

**Heat Tolerance as a Predictor of Amphibian Community Composition Along a Thermal
Landscape Gradient in Ecuadorian Chocó Tropical Forests**

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ABSTRACT:

Habitat conversion and associated extinction events are a growing threat to neotropical rainforest communities, and ectothermic species are at particularly high risk due to a need for specific environmental temperatures to regulate body temperatures. For this reason, uncovering the complex relationship between heat tolerance and amphibian community composition patterns across forest types differing in thermal landscape is an important research goal. To address this need, we measured operative temperatures across early reforestation plots and mature forests and then examined the heat tolerance (fundamental and realized thermal niche) of 28 species of amphibians native to the Mache-Chindul Reserve, northwest Ecuador. Using biodiversity data, we assessed the strength of heat tolerance and body size as predictors of community composition. Reforestation temperatures were higher than control forest temperatures across two years. We find no evidence of a relationship between heat tolerance and forest type; however, larger frogs dominated the restoration forests. The former suggests that behavioral thermoregulation via shuffling between microclimates is sufficient in keeping cool-adapted species at body temperatures below their heat tolerance maximums. A study of *Pristimantis achatinus*, indicates that a population within a cacao plantation has not evolved a higher heat tolerance than its primary forest counterpart. Finally, we find mixed support for a body size and heat tolerance association with greater mass contributing to longer periods of tolerance. Overall, we conclude that despite great differences in thermal landscape across reforestation and mature forests, key mechanisms including behavioral thermoregulation allow less heat tolerant species to persist within warmer areas. We argue that future studies within the region should consider a

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dynamics as the reforestation forest succeeds and continues to cool.

Introduction:

Deforestation is a global crisis that has had numerous catastrophic effects on our forests, with more damage expected in years to come. In tropical rainforests, large areas of forest are cleared every year (González-del-Piego et al., 2020) for pastureland, cacao production, palm oil, and timber (Chakravarty & Shukla, 2012; Perlin & Leguizamón, 2024). Beyond the immediate loss of habitat and resources, deforestation can have significant impacts on fauna and flora through the alteration of local macro and microclimates. Deforestation results in elevated solar radiation, air temperatures, and soil temperatures †significantly increasing the temperature of available microclimates (Lawrence & Vandecar, 2015; Nowakowski et al., 2018; Machado et al., 2023) and reducing the availability of cool refuges (Pringle et al., 2003; Boyle et al., 2025). Changes in the thermal landscape within a forest can greatly influence biotic communities (Nowakowski et al., 2017).

Ectotherms are particularly vulnerable to changes in microclimate, and differences in thermal niche between species is predicted to drive patterns of species composition change due to deforestation (Huey & Kingsolver, 1989; Huey et al., 2009; Frishkoff et al., 2015; Nowakowski et al., 2017; Palmeirim et al., 2017; Veselka et al., 2023; Camacho et al., 2024). Specifically, animals adapted to higher temperatures are expected to dominate in disturbed and cleared forests (Williams et al., 2020; Piñanez-Espejo et al., 2024). For example, two frog species (*Craugastor fitzingeri* & *Craugastor crassiditigus*), exhibit thermal niche partitioning as *C. fitzingeri*, a more heat-adapted species, dominates warmer low elevation forest and pastureland, while *C. crassiditigus*, a more cool-adapted species, dominates cooler high elevation forest (Frishkoff et al., 2015). In another global dataset analysis, researchers found that

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approached their thermal maximums (Williams & Newbold, 2021). An additional study determined that tropical lizard species from warmer open microhabitats exhibit higher heat tolerances than species from cooler forest microhabitats (Brusch et al., 2016). More warm-adapted species are better able to persist within disturbed landscapes because experienced temperatures are farther from their heat tolerance limits.

Body size is another trait that can be associated with community filtering during deforestation (Neckel-Oliveira & Gascon, 2006; Nichols et al., 2007; Torralvo et al., 2022), which could be at least partially mediated by relationships between size and physiological tolerances. For example, body size is associated with heat tolerance in a wide range of terrestrial and aquatic ectotherms, though the direction and strength of the association can differ across taxonomic groups. In some taxa, including mollusks, arthropods, fish, and reptiles, the relationship between body size and heat tolerance is often negative, meaning larger individuals are less tolerant (Peralta-Maraver et al., 2021). In contrast, a study of several Amazonian frog species found that body size was positively correlated with physiological heat tolerance, where smaller Strabomantidae had lower heat tolerances than larger Hylidae frogs (von May et al., 2019). Further, a study of behavioral heat tolerance (voluntary thermal maximum, VT_{max}) in two Brazilian frogs, *Physalaemus cuvieri* and *P. nattereri*, found that body size was positively correlated with VT_{max} (Diaz-Ricaurte et al., 2020). Large ectotherms also have greater thermal inertia, allowing them to resist extreme body temperatures for longer periods of time (Peralta-Maraver et al., 2021; Gunderson, 2024). In addition, large body size may influence persistence in deforested areas via effects on evaporative water loss. Large organisms have lower relative evaporative water loss rates than small organisms due to lower surface area-to-volume ratios

(Tracy et al., 2010), which may help large organisms in the hotter and less humid microclimates found in deforested areas.

The relationship between forest loss and thermal tolerance in amphibians is particularly relevant for the Chocó rainforests, which extend from northwest Ecuador into southwestern Colombia. The Chocó combines high rates of biodiversity and endemism, including 97 amphibian species, 28 of which are endemic (Ron et al., 2024), with high rates of deforestation for pastureland and cacao production (Jaimez et al., 2022). It is estimated that 61 - 89% of Ecuadorian Chocó primary forest has been deforested (Finer & Mamani, 2019; Escobar et al., 2025). However, a restoration project has been implemented to restore tropical forests to their native state. The restoration project offers a unique opportunity to study the factors that influence amphibian community composition due to deforestation and during the process of reforestation.

We investigated interactions between amphibian community dynamics and thermal biology during the reforestation of deforested land in the Ecuadorian Chocó, integrating data on microclimates within deforested and intact forests, amphibian physiology, and surveys of amphibian community composition. We tested several hypotheses: (1) temperatures within an early restoration forest are higher than temperatures within a healthy intact forest; (2) more heat-tolerant species will dominate the warmer restoration forests; (3) more cool tolerant species will establish populations in later restoration; (4) warming tolerance (WT) among species within the warmer restoration forest will be lower than species within cool mature forests and that the WT of the restoration species will increase over time as the restoration forests succeed. We also tested whether populations of the most locally abundant frog species, *Pristimantis achatinus*, in disturbed (cacao) vs. mature forest habitats differ in their heat tolerance; here, we hypothesized

greater heat tolerance amongst the disturbed population than the mature forest population. Additionally, we examined the association between body size, heat tolerance, and amphibian community composition in restoration areas. We tested two hypotheses: (1) body size will be positively correlated with heat tolerance (von May et al., 2019); and (2) body size of restoration species will be higher than that of mature forest species.

Materials and Methods

Study Area

Data were collected at the FCAT Reserve adjacent to REMACH within the Chocó rainforest region in the Esmeraldas province of Ecuador (0°22'22.7"N 79°39'53.6"W). A previous survey of the tropical rainforest within this reserve estimated 37 species of amphibians (Ortega-Andrade et al., 2010; Jongsma et al., 2014), yet this is likely a modest estimate given the recent discovery of two new species within the region, *Leucostethus bilsa* (Jones et al., 2024), and *Engystomops coloradorum*. Amphibians within these forests primarily belong to the *Bufo* family, *Dendrobatidae*, *Strabomantidae*, *Hylidae*, *Centrolenidae*, and *Leptodactylidae* families. Within this area, mean air temperatures range from 21-25 C and average precipitation reaches upwards of 3 m (Charlat et al., 2000; Mazanec 2022). The reserve is situated within a low to mid elevation tropical rainforest (~100-700 meters) (Mazanec et al., 2022). As highlighted in the introduction, efforts have been made throughout the past several decades to minimize the impact of logging on the Reserva Ecológica Mache Chindul (REMACH) to protect the remaining Chocó forest (Perlin & Leguizamón, 2024). Despite the existence of REMACH, deforestation rates have remained high in the region due to cacao production (Jaimez et al., 2022; Perlin & Leguizamón, 2024). Adjacent to REMACH is the Fundación para la Conservación de los Andes Tropicales (FCAT).

Established in 2018, FCAT has directed several community-engaged conservation projects including a reforestation project employing a technique called applied nucleation. This process involves planting fruit-bearing plants in island patches such that frugivores can ingest seeds and disperse them across the landscape, increasing the connectivity of the forest islands.

Environmental Operative Temperatures

Using copper models we measured operative temperatures (T_e), which are defined as the hypothetical experienced body temperature of an organism in a given microclimate (Huey 1991; Huey et al., 2009; Gunderson & Leal, 2012). Measurements were taken along transects (identical to the transects in the biodiversity monitoring project discussed below) in three restoration and two control forest plots from July 7th – July 8th, 2023, and from July 15th – July 20th, 2025. The restoration plots, 3B, 3C, and 2D, are only a few years old and were previously pastureland. Both control forests used in our study were considered healthy secondary forests (**Fig. 1**). Along each transect, two T_e values were recorded at randomly generated locations every four meters; we measured temperatures along each transect for a period of 50-60 minutes. Variables including weather conditions, sun exposure, and air temperature were recorded. Additionally, if a herptile was found, a copper model was placed in that exact location, and an operative temperature was recorded. This process continued across five days, with a rotation in the time period at which each plot was visited.

Amphibian Collection

Data was collected from May 16th until June 30th, 2025. We collected individuals nightly (20:00-0:00) from the forests surrounding the field station. Given the presence of highly venomous snakes in this area, including the bushmaster (*Lachesis acrochorda*) and eyelash pit

viper (*Bothriechis schlegelii*), we sampled within 5m of established trails. Additional collection occurred in and along streams, in cacao fields, in the restoration plots, and in the gardens surrounding the station. When a frog was captured, it was placed in a plastic bag with leaves, water, and air. GPS coordinates were recorded at the point of capture so that frogs could be returned to their approximate territory. Frogs were then brought to the field station for testing. Toads and large frogs, including several from the Leptodactylus family, were excluded from capture due to testing limits. Further, we only captured frogs whose IUCN status was listed as near threatened or below. For example, *Leucostethus bilsa*, was spotted on several occasions, but was not captured because it is considered critically endangered (Jones et al., 2024). We also collected 10 *P. achatinus* frogs from a cacao field and 10 from a primary forest. Collection procedures identical to our primary study were taken. We used *P. achatinus* playbacks within the cacao field to assist in frog detection and capture. Elevation was recorded as an additional analyzable covariate.

Heat Tolerance Experiment:

We measured voluntary thermal maximum (VTmax) to estimate heat tolerance limits of frogs. VTMax is the maximum body temperature at which an individual can voluntarily tolerate before it retreats to cooler temperatures (Camacho et al., 2018; Diaz-Ricaurte et al., 2020). VTmax was measured in 119 individuals across 13 species. Prior to experiments, we measured snout-vent length (SVL) to the nearest mm using a standard ruler and body mass to the nearest 0.001 g using a VEVOR Analytical Balance Lab scale 500g x 0.001g. Individuals were then placed in a container of water for 1 hour to allow them to reach 100% hydration (Díaz-Ricaurte et al., 2020). After hydration, frogs were placed into a dark heated chamber under a ceramic heater (Thrive Reptile Heat Emitter: 100 W) equilibrated to 39 C. The heat chamber featured a

box with mesh wire placed on top to block out light and simulate darkness for our nocturnal study species. Attached to the heat chamber via a swinging door was an unheated plastic tub with complete exposure to light (**Fig. 2**). Individuals consistently occupied the heat chamber and avoided the light until their body temperature was too high. When the frog left the heat chamber, their body temperature was immediately measured by inserting a wire thermocouple probe into the cloaca. This body temperature was recorded as the VTmax. After testing, frogs were returned to the container of water to cool and rehydrate. Each frog was then returned to their point of capture using the previously recorded GPS locality.

Data Analysis:

Environmental Temperature Analysis

We employed a linear mixed-effects model (LMM) to test for the effect of forest type on operative temperature, as well as year on operative temperature. Forest type was our fixed effect while year was our random effect.

Heat Tolerance & Community Composition

We used an ANOVA to test for a difference in the mean VTmax across all 13 species for which we had physiological data. We then used previously compiled biodiversity data to separate reforestation species from the regional species pool for analysis. We refer to the intact forest species as the regional species pool. Biodiversity data was collected by Holden Jones and FCAT (unpublished data) in two sampling periods each year from 2023 to 2025. This data was collected via visual encounter surveys along transects in the area surrounding the FCAT field station. We determined a species to be a restoration species if they were observed within the restoration sites for a minimum of two nights in the year. Four species were not present in the biodiversity data;

three of these species were placed in the regional species pool based on our locality data †the remaining species was omitted from our analyses. We bootstrapped the data by randomly sampling species from the regional species pool 1000 times to create a density estimate distribution of bootstrap means, which we compared to the observed VTmax mean of the restoration species group. For 2023 and 2025, to determine whether the species in the restoration forest exhibit significantly higher VTmax means than the regional species pool, we calculated the proportion of bootstrapped regional species pool VTmax means above our observed restoration VTmax mean, which became our p-value. We conducted an additional statistical analysis to test for a difference between restoration and non-restoration species (species only present within forest) heat tolerance. We used a t-test to detect the magnitude of difference and incorporated a Phylogenetic Generalized Least Squares (PGLS) analysis to correct for non-independence.

Warming Tolerance

Warming tolerance (WT) is a measure of thermal vulnerability defined as the difference between an individual's heat tolerance maximum and the environmental temperature maximum (Duarte et al., 2012; Simon et al., 2015; von May et al., 2019). For 2023 and 2025, we calculated the WT for each species in the restoration species group and the regional species pool. I will use the terms forest species and regional species pool synonymously given all species are found in the forest. I will also use the terms restoration, reforestation, and deforestation synonymously. Restoration species group $WT = \text{Species VTmax} - \text{Restoration Operative temperature maximum average}$. Regional species pool $WT = \text{Species VTmax} - \text{Control Forest Operative temperature maximum average}$. Specifically, each maximum was calculated as the mean of the daily maximum temperature across each 5-day collection period.

Body Size & Heat Tolerance

We calculated the mean weight (g), SVL (mm), and VTmax, for each species using data from 84 individuals across our 13 primary species. A PGLS model was used in R to phylogenetically correct our measure of the associations between these different variables: VTmax, weight (g), SVL (mm), and minutes. We then used a PGLS model to determine if body size was significantly greater in the restoration species group than non-restoration species group across 2023 and 2025.

RGBIF/BioClim

We employed the `rgbif` package in R from `rOpenSci` to retrieve species occurrence data. The `bioclim`, `geodata`, and `terra` packages in R from WorldClim were then used to acquire realized thermal niche data for 15 additional species present in the biodiversity dataset (but that we lacked heat tolerance data for). The realized thermal niche was created using BIO5 (maximum temperature of warmest month) and BIO1 (mean temperature during warmest quarter). We used simple linear models and PGLSs to compare realized thermal niches between restoration and forest species †this was followed by a bootstrap analysis. After retrieving V S Body size averages from `bioweb` (PUCE), we used a PGLS (maximum likelihood †) to compare log body size between restoration and forest species †we ran a bootstrap analysis in R to follow up. We used body size (mm) to assess the correlation between body size and realized thermal niche, or heat tolerance, while correcting for phylogenetic relatedness via a PGLM (to account for non-normality) from the `phylolm` package in R. Finally, we employed a PGLS to assess the correlation between VTmax and realized thermal niche (BIO5, BIO10). We retrieved data from the Open Tree of Life using the `ape` and `rotl` packages in R to generate a simple tree that illustrated the phylogenetic relatedness between all 28 study species (**Fig. 3**)

***P. achatinus* Populations**

We compared the mean VTmax of two *P. achatinus* populations: primary forest and cacao field. To compare, we sampled 10 frogs from each location and ran the same VTmax tests as were conducted in the primary experiment. Further analysis of our data allowed us to explore the relationship between weight (g), SVL (mm), the duration of the experiment (mins), and elevation (m) on VTmax, and the weight (g) on the duration of the experiment (mins).

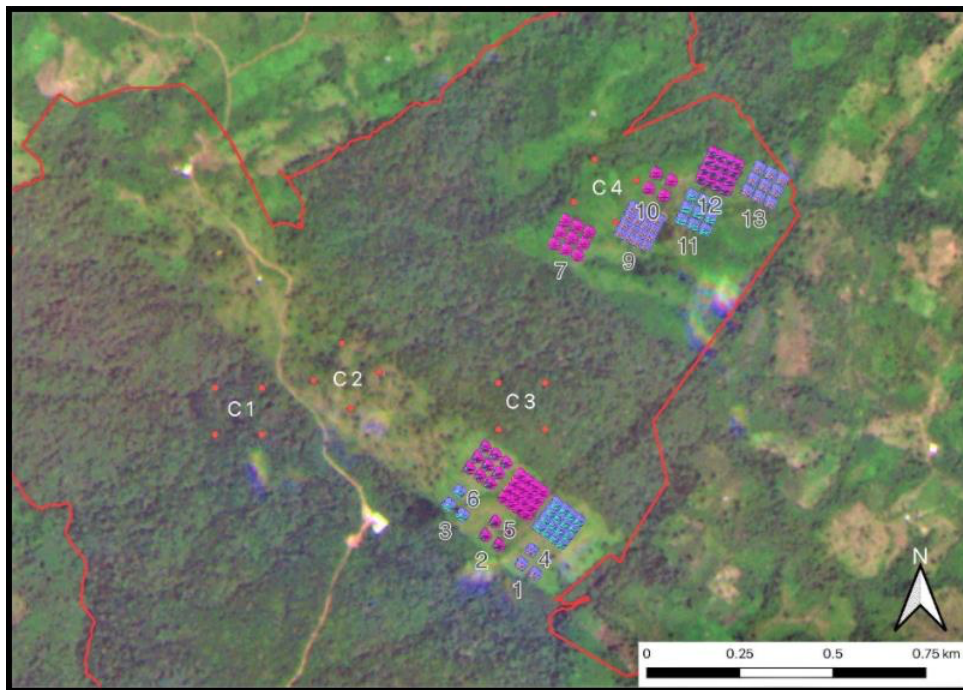


Figure 1: Map of FCAT reserve and the restoration plots within the reserve. The circles forming squares represent the restoration islands whereas C1, C2, C3, and C4 represent the control plots.



Figure 2: Testing chamber setup. A 100 W ceramic heat emitter bulb was used. A metal sheet was used to darken the heated chamber. A door was cut into the plastic tub and cardboard box to allow a frog to escape to the cooler but light plastic tub.

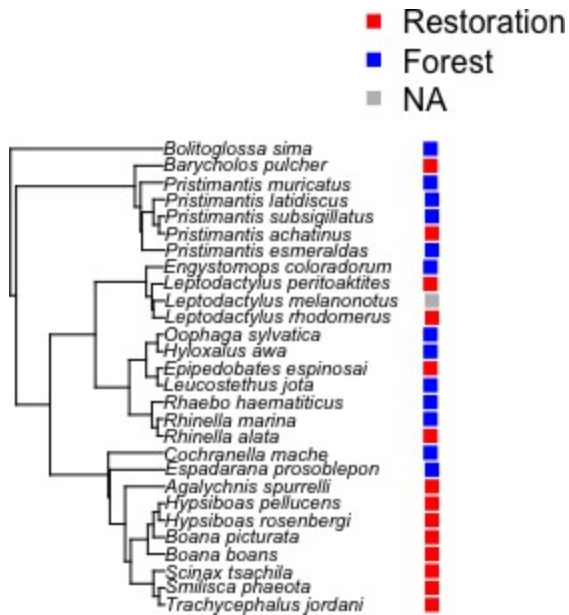


Figure 3: Phylogenetic tree describing the evolutionary relationships between the 28 species key to this study. Species are labeled as Restoration, Forest, or NA groups.

Results:

Environmental Temperatures:

In 2023, operative temperatures were higher in the early restoration forest (29.93 ± 3.52 °C; range 23.3 - 41.6 °C) than in the control forest (25.74 ± 1.33 °C.; range 23.8 - 31.2 °C) ($t = -14.87$, $p < 0.0001$, $df = 217.1$). Similarly, in 2025, operative temperatures were higher within the restoration forests (27.09 ± 2.41 °C; range 23.2 - 39.4 °C) than the control forest (25.56 ± 1.71 °C; range 22.4 and 30.9 °C) ($t = -6.35$, $p < 0.0001$, $df = 287.7$) (**Fig. 4**). A t-test yielded a significant decrease in operative temperatures within the restoration forest from 2023 to 2025 ($t = 8.77$, $df = 308.4$, $p < 0.0001$), but no significant difference in control forest operative

temperatures between years ($t = 0.98$, $df = 200.2$, $p = 0.327$). A LMM yielded a significant difference in operative temperatures across forest types, with restoration forests being significantly warmer than control forests (

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Species Heat Tolerance & Forest Type Analysis:

6 S H F LmHansVranffged from 70.6 °D to [33.9 °C (**Table 1; Fig. 5**). VTmax differed significantly among species (ANOVA, $F = 13.71$, $p < 0.001$). There were six species found in the restoration forest plots in 2023 and four species in 2025 (**Table 1**). A bootstrap of our 2023 biodiversity data determined that the restoration species group VTmax mean (32.33 ± 1.38 °C) was not significantly higher than the mean VTmax of the regional species pool (31.73 ± 0.46 °C) ($p = 0.118$) (**Fig. 6**). Further, a bootstrap of our heat tolerance data using 2025 biodiversity parameters revealed no significant difference in the mean VTmax of the restoration species group (32.38 ± 1.45 °C) and the regional species pool (31.72 ± 0.44 °C) ($p = 0.120$) (**Fig. 7**).

Restoration Species vs. Non-Restoration Species Analysis: 13 species

We analyzed our data to compare heat tolerance in restoration species vs. non-restoration species. This analysis differed from our bootstraps in that there was no overlap in the species that occurred in each forest type. A PGLS yielded no significant difference in the VTmax of the restoration species (32.33 °C) and non-restoration species (31.01 °C) in 2023 ($F = 0.261$, $p = 0.620$) and no significant difference in the VTmax of the restoration species (32.38 °C) and non-restoration species (31.32 °C) in 2025 ($F = 0.046$, $p = 0.834$) (**Fig. 5**).

Warming Tolerance: 13 species

We calculated the WT of each reforestation and forest species group for 2023 and 2025 (Table 1). The mean WT of the restoration species group increased from 6.34 °C in 2023 to 0.95 °C in 2025, and the mean WT of the forest species group decreased from 3.35 °C in 2023 to 2.94 °C in 2025 (**Fig. 8**).

Body Size * Restoration Analysis: 13 species

We used a PGLS to compare mean body size in our 2023 restoration species (3.40 g) and non-restoration species group (1.41 g); this yielded no significant difference ($F = 0.025$, $p = 0.878$). Additionally, we found no difference in mean body size of our 2025 restoration species (4.19 g) and non-restoration species (1.51 g) ($F = 2.521$, $p = 0.143$) (**Fig. 9**).

Body Size * Heat Tolerance Analysis: 13 species

Frog SVL ranged from 15-68mm, and weight ranged from 0.292-26.55g. Using a linear model, we found a significant association between mass and VTmax ($F = 7.62$, $p = 0.019$); however, when we employed a PGLS model, it yielded no significant positive correlation between mean weight and mean VTmax ($F = 1.483$, $p = 0.251$) (**Fig. 10**). Additionally, SVL and VTmax were significantly correlated ($F = 22.47$, $p < 0.001$); however, this correlation disappeared upon using a PGLS ($F = 0.536$, $p = 0.481$) (**Fig. 10**). Our analysis of further covariates via PGLS yielded a significant correlation between length of exposure and VTmax ($F = 12.48$, $p = 0.005$) (**Fig. 10**). Finally, we found that mass is positively correlated with the length of exposure †individuals with greater mass were able to tolerate the heat for longer periods of time ($F = 24.91$, $p < 0.001$) (**Fig. 10**).

RGBIF/Bioclim Analysis: 28 species

A PGLS yielded no significant difference in the realized thermal niche (BIO5; max temperature of hottest month) between restoration and forest species ($F = 2.499$, $p = 0.127$); a simple linear model also showed no significant difference ($F = 1.115$, $p = 0.301$). An additional PGLS yielded no significant difference in the realized thermal niche (mean temperature of warmest quarter) between restoration and forest species ($F = 1.58$, $p = 0.2204$) (**Fig. 11**); a simple linear model also showed no significant difference ($F = 0.967$, $p = 0.335$). Bootstrapping of these two analyses also indicted no significant difference in realized thermal niche between forest and restoration species ($p = 0.234$; $p = 0.241$). A PGLS yielded a significant difference in log body size between restoration and forest species ($F = 5.66$, $SE = 0.518$, $p = 0.025$) (**Fig. 11**); a bootstrap analysis indicated a marginally significant difference ($p = 0.075$). We found a significant correlation between body size (mm) and realized thermal niche (bioclim5; max temp of the hottest month) ($t = 2.464$, $SE = 1.597$, $p = 0.021$), and a marginally significant correlation between body size and realized thermal niche (bioclim10; mean temp of the warmest quarter) ($t = 1.939$, $SE = 1.725$, $p = 0.064$) (**Fig. 12**).

VTmax * Realized Niche Analysis:

We employed a PGLS to assess the association between VTmax & realized niche across 13 species for which we had VTmax means; we found no significant association between VTmax & max temp in hottest month ($F = 0.049$, $p = 0.830$) and no significant association between VTmax & mean temp in the warmest quarter ($F = 0.031$, $p = 0.863$) (**Fig. 13**).

P. achatinus Populations Analysis

A within-species analysis of *P. achatinus* found no significant difference in the VTmax of primary forest (31.58 ± 0.92 °C) vs. cacao field individuals (30.91 ± 0.90 °C) ($t = 1.642$, $p >$

0.05) (**Fig. 14**). Regarding covariate analyses of our *P. achatinus* data, we found a significant positive correlation between weight and VTmax ($F = 4.949, p < 0.05$) (**Fig. 15**), however, there was no significant correlation between SVL and VTmax ($F = 1.201, p > 0.05$) (**Fig. 15**). Further, we found a significant positive association between the duration of the experiment and VTmax ($F = 5.25, p < 0.05$) (**Fig. 15**) and a significant positive correlation between weight and the duration of the experiment ($F = 10.01, p < 0.01$) (**Fig. 15**). Finally, we found no effect of elevation on VTmax ($F = 1.02, p > 0.05$) (**Fig. 16**).

Discussion:

P1-4: Readdress primary question and discuss and interpret results

This study addressed the relationship between heat tolerance, body size, and amphibian community composition in deforested areas of the Chocó biogeographic zone. We did not find support for the hypothesis that warmer restoration forests are dominated by more heat tolerant species. We can, however, conclude that larger-bodied frogs dominate warmer restoration areas whereas smaller-bodied frogs are limited to cooler mature forests. We find support for our hypothesis that warming tolerances of restoration species would be lower than forest species, and that warming tolerances of restoration species would increase temporally as the forest succeeded. Finally, we found that phylogeny explains amphibian heat tolerance more greatly than body size.

Temporal & Spatial Patterns in Environmental Temperatures

We predicted that environmental temperatures would be higher in the restoration forest sites than in the control forest sites. Indeed, restoration forests were warmer than intact forests in both sampling years. Further, we found that restoration forests cooled from 2023 to 2025 due to rapid forest growth increasing shade. This is consistent with findings in other tropical forests

where reforestation led to significant cooling in a short time span. A study of a regenerated Amazon rainforest showed a 1.2 C decrease in temperature over a 30-year period (Cooley et al., 2025). An additional global study found that regeneration initiatives can lower tropical forest temperatures by 2.03 C (Alibakhshi et al., 2024). Restoration efforts help to cool forests, thus buffering ectotherms from warming climates and providing more thermally suitable habitat.

Heat Tolerance as a Predictor of Amphibian Biodiversity

Understanding how heat tolerance shapes amphibian community composition can help improve conservation forecasting. We did not find evidence to support our hypothesis that more heat tolerant species are present in warmer restoration forests. This result is contrary to other studies of tropical ectotherms which found that community composition is linked to heat tolerance, as more heat tolerant lizards dominate open habitats (Brusch et al., 2016). An additional study of two *Craugastor* frogs found that the more deforestation-tolerant species had a higher heat tolerance than the forest-affiliated species (Frishkoff et al., 2015). However, this pattern is not always observed (Diaz-Ricaurte et al., 2020). Our findings suggest that other

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facilitate persistence in altered habitats (Kearney et al., 2009). Shaded microclimates within restoration forests may be sufficient to keep amphibian body temperatures below their heat tolerance limits. Furthermore, many of the species in our study are nocturnal and may not be exposed to extreme temperatures during the day where they often reside in hides such as leaf litter (Scott, 1976). Despite our results, continual cooling of the restoration forest may still influence future amphibian assemblages †less heat-adapted species may establish populations within restoration forests. (Díaz-García et al., 2017).

Positive Trends in the Warming Tolerance of Restoration Species

We hypothesized lower warming tolerances in restoration forests than control forests across years, and an increase in warming tolerance in the restoration forest from 2023 to 2025. We found that the warming tolerance of restoration species was much lower than that of the control forest species. Intact forests kept amphibians from experiencing body temperatures close to their upper thermal limit, suggesting that healthy forest buffers amphibians from overheating even as the climate warms. The warming tolerance of species within the restoration forests were well below zero in 2023, suggesting they were at a great risk of overheating. However, the warming tolerance of the restoration species approached zero in 2025, consistent with the cooling of restoration forests. We expect a continued increase in warming tolerance for the next several years as the restoration forest continues to regenerate, and extreme temperatures are limited by greater canopy cover and denser vegetation. Increasing temperatures via climate change threaten tropical amphibians, especially species that inhabit deforested areas (Frishkoff et al., 2015), however restoring forests can buffer amphibians from increasing temperatures and exposure to otherwise lethal temperatures (Pottier et al., 2025). One study in southern Mexico found that restoration initiatives carried out over a 7-year period helped to cool temperatures and facilitate the return of amphibian biodiversity in restoration forests to a similar level of that found in the reference tropical montane cloud forest †with a high diversity of forest specialists and habitat generalists (Díaz-García et al., 2017). Future efforts within our study system will continue to address this question via a longitudinal study and will additionally assess changes in heat tolerance across restoration species as restoration forest temperatures decrease.

Body Size and Community Composition Patterns Across Forest Types

We did not find evidence to support our hypothesis that body size influences amphibian biodiversity in deforested areas. In fact, body size is similar across both warm restoration forests

and cool healthy forests. This result contrasts with a study of Amazonia tropical amphibians which found that deforestation was a strong filter of amphibian assemblages; larger-bodied frogs were dominant in warm deforested areas whereas small-bodied frogs were virtually nonexistent (Torralvo et al., 2022). Additional studies of tropical amphibians have found that larger-bodied frogs are associated with warmer deforested sites (Frishkoff et al., 2015; Galindo-Urbe et al., 2022). Conversely, a study of neotropical ectotherms found that larger-bodied herpetofauna were more limited to intact forests and less present within human-altered forests (Romero & Urbina-Cardona, 2025). Large body size and small body size in amphibians are both associated with trade-offs (Tracy et al., 2010), which may influence distribution patterns. Small frogs can more effectively use thermal refugia to regulate body temperature, while large frogs can withstand high temperatures for longer periods of time. Both mechanisms provide support for our findings, which point towards a diversity of size within restored areas.

A Mixed Relationship Between Body Size and Heat Tolerance

We evaluated the correlation between body size and heat tolerance and hypothesized that greater body size is associated with higher heat tolerance. Body size was positively correlated with heat tolerance; however, this association disappeared when accounting for phylogenetic relatedness. The species *S. phaeota*, *B. picturata*, and *B. pellucens* had the highest heat tolerances and largest body sizes, but these species are closely related within the family Hylidae (**Fig. 3**). This result contrasts with a study of 56 species of Amazonian lowland tropical frogs that found a positive correlation between body size and heat tolerance that persisted after accounting for phylogenetic relatedness (von May et al., 2019). However, we did find that larger frogs can withstand high temperatures for longer periods of time (**Fig. 10**). This positive correlation

strongly agrees with previous literature and is due to greater thermal inertia and lower rates of water loss (Tracy et al., 2010).

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We assessed the relationship between realized thermal niche data in restoration and forest species, whether body size (mm) differed between these two groups, and whether body size and/or VTmax correlated with realized thermal niche. We found no evidence to support our

hypothesis. V L V W K D W V S H F L H V of 11 sites. Habitat data.] H G W

forest sites. Specifically, both maximum temperature in the hottest month and mean temperature in the warmest quarter, which are measures of realized thermal niches, did not differ between groups. However, we can conclude that body size (mm) is greater in restoration species than forest species (**Fig. 11**). Additionally, we find that body size correlates with realized thermal niche; large-bodied frogs are characterized by hotter thermal niches than small-bodied frogs (**Fig. 12**). Smaller frogs, who are characterized by lower thermal inertia and greater EWL, are, in general, filtered out from warm habitats. Greater thermal inertia and lower EWL (Tracy et al., 2010) may enable larger frogs to persist within warmer habitats. However, as the restoration forest continues to cool, we may see small-bodied frogs (i.e., *Strabomantidae* or *Dendrobatidae*) establish populations. Finally, we can't argue that VTmax is correlated with realized thermal niche; rather, we find that species with lower heat tolerances can fill hotter niches, and species with higher heat tolerances can fill cooler niches. These results suggest that morphological factors including body size may be more influential in shaping amphibian distributions than heat tolerance (both realized and fundamental thermal niche).

Heat Tolerance Patterns in Two Distinct Populations of *Pristimantis achatinus*

We tested whether two populations of *P. achatinus* exhibit differences in heat tolerance given distinct habitat types and thus thermal landscapes. We did not find evidence to support our hypothesis that a *P. achatinus* population within a warmer cacao field has a higher heat tolerance than a *P. achatinus* population within a cooler primary forest. Despite drastic differences in canopy cover and thus thermal landscapes between the two habitats, we cannot argue that the population within the cacao field exhibits heat tolerance trait plasticity, as its heat tolerance is very consistent with those from cooler habitats. The presence of tall grass and the cover from cacao trees may provide a buffer against extreme temperatures as individuals thermoregulate † suggesting again that even minimal vegetation may provide enough shaded microclimates for efficient behavioral thermoregulation (Kearney et al., 2009). Further, *P. achatinus* is a nocturnal species and may retreat to rest in thick vegetation such as cacao when daytime temperatures reach extremes. Previous literature suggests that intraspecific variation in heat tolerance plasticity, specifically between populations, can occur across both small and large geographic scales, and can be both reversible and non-reversible (Cocciardi & Ohmer, 2024). Several studies have found intraspecific variation in heat tolerance (Sorte et al., 2011; von May et al., 2019; Riquelme et al., 2017), suggesting that future divergence of the thermal landscapes of two geographically distinct populations may contribute to heat tolerance differences.

Conclusion

Amphibian community composition patterns across forest types were not driven directly by heat tolerance; however, we can argue that body size influences community composition. Despite great differences in temperature means and extremes between reforestation and control forests (**Fig. 7-8**), heat tolerance averages between the two habitat types remained similar. Thermal refugia within the warmer restoration forests can buffer individuals from extreme

temperatures (Scheffers et al., 2013; Frishkoff et al., 2015; Nowakowski et al., 2017; Diaz-Garcia et al., 2017; Nowakowski et al., 2018) and enable less heat tolerant species to persist. Larger-bodied frogs such as Hylidae, have greater thermal inertia and resistance to dehydration, which enable them to remain in hotter and dryer areas for longer periods of time without needing to thermoregulate as frequently. We do, however, expect that the continual cooling of the restoration forest through time will assist in the establishment of less heat tolerant species. Overall, this study highlights the importance of future assessments of the relationship between heat tolerance and amphibian biodiversity patterns and shifts as tropical forests are continually fragmented.

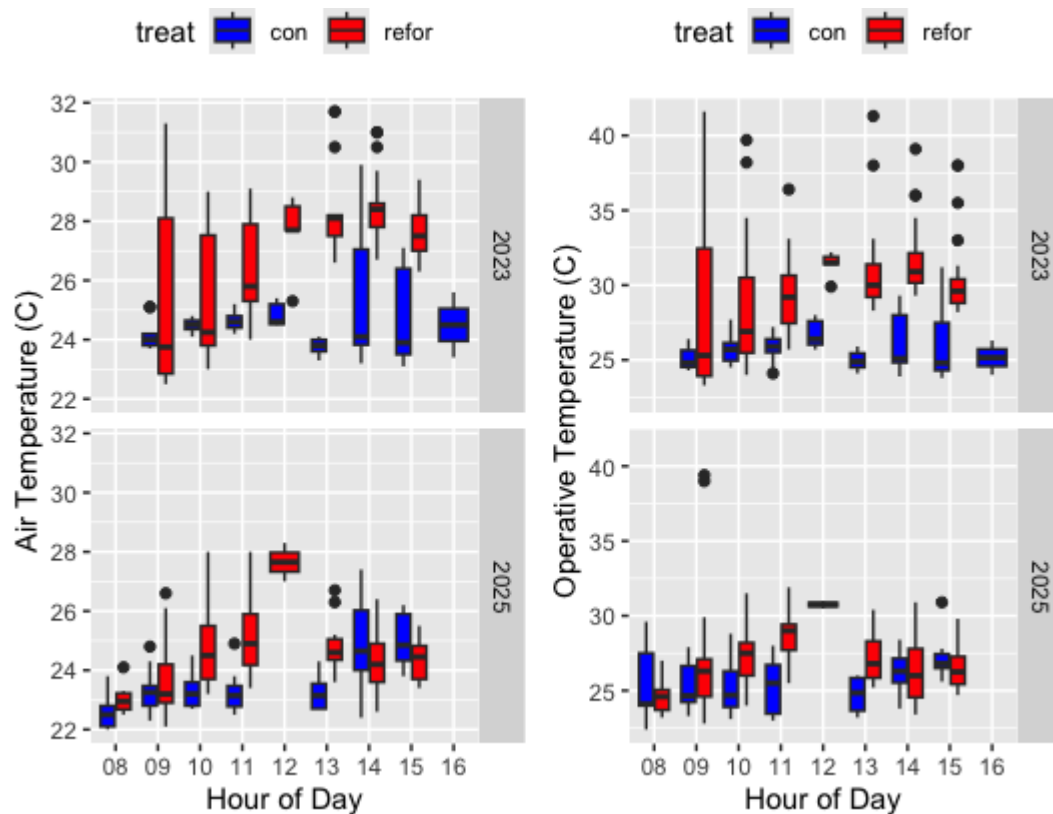


Figure 4: The distribution of (A) air temperatures and (B) operative temperatures throughout the day in the control vs. restoration forests for 2023 and 2025.

Species	N	Average VTmax (C)	Average Mass (g)	Average SVL (mm)	Restoration n 2023	Restoration 2025	WT 2023	WT 2025
<i>Pristimantis achatinus</i>	19	31.18	1.87	28.85	Y	Y	-7.37	-0.26
<i>Epipedobates espinosai</i>	8	30.96	0.36	16	Y	N	-7.59	2.20
<i>Boana picturata</i>	13	33.39	5.57	51.62	Y	Y	-5.16	1.95
<i>Smilisca phaeota</i>	11	33.85	8.4	49.09	Y	Y	-4.70	2.41
<i>Oophaga sylvatica</i>	14	30.56	1.63	25.7	N	N	2.21	1.80
<i>Pristimantis latidiscus</i>	7	31.16	3.38	33.14	N	N	2.81	2.40
<i>Engystomops coloradorum</i>	8	31.09	1.06	22.29	N	N	2.74	2.33
<i>Barycholos pulcher</i>	5	31.1	0.91	21.4	Y	Y	-7.45	-0.34
<i>Hyloxalus awa</i>	4	30.93	0.83	19.5	N	N	2.58	2.17
<i>Leptodactylus melanonotus</i>	2	32.25	12.49	54	N/A	N/A	N/A	N/A
<i>Espadarana prosoblepon</i>	2	30.75	0.95	26.5	N	N	2.4	1.99
<i>Boana pellucens</i>	1	33.5	3.32	43	Y	N	-5.05	4.74
<i>Pristimantis esmeraldas</i>	1	31.6	0.58	20	N	N	3.25	2.84

Table 1: Table of descriptive statistics for the 13 study species. Sample size (N), mean VTmax (C), Mass (g), SVL (mm), and WT are presented. Additionally, species were labeled as restoration species (Y), non-restoration species (N), or not applicable (NA), using the biodiversity dataset.

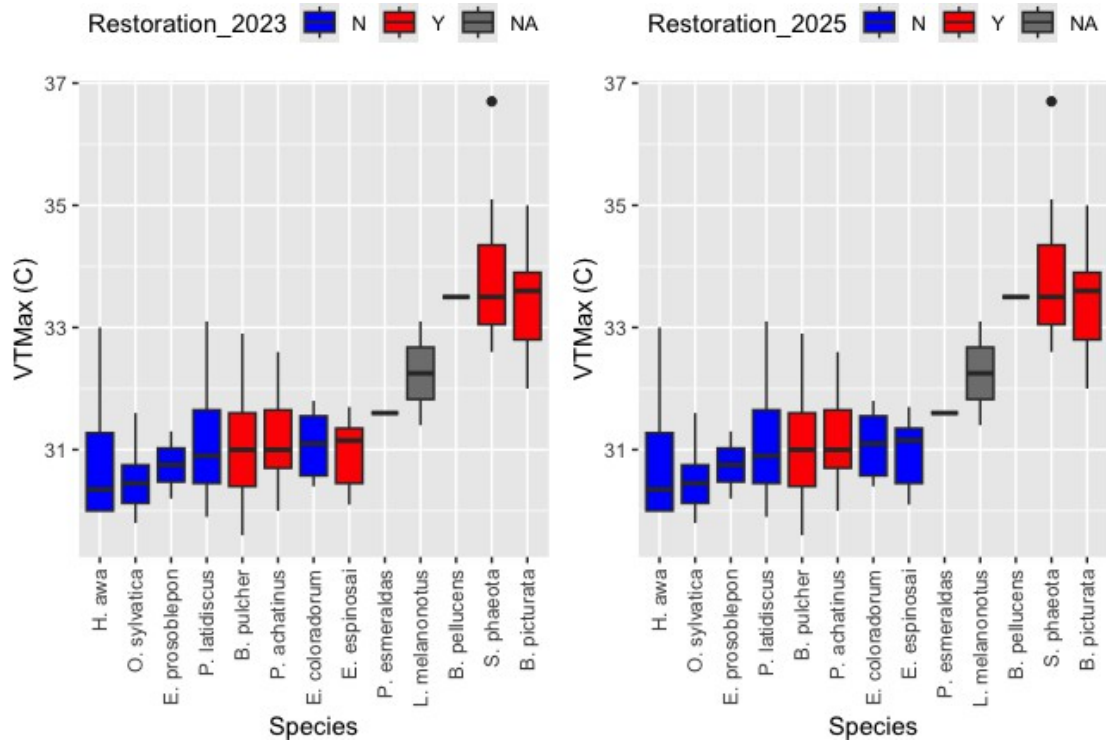


Figure 5: Distribution of VTmax (C) means across all 13 species in the study in (A) 2023 and (B) 2025. Species in orange represent restoration species in 2023; green represents non-restoration species; gray represents species not present in the biodiversity dataset.

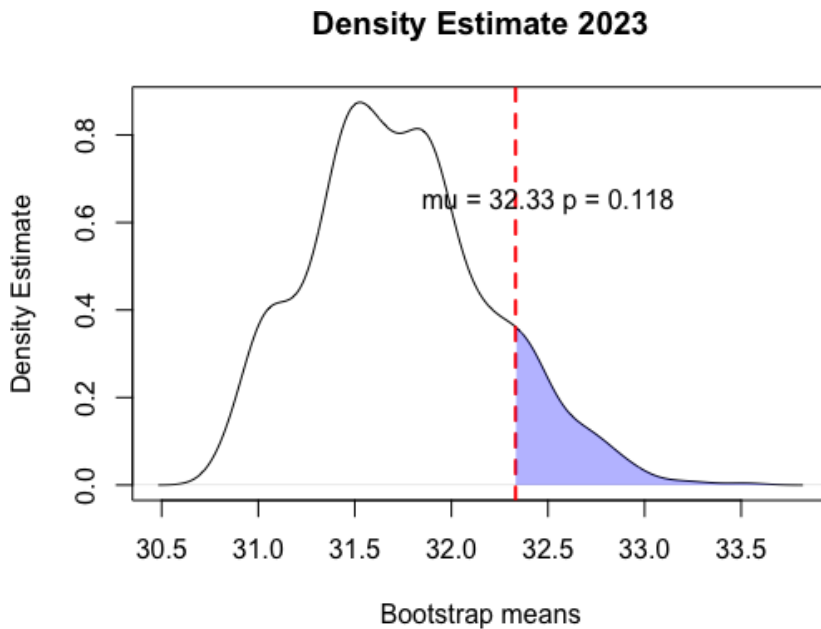


Figure 6: 2023; A density estimate of the bootstrap means compared to the observed mean. 6 U D Q G R P V S H F
VTmax (C) were chosen and bootstrapped 1000 times. This distribution of means was compared to the mean
VTmax (C) of the species observed in the restoration forests.

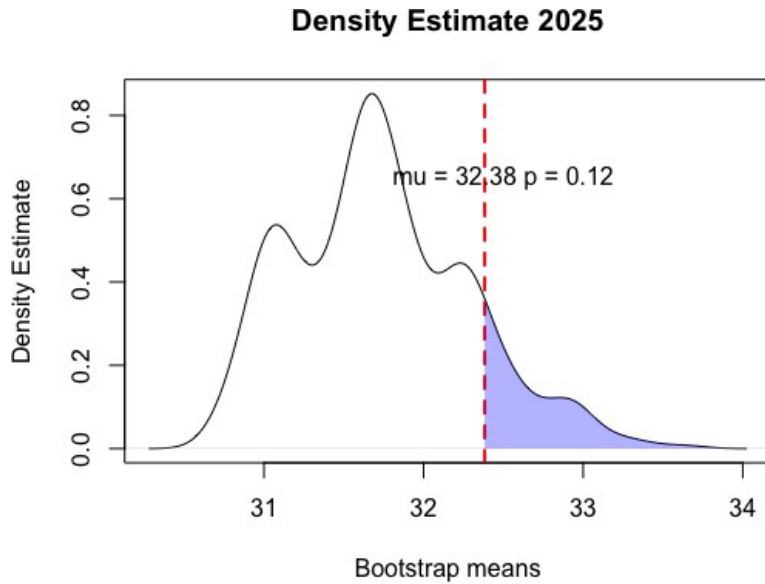


Figure 7: 2025; A density estimate of the bootstrap means compared to the observed mean. 4 U D Q G R P V S H F
VTmax (C) were chosen and bootstrapped 1000 times. This distribution of means was compared to the mean
VTmax (C) of the species observed in the restoration forests.

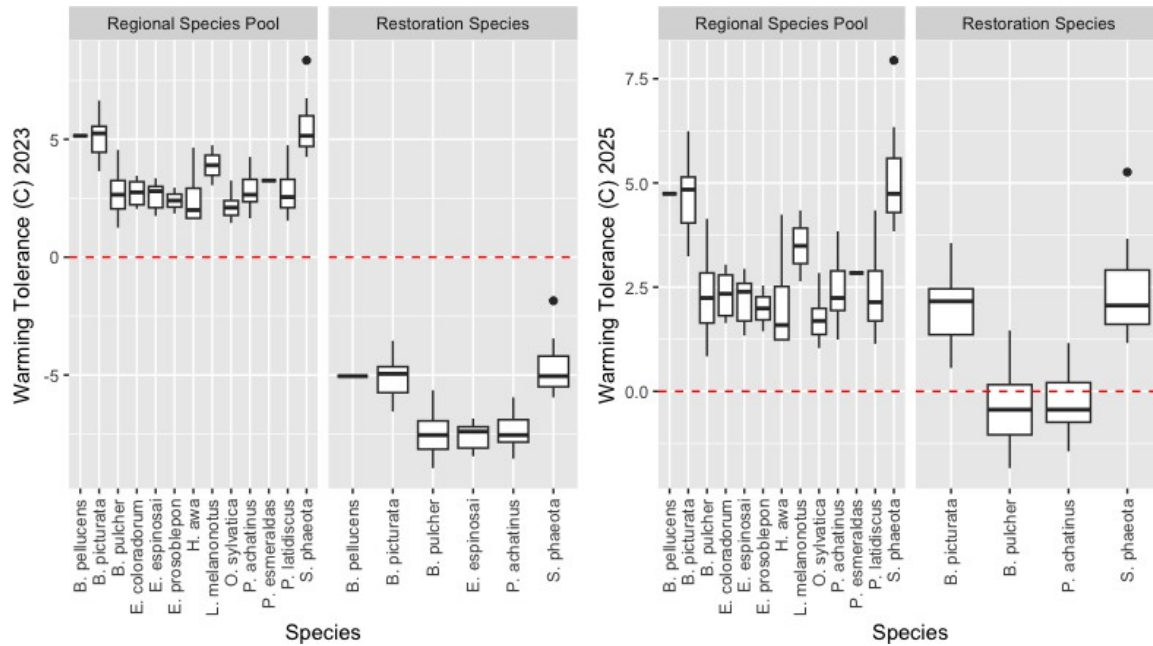


Figure 8: Warming Tolerance (WT) for the reforestation group and the Regional Species Pool in 2023 (A) and 2025 (B). Dashed lines represent the mean WT across all species within the group.

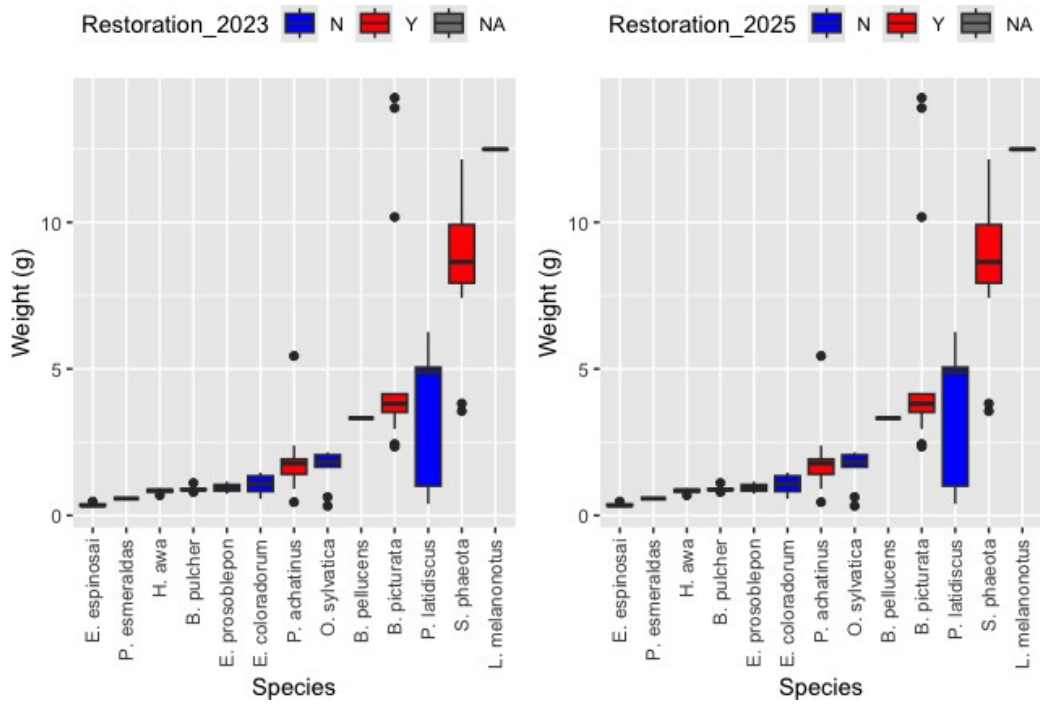


Figure 9: Distribution of weight (g) means across all 13 species in the study in (A) 2023 and (B) 2025. Species in orange represent restoration species in 2023; green represents non-restoration species; gray represents the species that are not present in the biodiversity dataset.

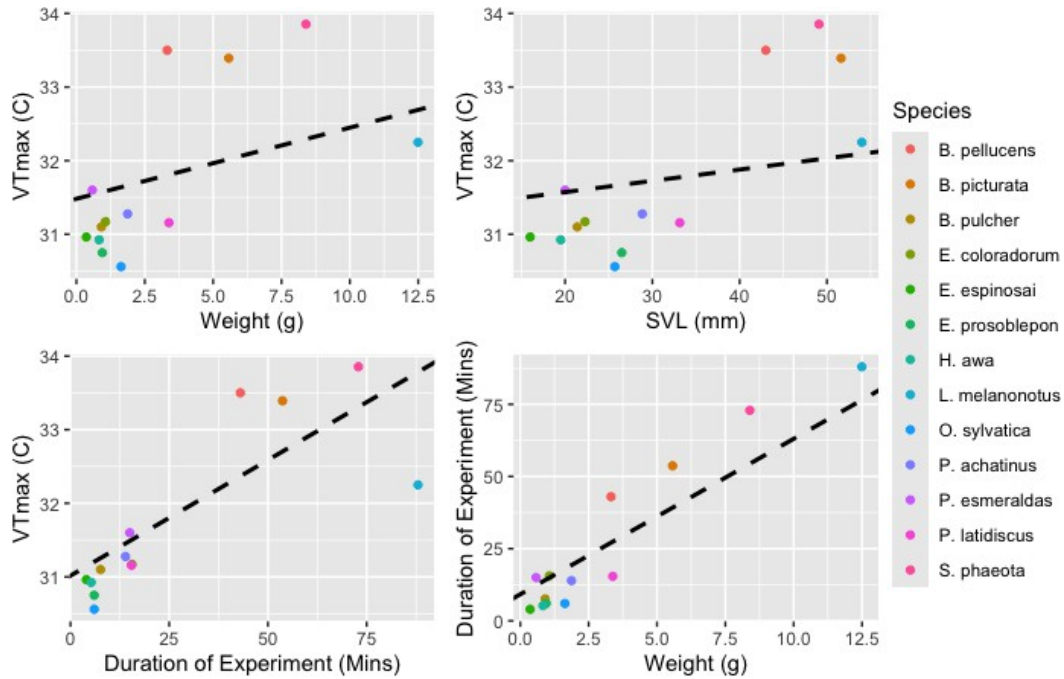


Figure 10: Linear plots describing the association between (A) weight and VTmax, (B) SVL and VTmax, (C) Duration of Experiment (mins) and VTmax, (D) weight and Duration of Experiment (Mins). Dashed lines represent the PGLS line of best fit.

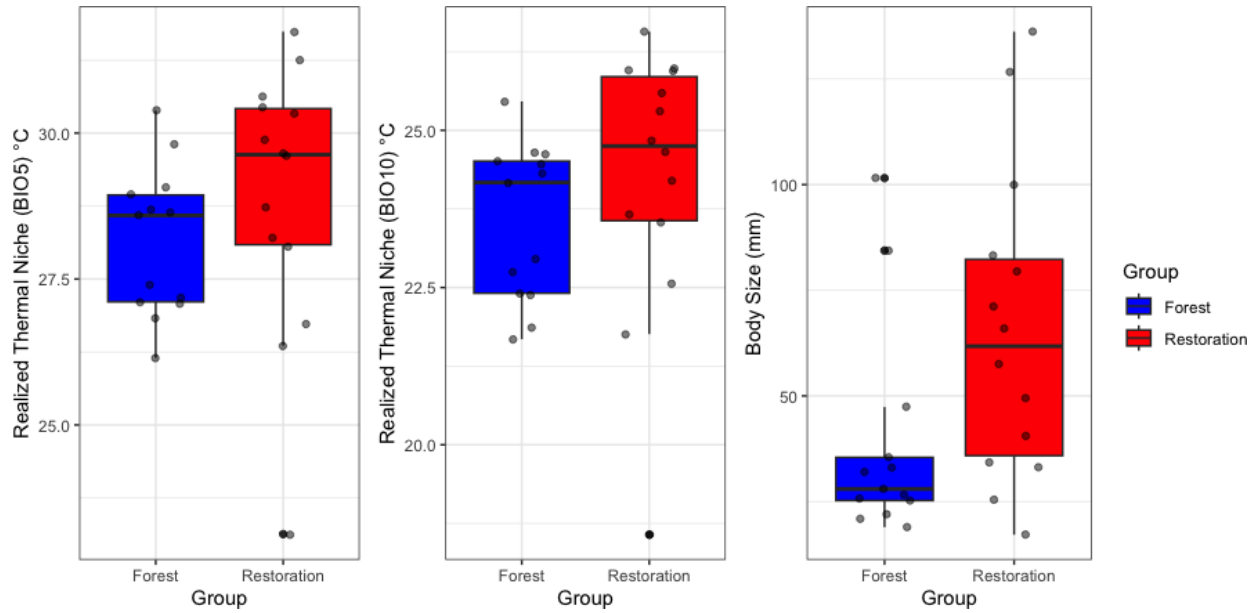


Figure 11: Boxplots highlighting the difference in (A, B) realized thermal niche (BIO5, BIO10) between the restoration and forest species groups and (C) the difference in body size (mm) between the restoration and forest species groups.

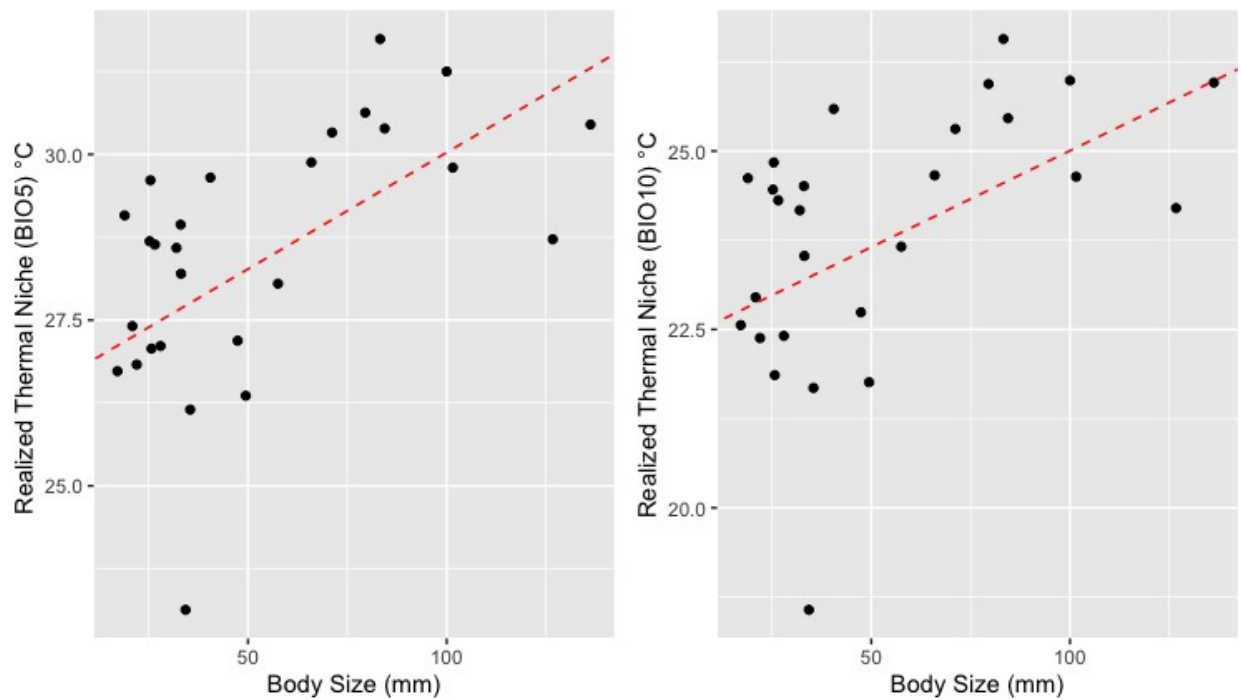


Figure 12: Linear plots for the association between (A) body size (mm) & realized thermal niche (BIO5) and (B)

body size (mm) & realized thermal niche (BIO10). ' R W V U H S U as Hed V ind H re Q res W nt the V GLSS H F L H V
 line of best fit.

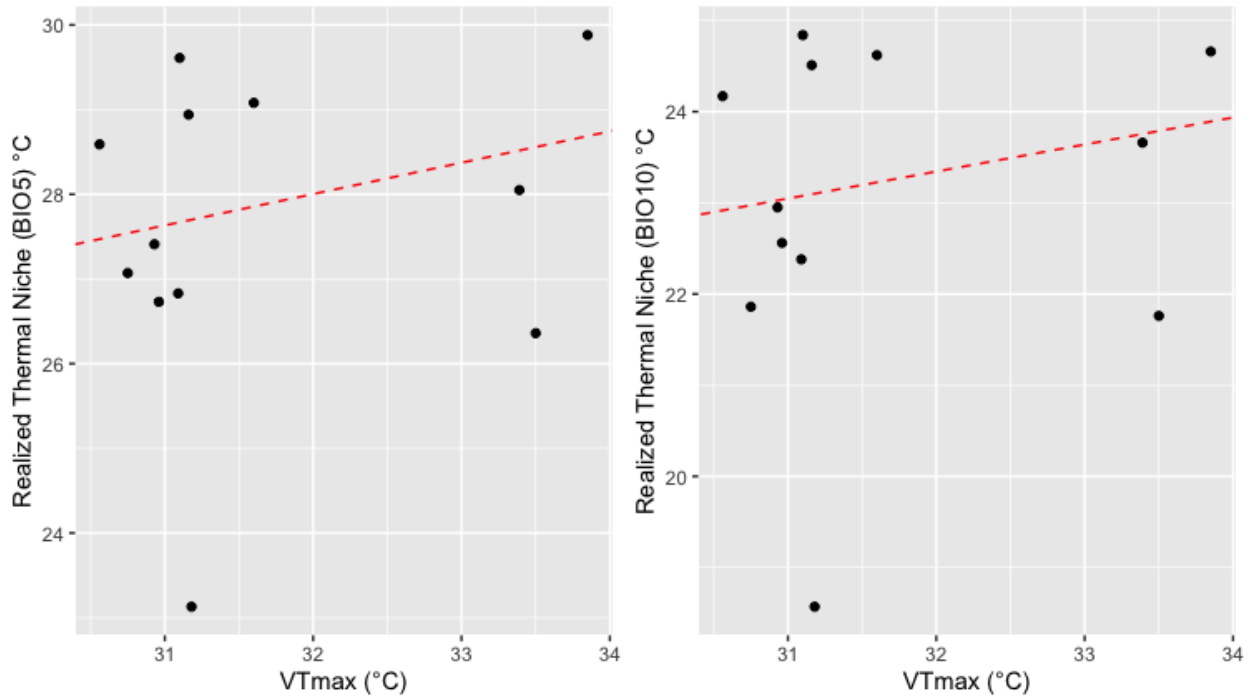


Figure 13: Linear plots illustrating the association between (A) VTmax & realized thermal niche (BIO5) and (B) VTmax & realized thermal niche (BIO10). Dots represent V S H F L as Hed V ind H re Q res W nt the V GLSS H F L H V
 line of best fit.

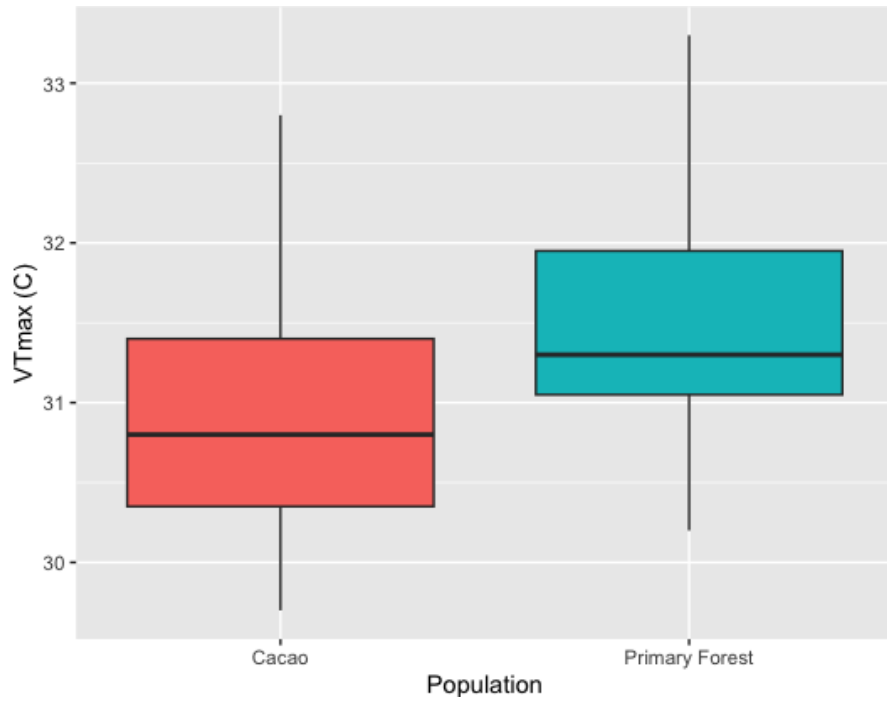


Figure 14: Boxplot describing the distribution of VTmax for the *P. achatinus* cacao and primary forest populations.

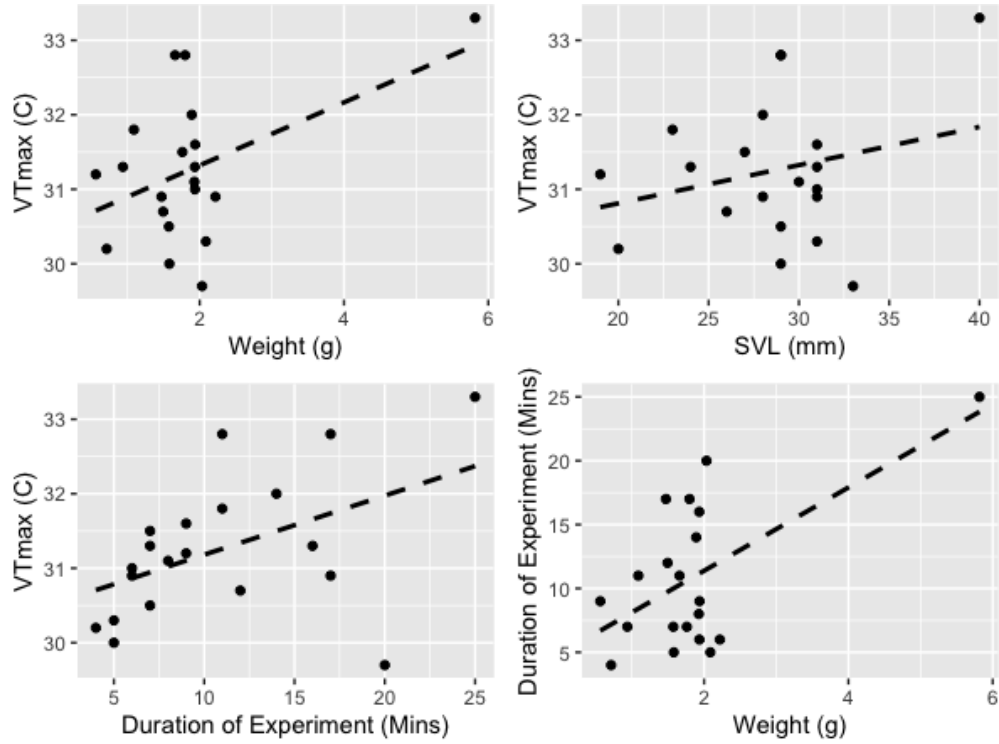


Figure 15: A linear model describing the association between (A) weight & VTmax, (B) SVL & VTmax, (C) duration of experiment (Mins) & VTmax, and (D) weight & duration of experiment (Mins) for two populations of *P. achatinus* from a primary forest and a cacao field.

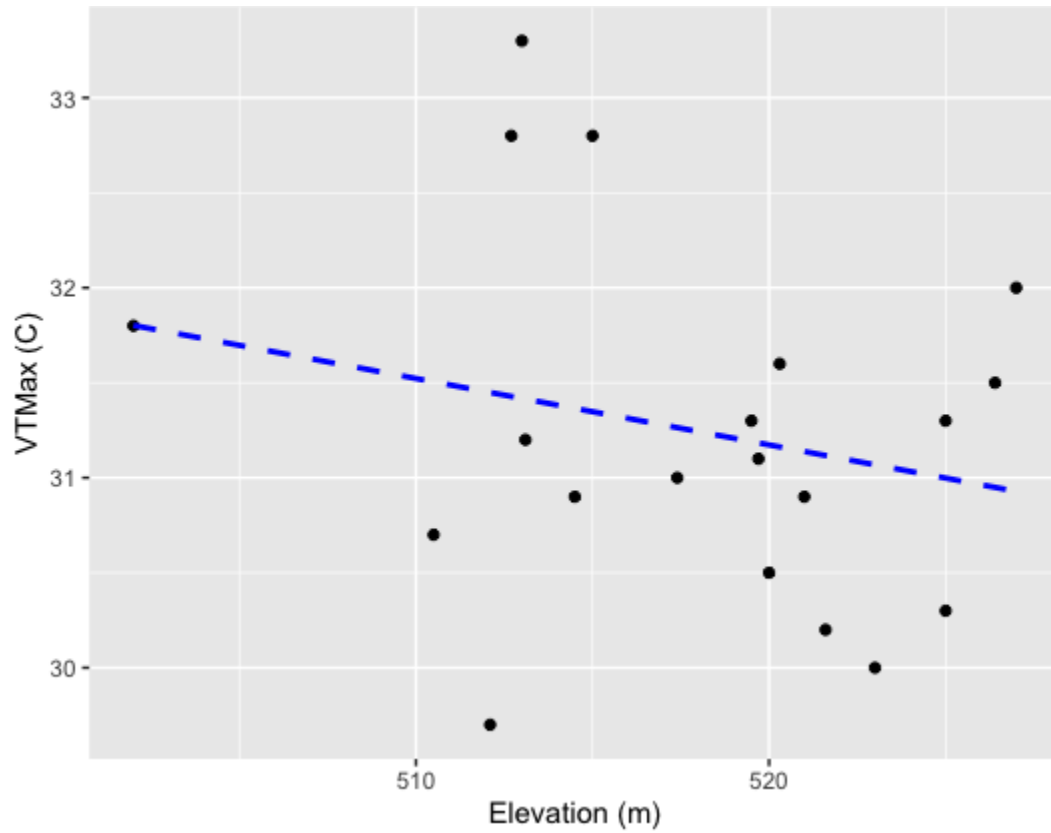


Figure 16: A linear model illustrating the relationship between elevation (m) and VTMax (C) across the two populations of *P. achatinus* from the cacao plantation and primary forest.

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