with the monthly average temperatures reported at Mashpi Reserve. Although *Bd* thermal tolerance needs to be further studied, low *Bd* performance is usually associated

with higher temperatures (Stevenson et al. 2013).

To elucidate vertical stratification dynamics of amphibian populations, future research should prioritize investigating the behavior and life-history traits of anurans partially or fully inhabiting the canopy. While our findings suggest a low presence of amphibians in the canopy of Mashpi Reserve, this may reflect a need for a more complete exploration of canopy herpetofauna. Direct-developing anurans, such as species of *Pristimantis*, may occupy alternative microhabitat within the canopy, such as tree holes, moss, soil accumulations, and other epiphytes. These species do not undergo a tadpole stage and are not reliant on a body of water for survival, allowing them to inhabit microhabitats beyond bromeliads.

In this context, it is necessary to consider species that are obligate or facultative bromeliad breeders. For instance, Basham et al. (2022) reported individuals of the bromeligenous species, Yellow-bellied Poison Frog (*Andinobates fulguritus*), using alternative microhabitats such as *Ludovia* epiphytes, showing the flexibility of some bromeliad-associated species. Therefore, determining whether bromeliad breeders, such as some species from the family Dendrobatidae, are present in the canopy of Mashpi will reveal critical insights into canopy amphibian dynamics and habitat use.

Additionally, seasonal dynamics also merit further investigation. Some arboreal anurans tend to descend to the forest floor during dry seasons to avoid desiccation (Doan 2004; Basham and Scheffers 2020), underscoring the importance of seasonality in driving anuran behavior. Yet, most studies, including ours, have been conducted during a single season, limiting our understanding of seasonal shifts in habitat use (Basham et al. 2023). Notably, trees within our sampling sites typically harbored more than about 30 bromeliads, potentially reducing the probability of detecting amphibians in the tree. Therefore, we recommend that future investigations concentrate on increasing the number of sampled bromeliads per tree and expanding the sampling scope to encompass diverse elevational gradients and environmental contexts, including agroforestry, and primary and secondary forests.

Our findings contribute to the expanding body of literature investigating the canopy of the Andean Chocó region. Given the potential threat of amphibian population declines compounded by habitat loss and disease, safeguarding natural habitats becomes imperative. Conservation efforts should also focus on preserving the canopy and subcanopy environments

and recognize their ecological significance in providing stable niches for amphibian populations.

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