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Thermal niche variation among individuals of the poison frog, *Oophaga pumilio*, in forest and converted habitats

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Abstract

The conversion of natural habitats to human land uses often increases local temperatures, creating novel thermal environments for species. The variable responses of ectotherms to habitat conversion, where some species decline while others persist, can partly be explained by variation among species in their thermal niches. However, few studies have examined thermal niche variation within species and across forest-land use ecotones, information that could provide clues about the capacity of species to adapt to changing temperatures. Here, we quantify individual-level variation in thermal traits of the tropical poison frog, *Oophaga pumilio*, in thermally contrasting habitats. Specifically, we examined local environmental temperatures, field body temperatures (T_b), preferred body temperatures (T_{pref}), critical thermal maxima (CT_{max}), and thermal safety margins (TSM) of individuals from warm, converted habitats and cool forests. We found that frogs from converted habitats exhibited greater mean T_b and T_{pref} than those from forests. In contrast, CT_{max} and TSM did not differ significantly between habitats. However, CT_{max} did increase moderately with increasing T_b, suggesting that changes in CT_{max} may be driven by microscale temperature exposure within habitats rather than by mean habitat conditions. Although *O. pumilio* exhibited moderate divergence in T_{pref}, CT_{max} appears to be less labile between habitats, possibly due to the ability of frogs in converted habitats to maintain their T_b below air temperatures that reach or exceed CT_{max}. Selective pressures on thermal tolerances may increase, however, with the loss of buffering microhabitats and increased frequency of extreme temperatures expected under future habitat degradation and climate warming.

Abstract in Spanish is available with online material.

KEYWORDS

amphibians, body temperature, Costa Rica, CT_{max}, ectotherm, habitat loss, land use, tropical wet forest

1 | INTRODUCTION

The conversion of natural habitats to areas of human land use is one of the most widespread and immediate threats to terrestrial biodiversity (Vié, Hilton-Taylor & Stuart, 2009). Habitat conversion often leads to shifts in the abundances, distributions, and composition of species in an area (Newbold et al., 2015; Nowakowski, Frishkoff, Thompson, Smith & Todd, 2018). The exact mechanisms underlying these shifts are not always well understood but may include resource availability, severity of disturbance, and niche specialization of species (Clavel, Julliard & Devictor, 2011; Driscoll, Banks, Barton, Lindenmayer & Smith, 2013; Keinath et al., 2017). Habitat conversion also frequently alters microclimates from those found in natural habitats (González del Pliego et al., 2016; Senior, Hill, González del Pliego, Goode & Edwards, 2017; Todd & Andrews, 2008). Ectotherms, such as amphibians, are particularly sensitive to temperature changes because their physiological performance—including reproduction, foraging, and growth—depends on environmental temperatures (Huey & Stevenson, 1979). As a result, the responses of ectotherms to habitat conversion may in part be explained by species-specific thermal biology and changes in thermal conditions (Nowakowski, Watling, et al., 2018; Thompson, Halstead & Donnelly, 2018; Tuff, Tuff & Davies, 2016).

The conversion of forest into lands for grazing and agriculture generally reduces canopy cover and exposes the ground to more direct solar radiation, thereby increasing near-ground temperatures in these converted habitats and reducing availability of thermal refugia (González del Pliego et al., 2016; Pringle, Webb & Shine, 2003). Because many tropical ectotherms have narrow thermal safety margins (Huey et al., 2012)—they are exposed to temperatures close to their upper thermal maxima (Deutsch et al., 2008; Sunday et al., 2014)—these species are expected to be more sensitive to the increased temperatures of converted habitats. Changes in thermal environments may in part explain the shifts in spatial distributions of ectotherm populations seen following habitat conversion (Frishkoff, Hadly & Daily, 2015; Nowakowski, DeWoody, Fagan, Willoughby & Donnelly, 2015; Nowakowski, Watling, et al., 2018).

Recent studies have examined why some ectotherm populations decline while others persist in converted habitats by identifying traits associated with species' responses to habitat conversion (Frishkoff et al., 2015; Nowakowski, Watling, et al., 2018). Traits that represent aspects of species' climatic niches, including thermal tolerances, can explain more variation in species' responses to habitat conversion than non-thermal traits. Specifically, species adapted to warm conditions—that is, those with greater upper thermal tolerances—are more likely to persist in converted habitats, whereas species adapted to cooler conditions are often restricted to forest remnants (Nowakowski, Watling, et al., 2018). The changes in the thermal conditions following habitat conversion are therefore capable of driving changes in ectothermic assemblages, filtering species in part by their thermal traits (Frishkoff, Gabot, Sandler, Marte & Mahler, 2019; Frishkoff et al., 2015; Nowakowski, Watling, et al., 2018).

Thermal traits vary not only among species but also within species, and this intraspecific variation can provide clues about how species may adapt or acclimate to changing thermal environments. The potential for species to shift their thermal niches has consequences for predicting their responses to both the rapid temperature changes that result from habitat conversion and the more gradual changes resulting from climate warming (Sinclair et al., 2016). Critical thermal tolerances and preferred body temperatures have been found to vary among populations living in regions with different climate conditions (Barria & Bacigalupe, 2017; Riquelme, Díaz-Páez & Ortiz, 2016; Simon, Ribeiro & Navas, 2015). Furthermore, acclimation experiments have shown capacity for modest changes in individuals' thermal tolerances as a response to exposure to different experimental temperatures. For example, mean increases in CT_{max} were on the order of ~0.02–0.15°C per 1°C increase in acclimation temperature in studies of frogs and lizards (Clusella-Trullas & Chown, 2014; Riquelme et al., 2016; Simon et al., 2015). How thermal traits of individuals of a species vary in altered landscapes may also be shaped by adaptation or acclimation to different thermal conditions (Richter-Boix et al., 2015). The different temperature regimes experienced in forest and in open-canopy, converted habitats likely exert differing environmental selection pressures on populations living in these habitats. Therefore, the magnitude of variation in thermal traits within and among populations in these thermally contrasting habitats may provide insights into the potential (or lack of potential) for species to adapt or acclimate to rapidly changing thermal environments.

Here, we examined multiple aspects of the thermal niche of a tropical poison frog, *Oophaga pumilio*, that occurs in both forest and converted habitats in lowland Costa Rica. To determine the amount of thermal niche variation within this species and whether thermal traits differ between individuals in thermally contrasting habitats, we measured environmental temperatures at the location of each individual frog (i.e., microclimate), field body temperatures (T_b), preferred body temperatures (T_{pref}), and critical thermal tolerances (CT_{max}) of individuals captured from relatively cool forest habitats and those from warmer converted habitats. We also examined whether intrinsic thermal traits, T_{pref} and CT_{max}, were associated with microscale temperature, which can vary considerably within habitats (Nowakowski, Frishkoff, Agha, Todd & Scheffers, 2018; Scheffers et al., 2017). Finally, we determined whether frogs in forest and converted habitats had different thermal safety margins (TSM), defined here as the difference between CT_{max} and T_b (Gunderson & Stillman, 2015; Sinclair et al., 2016). We expected that individuals occurring in open-canopy, converted habitats would be exposed to warmer microclimates, and thereby experience greater T_b, than in forests. We also expected that individuals in converted habitats would exhibit higher mean T_{pref} and CT_{max} and would have narrower thermal safety margins than those found in forests. By examining the amount of variation within thermal traits and how this variation is partitioned within and between habitats for this species, we aim to contribute to the understanding of how ectotherms respond to rapid changes in temperature regimes caused by habitat conversion.

2 | METHODS

2.1 | Study area and focal species

We conducted this study at La Selva Biological Station forest reserve (10.431111 N, 84.003889 W) and in surrounding areas of the Sarapiquí region of northeastern Costa Rica, between June and August 2017. The landscape is composed of wet tropical forest remnants in an agricultural matrix of croplands, plantations, and cattle pastures (Fagan et al., 2013). The region was completely forested until the expansion of the cattle industry drove widespread deforestation, beginning in the 1950s (Butterfield, 1994). The mean annual temperature of this region is 25°C, and the mean annual rainfall is 4 m (Sanford, Paaby, Luvall & Phillips, 1994). We collected frogs and measured body temperatures and microclimates in forests and in open-canopy, converted habitats located both inside and outside La Selva Biological Station. Forest frogs were sampled in several closed-canopy locations within the ~1500 ha La Selva reserve and within two large forest fragments in the surrounding landscape. Areas within La Selva and in one large fragment consisted of remnant forest, whereas the third forest site was previously an agroforestry site that was abandoned in 1966 and regenerated. Previous work in the system shows that vegetations structure in second growth fragments recovers quickly, however, and resembles old growth forest within 21–30 years, in terms of both biomass and species richness (Letcher & Chazdon, 2009). Open, converted habitats primarily consisted of three separate cattle pastures (e.g., Figure S1). However, we did measure several individuals in a large clearing within La Selva reserve and we measured one individual in an open-canopy, heart-of-palm plantation adjacent to one of our forest sites; the results reported below are qualitatively identical if this heart-of-palm individual is removed from the dataset. Replicate sample sites of the same habitat type (considering La Selva as a single site) were separated by ≥ 900 m. All sites were at lowland elevations, between 46 and 214 m asl (x = 85 m).

Our study species was the poison frog *Oophaga pumilio*, a small diurnal amphibian that is among the most common vertebrates in the region; however, populations in the La Selva forest reserve have declined (Whitfield et al., 2007) and local populations have disappeared from other forest remnants in highly agricultural areas (Nowakowski unpubl.). The species is most abundant in forest habitats, but also occurs in converted habitats at lower abundances (Kurz, Nowakowski, Tingley, Donnelly & Wilcove, 2014). In converted habitats, the species is typically associated with small patches of remnant vegetation, such as remnant scattered trees, that can provide cooler microhabitats in otherwise open-canopy areas (Robinson, Warmsley, Nowakowski, Reider & Donnelly, 2013); however, air temperatures of these shaded microhabitats are still warmer, on average, than air temperatures in forest (Nowakowski, Frishkoff, Agha, et al., 2018; Robinson et al., 2013). Individuals of *O. pumilio* maintain very small home ranges (~10 m^2) and movement of adults between forest and pastures may be rare (Donnelly, 1989; Robinson et al., 2013).

2.2 | Field body temperatures and microclimates

In the field, we measured body temperatures during the day of individuals encountered in forest and converted habitat sites using an infrared (IR) thermometer (Mastercool, Class II Laser Product, 52224-A). We slowly walked through a given sampling area, haphazardly searching leaf litter, tree buttresses, and other microhabitats. We sampled each area only once to avoid measuring the same individual multiple times. When we encountered a frog, we quickly placed a plastic mesh cylinder around the individual to temporarily limit movement while avoiding handling that could alter body temperatures. Through the opening in the top of the mesh cylinder, we then took three direct measurements of dorsal body temperatures for each individual from a distance of ~5 cm using the IR thermometer; we then calculated the mean of the three measurements for each individual. We measured the temperatures of perch substrates in the same way using the IR thermometer. We ultimately measured T_b of 111 individuals (53 in forest and 58 in converted habitats). We also measured air temperatures every 5 min using iButton temperature sensors (Maxim Integrated Products) attached to 1.5-m-long PCV poles (at approx. 0.5 m from ground); these PCV poles were carried by each observer so that iButtons functioned as mobile sensors, recording air temperature at the location of each individual frog in the field. We later extracted air temperature measurements recorded by sensors during the observation time of each individual. Snout-to-vent (SVL) length was recorded using calipers. A subset of individuals was captured from each habitat type to measure T_{pref} and CT_{max} using laboratory experiments.

2.3 | Preferred body temperatures

We measured preferred body temperatures (T_{pref}) selected by individuals collected in forest and converted habitat sites by placing them in an experimental thermal gradient of ~10–35°C. Temperature preference trials were conducted in two-shaded, ambient-air laboratories, one within La Selva Biological Station and the other just outside the reserve; this was done to avoid transporting individuals across the boundary of the protected area. We measured T_{pref} of individuals captured from forest and converted habitats at the laboratory outside the reserve, and of forest individuals only inside the reserve. To confirm that these thermal gradients were standardized, we compared temperatures between laboratories using a linear model. The maximum and minimum temperatures of the thermal gradients throughout the study and the T_{pref} of forest individuals in each laboratory were not significantly different (Figure S2, $p > .05$). Thermal gradients were constructed using aluminum material that was fashioned into 20 × 30 × 80 cm enclosures (Figure S3). Each enclosure was covered with a screen-mesh lid and contained sand as substrate. The thermal gradient was produced by attaching a heating pad under one end of the enclosure and placing ice packs under the opposite end. For each set of trials, frogs were randomly assigned to one of three enclosures, and the orientation of each enclosure was alternated by at least 90 degrees; this was done to control for

possible effects of external, directional stimuli on behavior. Prior to each trial, we sprayed the sand substrate with collected rainwater, until the top layer was completely wetted, to provide uniform substrate moisture across the thermal gradient. The enclosures were surrounded by a plain white sheet used as a visual barrier during the trials to minimize the influence of external visual cues on behavior. Each trial began by placing an individual frog at the center of the enclosure and allowing it to acclimate for 10 min. We then measured dorsal temperature with an IR thermometer from a distance of ~5 cm at the start of the trial and every 15 min for 2.5 hr. This protocol yielded 11 repeated T_{pref} measurements of each individual, resulting in 354 total measurements for 32 individuals (16 individuals from forest and 16 from converted habitats). For approximately 30 s during each measurement, the observer placed a small plastic mesh cylinder around the frog to limit its mobility inside the larger aluminum enclosure while taking the three dorsal temperatures, which were averaged to obtain a mean T_{pref} for each 15 min time interval.

2.4 | Measuring CT_{max}

We measured the CT_{max} of individuals collected from forest and open-canopy habitats by placing them into a water bath and raising the water temperature by 0.5°C/min from an initial set point of 26°C by slowly adding and circulating heated water while monitoring the temperature with a thermocouple. The individuals were turned on their back at the end of each 1-min interval using a plastic-slotted ladle to determine whether they could still right themselves. We recorded the water temperature and the ventral temperature (out of the water) using a thermocouple when loss of righting response occurred for 5 s. We analyzed both water temperature and ventral temperature as measurements of CT_{max} because body temperatures of these small frogs (~20 mm SVL) rapidly conform to water temperatures, and although ventral temperature is a more direct measurement, body temperatures could change during the several seconds required to obtain a measurement outside of the water. Animals were then immediately placed into an ambient-temperature water bath following the trial. We measured CT_{max} of 53 individual frogs, 27 from forest and 26 from converted habitats. Frogs from both T_{pref} and CT_{max} experiments were returned to their site of capture following measurements.

2.5 | Data analysis

We first examined simple pairwise relationships among local air temperatures, substrate temperatures, habitat type, and T_b by fitting linear mixed effects models (LMMs) with hour nested within date as random intercepts to account for non-independence of observations on the same time of day or date. We also checked whether prevailing weather conditions could have introduced biases in our temperature measurements taken in different habitats. To do this, we analyzed temperature measurements from the weather station at La Selva taken during the specific days and times that we measured T_b, air, and substrate temperatures for individual frogs. We compared these weather station temperatures by grouping them by the times that we sampled in forest versus in converted habitats—there was no difference in weather station temperatures when sampling in different habitats (also, see results).

To compare competing models of variation in T_b, we again included hour nested within date as random intercepts, and we fit a full LMM with habitat type, substrate temperature, and SVL, as predictor variables (we did not include air temperatures in model selection because this variable was correlated with substrate temperatures). The relationship between T_b and environmental (air and substrate) temperatures was curvilinear; therefore, we fit models with a quadratic term for these predictors, which resulted in improved model fit as judged by Akaike's information criterion corrected for small sample sizes (AICc). We then fit all subsets of the full model, including an intercept-only model, and compared the models using AICc. Because we observed a curvilinear relationship between T_b and environmental temperatures, possibly indicative of thermoregulation, we also performed a post hoc breakpoint regression to determine the temperature threshold at which frogs may be induced to mitigate exposure to warm temperature through thermoregulation.

To analyze variation in T_{pref}, we fit LMMs with individual ID as a random intercept to account for non-independence of observations of the same individual. It was not possible to fit models with varying slopes among individuals because individuals were either captured from forest or converted habitats and were therefore not exposed to both habitat types. We first fit a full model with habitat type and enclosure orientation as predictor variables. We then fit all subsets of this model, including an intercept-only model. We compared the fit of these models using AICc. Due to some missing values for SVL and T_b, we fit individual models with these predictor variables, rather than including them in the full model selection procedure.

To analyze variation in CT_{max}, we fit separate linear models with habitat type, SVL, and T_b as single predictor variables as well as an intercept-only model. Due to missing values of some predictor variables, resulting in slightly different sample sizes across models, we did not compare these models using AICc. To compare thermal safety margins between habitat types, we fit an LMM with hour of T_b measurement as a random intercept. All analyses were performed in R version 3.4.4 (2018), and LMM analyses were performed using "lme4" package (Bates, Mächler, Bolker & Walker, 2014).

3 | RESULTS

Frogs in open, converted habitats were exposed to local air temperatures (sample $\bar{X}_{Converted}$ = 29.5, SD = 2.3, range = 25.1–35.2°C) that were significantly greater than those in forest ($\bar{X}_{Forest}$ = 26.9, SD = 1.1, range = 24.9–28.4°C; model estimates: $\beta_{Converted}$ = 2.336, $SE_{Converted}$ = 0.515, X^2 = 20.6, p < .001 P; Figure 1). Substrate temperatures associated with individual frogs were also greater in converted habitats ($\bar{X}_{Converted}$ = 26.6, SD = 1.9, range = 22.4–32.8°C) than in forest ($\bar{X}_{Forest}$ = 24.9, SD = 0.9, range = 22.8–27.1°C; $\beta_{Converted}$ = 1.606, $SE_{Converted}$ = 0.397, X^2 = 16.4, p < .001; Figure 1). There were no biases

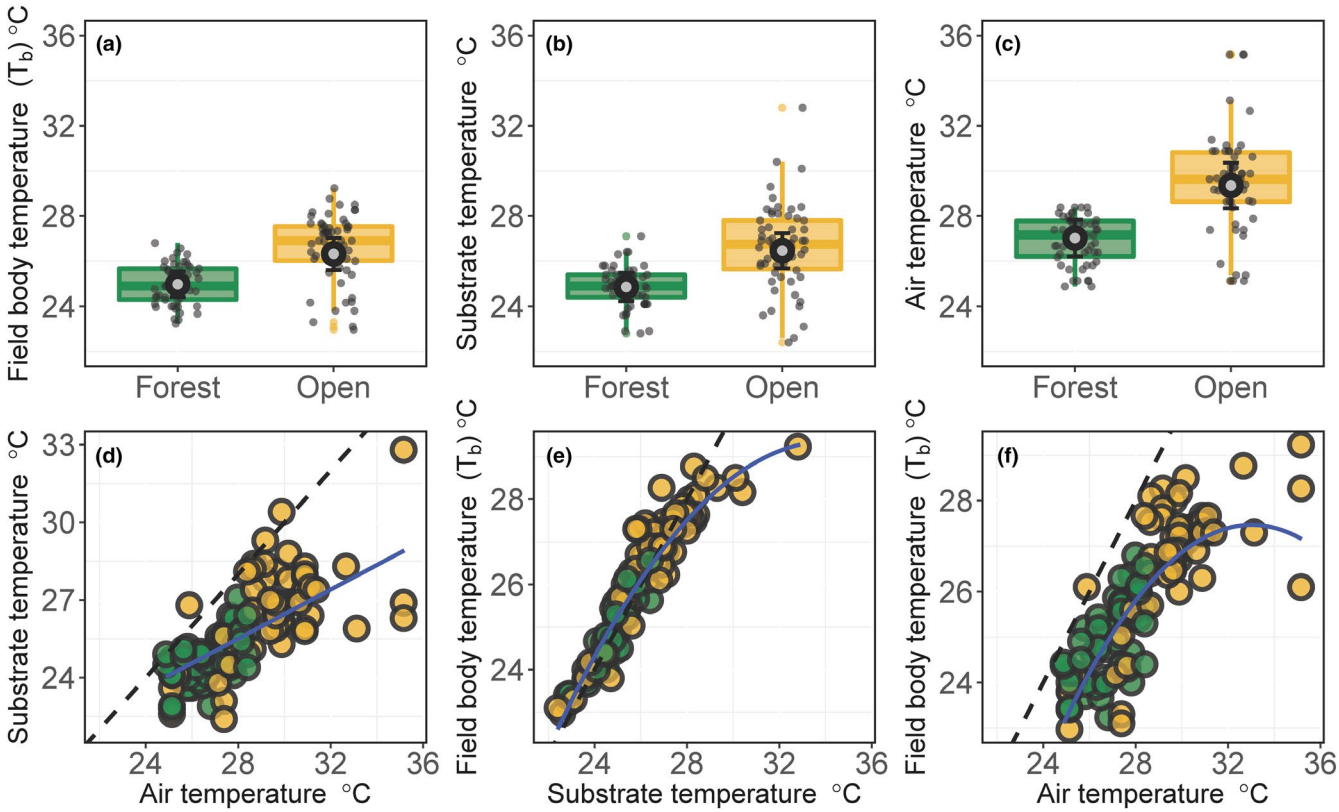

FIGURE 1 Box plots show (a) field body temperatures (T_b), (b) substrate temperatures, and (c) air temperatures experienced by individuals of *Oophaga pumilio* in forests and open, converted habitats. Boxplots indicate the median, interquartile range (IQR), and 1.5*IQR. Dots are individual data points, and circles and error bars indicate predicted mean and 95% CIs from linear mixed models. Scatterplots show relationships between (d) substrate temperature and air temperature, (e) T_b and substrate temperatures, and (f) T_b and air temperatures. Blue lines indicate predicted relationships from linear mixed models, and dotted lines are 1:1 expectations

in prevailing weather conditions when sampling in forest versus converted habitats based on comparisons of air temperatures from the weather station at La Selva ($\beta_{Converted}$ = −0.128, $SE_{Converted}$ = 0.326, X^2 = 0.2, p = .695). There was also no bias in time of day when sampling frogs in forest versus converted habitats (p = .115).

When analyzing variation in T_b, the best fit model included habitat type and substrate temperature as predictor variables (Table 1). After controlling for substrate temperature (β_{Tsub} = 13.106, SE_{Tsub} = 0.544, $\beta_{Tsub}{}^2$ = −2.657, $SE_{Tsub}{}^2$ = 0.421, X^2 = 597.0, p < .001; Figure 1e), T_b was still significantly greater in converted habitats ($\bar{X}_{Converted}$ = 26.6 SD = 1.5, range = 22.3–29.2°C) than in forests ($\bar{X}_{Forest}$ = 25.0, SD = 0.9, range = 23.2–26.8°C; $\beta_{Converted}$ = 0.266, $SE_{Converted}$ = 0.112, X^2 = 5.7, p = .017; Figure 1), possibly due to unmodeled differences in direct solar insolation, air temperatures, or thermoregulatory behavior between habitats that can affect T_b. Based on a post hoc analysis of the relationships between T_b and environmental (air and substrate) temperatures using breakpoint regression, estimated breakpoints for predictors were 26.9°C (SE = 0.25) for substrate temperature and 30.1 (SE = 0.52) for air temperatures. These breakpoints corresponded to T_b values of 27.1°C and 27.3°C, respectively (Figure S4).

We also found that individuals from converted habitats preferred higher body temperatures ($\bar{X}_{Converted}$ = 25.0, SD = 3.6°C), on average, than individuals from forests ($\bar{X}_{Forest}$ = 23.0, SD = 4.3°C) when placed in experimental thermal gradients ($\beta_{Converted}$ = 1.965, $SE_{Converted}$ = 0.752, X^2 = 6.8, p = .009, Figure 2; Table 2). There was no significant relationship, however, between T_{pref} and SVL (β_{SVL} = −0.204, SE_{SVL} = 0.427, X^2 = 0.2, p = .633; Figure S5) or between T_{pref} and T_b (β_{Tb} = 0.459, SE_{Tb} = 0.361, X^2 = 1.6, p = .203; Figure S6). We found no significant difference in CT_{max} between converted habitats ($\bar{X}_{Converted}$ = 30.0, SD = 1.9°C) and forest ($\bar{X}_{Forest}$

TABLE 1 Comparison of linear mixed models explaining variation in field body temperatures (T_b) of *Oophaga pumilio* individuals. Model support is indicated by Akaike's information criterion corrected for small sample sizes (AICc), increase in AICc (ΔAICc) from best-supported model, and model weights

Model	*df*	AICc	ΔAICc	Weight
Habitat + T_{sub}	7	134.4	0	0.613
Habitat + T_{sub} + SVL	8	136.5	2.08	0.217
T_{sub}	6	137.6	3.22	0.123
SVL + T_{sub}	7	139.5	5.12	0.048
Habitat	5	307.6	173.16	<0.001
Habitat + SVL	6	308.4	173.98	<0.001
Null	4	317.3	182.92	<0.001
SVL	5	318.5	184.14	<0.001

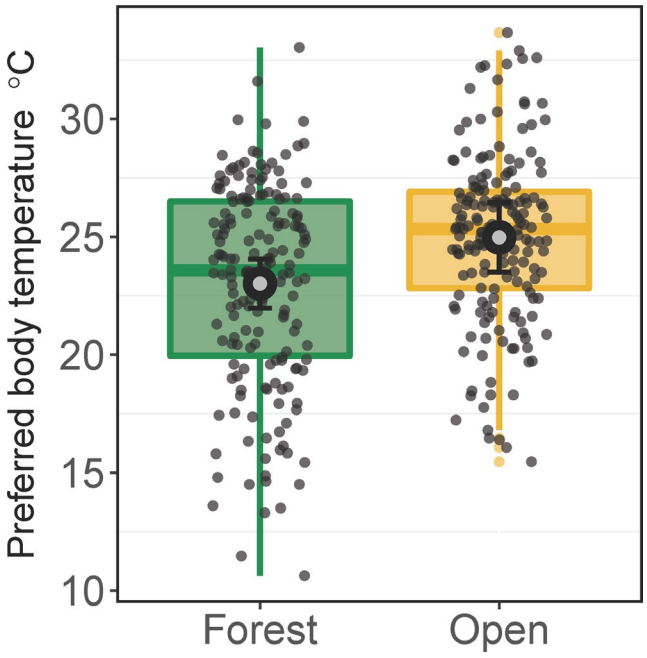

FIGURE 2 Box plots show preferred body temperatures (T_{pref}), measured in thermal gradients, of individuals of *Oophaga pumilio* captured from forests and open, converted habitats. Boxplots indicate the median, interquartile range (IQR), and 1.5*IQR. Dots are individual data points, and circles and error bars indicate predicted mean and 95% CIs from linear mixed models

TABLE 2 Comparison of linear mixed models explaining variation in preferred body temperatures (T_{pref}) of *Oophaga pumilio* individuals, measured in thermal gradients. Model support is indicated by Akaike's information criterion corrected for small sample sizes (AICc), increase in AICc (ΔAICc) from best-supported model, and model weights

Model	*df*	AICc	ΔAICc	Weight
Habitat	4	1940.3	0	0.87
Null	3	1944.4	4.1	0.11
Habitat + Orientation	9	1948.9	8.6	0.01
Orientation	8	1949.2	8.9	0.01

= 29.1, SD = 1.9°C; $\beta_{Converted}$ = 0.844, $SE_{Converted}$ = 0.518, t = 1.6, p = .109; Figure 3), and there was no support for a relationship between CT_{max} and SVL (β_{SVL} = 0.156, SE_{SVL} = 0.212, t = 0.7, p = .466; Figure S5). Using T_b as a predictor of CT_{max}, there was a significant positive relationship between water temperature at CT_{max} and mean T_b (β_{Tb} = 0.453, SE_{Tb} = 0.216, t = 2.1, p = .045; Figure 3); however, this relationship was marginally non-significant when using ventral temperature as a measurement of CT_{max} (β_{Tb} = 0.315, SE_{Tb} = 0.167, t = 1.9, p = .070). Although CT_{max} estimates using water temperature and ventral temperature measurements were highly correlated (r = .98), these measurements deviated slightly from a 1:1 relationship at high temperatures (Figure S7). Thermal safety margins did not differ between forest ($\bar{X}_{Forest}$ = 4.6, SD = 2.1°C) and converted habitats ($\bar{X}_{Converted}$ = 4.4, SD = 1.8°C; $\beta_{Converted}$ = 0.145, $SE_{Converted}$ = 0.758, X^2 = 0.04, p = .849; Figure S8).

4 | DISCUSSION

Habitat conversion is driving the decline of many species worldwide (Newbold et al., 2014). Some species such as *O. pumilio*, however, persist in these converted habitats while others do not (Kurz et al., 2014; Nowakowski, Frishkoff, Thompson, et al., 2018). The novel microclimatic conditions that species are exposed to following habitat conversion may be exerting selective pressures on populations. Therefore, the extent to which species can acclimate or adapt to these changing thermal conditions will likely determine the success of species in the face of continued habitat conversion (Richter-Boix et al., 2015). Here, we found that individuals of *O. pumilio* were exposed to greater environmental temperatures in converted habitats than in forests. This species exhibited intraspecific variation in aspects of its thermal biology, including T_b, T_{pref}, and CT_{max}, and individuals had significantly greater T_b and T_{pref} in converted habitats than in forests. However, we found less divergence in CT_{max} between thermally contrasting habitats. The standing variation in thermal traits may allow for adaptive shifts in response to rapid temperature changes that could delay or forestall changes in distributions expected under changing thermal environments (e.g., climate change). By examining intraspecific variation in thermal traits between habitats, our results contribute to the understanding of species responses to the rapidly changing thermal conditions that arise from habitat conversion and may also provide insights into more gradual temperature increases resulting from climate change (Nowakowski, Watling, et al., 2018; Tuff et al., 2016).

Converted, open-canopy habitats tend to have hotter, drier conditions than those in natural forest habitat (Nowakowski, Frishkoff, Agha, et al., 2018; Senior et al., 2017). At randomly sampled points, maximum air temperatures in converted habitats in the study area can surpass those in forest by more than 10°C, reaching temperatures that exceed the CT_{max} of many tropical ectotherms (Nowakowski, Watling, et al., 2018; Robinson et al., 2013; Sunday et al., 2014). Individuals that persist in converted habitats may avoid extreme temperatures and thermal stress, however, by exploiting thermal heterogeneity at microscales and by limiting their fine-scale distributions to cooler microhabitats within converted habitats. (González del Pliego et al., 2016; Scheffers, Edwards, Diesmos, Williams & Evans, 2014; Sunday et al., 2014). In this study and others, *O. pumilio* were almost exclusively found near remnant native vegetation in converted habitats, such as single trees (Kurz et al., 2014; Robinson et al., 2013; Thompson et al., 2018). These scattered structures provide important patches of relatively cool microhabitats within converted habitats that are otherwise inhospitable for many ectotherms (Manning, Fischer & Lindenmayer, 2006; Nowakowski & Veiman-Echeverria, 2016; Nowakowski, Watling, et al., 2018; Thompson et al., 2018). Even when using these cooler microhabitats,

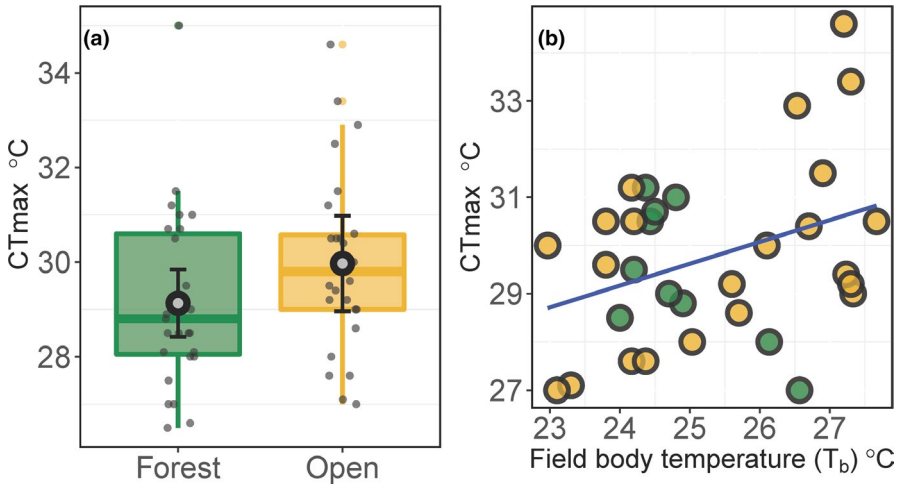

FIGURE 3 Box plots (a) show critical thermal maxima (CT_{max}) of individuals of *Oophaga pumilio* captured from forests and open, converted habitats, measured in water baths and recorded as loss of righting water temperature. Boxplots indicate the median, interquartile range (IQR), and 1.5*IQR. Dots are individual data points, and circles and error bars indicate predicted mean and 95% CIs from linear mixed models. Scatterplot (b) shows effect of field body temperatures (T_b) of individuals of *Oophaga pumilio* in forests and open-canopy habitats on critical thermal maxima (CT_{max}) measured in water baths and recorded as loss of righting response water temperature. Blue line indicates predicted relationships from linear mixed models

environmental temperatures and T_b of *O. pumilio* were warmer, on average, than those measured in forest (Figure 1). As substrate and air temperatures exceeded 27°C and 30°C in converted habitats, respectively, T_b of individuals became decoupled from environmental temperatures (Figure 1e,f and Figure S4), a pattern that possibly indicates that frogs were thermoregulating as a means of avoiding thermal stress. Maintenance of body temperatures below thermal limits through thermoregulation can incur costs, however, such as greater energetic demands on individuals in converted habitats (Huey & Slatkin, 1976).

We found that individuals from converted habitats had greater mean T_{pref} than those from forests. This difference in behavior may result from acclimation or adaptation of T_{pref} to the elevated temperatures individuals are exposed to in converted habitats. A previous study reported intraspecific variation in preferred temperatures of wood frog tadpoles from thermally contrasting ponds (Freidenburg & Skelly, 2004), and studies measuring preferred temperatures of individuals along an elevational gradient have shown selection of higher temperatures by individuals from warmer habitats at lower elevations (Barria & Bacigalupe, 2017). If T_{pref} is often labile, then individuals may be able to behaviorally adapt to novel temperature regimes in converted habitats. In some species, T_{pref} can be tightly coupled with physiological thermal optima, the temperature at which an individual maximizes its physiological performance (Huey et al., 2012; Sinclair et al., 2016; but see Gvoždík, 2015). It is possible, therefore, that observed shifts in T_{pref} may also indicate changes in thermal optima for underlying physiological processes, such as digestion, rate of muscle contraction, or immune function (Angilletta, Hill & Robson, 2002). These results add to a limited number of studies indicating potential for behavioral adaptations to geographic temperature variation. Here, we observed evidence of incipient divergence in T_{pref} among local populations in forest and converted, open-canopy habitats separated, in some cases, by only a few hundred meters.

In contrast, we found no significant difference in CT_{max} between habitats, suggesting that physiological upper tolerances are less labile between habitats than T_{pref} in this species. This finding is consistent with an emerging literature showing that although CT_{max} can vary through acclimation and local adaptation (Richter-Boix et al., 2015), the magnitude of these changes is usually small. In fact, CT_{max} in ectotherms is often phylogenetically conserved (Kellermann et al., 2012; Hoffmann, Chown & Clusella-Trullas, 2013; but see von May et al., 2017), typically does not increase substantially in acclimation or selection experiments (Clusella-Trullas & Chown, 2014; Gunderson & Stillman, 2015; Hoffmann et al., 2013; Simon et al., 2015), and exhibits lower rates of evolution than other thermal traits (Muñoz & Bodensteiner, 2019). We did, however, observe that CT_{max} increased moderately with T_b (though this effect was only marginal), suggesting that acclimation or adaptation of CT_{max} could be driven more by the microhabitat temperatures experienced by individuals and local populations than by mean habitat conditions. Individual *O. pumilio* maintain very small home ranges and may only experience a subset of available microclimates, which can be highly heterogenous within forest or converted habitats (Figure 1; González del Pliego et al., 2016; Scheffers et al., 2017). Within converted habitats, some individuals were exposed to air and substrate temperatures that approached or exceeded mean CT_{max}. As T_b exceeded 27°C, however, frogs maintained T_b below environmental temperatures (Figure 1e,f), possibly through evaporative water loss or behavioral thermoregulation. The ability to avoid deleterious effects of thermal stress through thermoregulation can further limit local adaptation of CT_{max}, a phenomenon known as the Bogert effect (Huey, Hertz & Sinervo, 2003).

Finally, we found that TSM did not differ significantly between habitats, which further supports the inference that individuals in pastures are currently buffered from acute thermal stress, on average, even though environmental temperatures are higher than in forest. The lack of difference in TSM is likely due to a combination of factors, including the moderate increase in CT_{max} with increasing T_b, the frequent use of cooler microhabitats within converted habitats (e.g., remnant trees), and the ability of individuals to maintain T_b below air temperatures and substrate temperatures that approach CT_{max} in converted habitats, possibly through thermoregulation and evaporative cooling (Figure 1). Given the standing variation in CT_{max} among individuals and its association with T_b, there may be some limited potential for CT_{max} to diverge between habitats over time, as observed in other ectotherms (ants, Diamond, Chick, Perez, Strickler & Martin, 2017). Selection pressure on thermal tolerances could increase if buffered microhabitats are lost and individuals experience greater temperature extremes that cannot be sufficiently ameliorated through thermoregulation under continued habitat degradation and climate change.

Assessing intraspecific variation in thermal traits may shed light on how species respond to habitat conversion. The ability to persist in converted habitats may, in part, depend on the degree to which species exhibit variation in thermal traits and can adapt to changing temperature regimes. Despite phenotypic variation in thermal traits among *O. pumilio*, there is currently little (CT_{max}) to moderate (T_{pref}) divergence in thermal traits between groups of individuals in forest and converted habitats suggesting that: (a) acclimation and adaptation potential of thermal limits are not sufficient to keep pace with the continuing increase in temperatures from habitat conversion and climate change (Gunderson & Stillman, 2015; Nowakowski et al., 2017) and/or (b) individuals in converted habitats are currently able to sufficiently buffer themselves from extreme environmental temperatures and are not yet experiencing strong directional selection on thermal traits (Muñoz et al., 2014). These findings suggest directions for future research that examines the consequences of thermal conditions in converted habitats for fitness and population dynamics of ectotherms. Linking thermal trait variation to population dynamics in thermally contrasting habitats may also provide insights into how species will respond to climate change, where similar temperature differences may be experienced over decades of warming. Our results indicate that individual poison frogs may be able to cope, currently, with higher temperatures in converted habitats through behavioral plasticity; however, this species may not be able to persist in these habitats if ongoing habitat degradation and climate warming continue to reduce availability of buffering microhabitats. In the future, resource managers will likely need to implement strategies for maintaining connectivity, remnant forests, and remnant vegetation in converted habitats across the landscape to ensure long-term persistence of *O. pumilio* populations and other lowland tropical ectotherms that are currently experiencing declines.

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DATA AVAILABILITY

Data available from Figshare: https://doi.org/10.6084/m9.figshare.8795141.v1

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