ARTICLE

Equivocal support for the climate variability hypothesis within a Neotropical bird assemblage

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Abstract

The climate variability hypothesis posits that an organism's exposure to temperature variability determines the breadth of its thermal tolerance and has become an important framework for understanding variation in species' susceptibilities to climate change. For example, ectotherms from more thermally stable environments tend to have narrower thermal tolerances and greater sensitivity to projected climate warming. Among endotherms, however, the relationship between climate variability and thermal physiology is less clear, particularly with regard to microclimate variation—small-scale differences within or between habitats. To address this gap, we explored associations between two sources of temperature variation (habitat type and vertical forest stratum) and (1) thermal physiological traits and (2) temperature sensitivity metrics within a diverse assemblage of Neotropical birds ($n = 89$ species). We used long-term temperature data to establish that daily temperature regimes in open habitats and forest canopy were both hotter and more variable than those in the forest interior and forest understory, respectively. Despite these differences in temperature regime, however, we found little evidence that species' thermal physiological traits or temperature sensitivity varied in association with either habitat type or vertical stratum. Our findings provide two novel and important insights. First, and in contrast to the supporting empirical evidence from ectotherms, the thermal physiology of birds at our study site appears to be largely decoupled from local temperature variation, providing equivocal support for the climate variability hypothesis in endotherms. Second, we found no evidence that the thermal physiology of understory forest birds differed from that of canopy or open-habitat species—an oft-invoked, yet previously untested, mechanism for why these species are so vulnerable to environmental change.

INTRODUCTION

An organism's thermal physiology is a critical component of its response to variation in environmental temperature. An influential framework for understanding geographic variation in thermal physiology is the climate variability hypothesis, which predicts that organisms experiencing less temperature variability will have narrower thermal tolerances (Addo-Bediako et al., 2000). According to this hypothesis, tropical species that experience relatively less temperature variability are predicted to have narrower thermal tolerances than their temperate-zone counterparts (Janzen, 1967). Consistent with this prediction, macrophysiological studies of ectotherms (Addo-Bediako et al., 2000; Deutsch et al., 2008; Shah et al., 2017; Sunday et al., 2011, 2019) and, to a lesser extent, endotherms (Araújo et al., 2013; Pollock et al., 2019; Sunday et al., 2019) have collectively demonstrated that species in the tropics have narrower thermal tolerances than their temperate counterparts. An important implication of the climate variability hypothesis is that tropical species will likely be more susceptible to climate warming. Tropical ectotherms, in particular, which often live close to their optimal temperatures, are thus predicted to be especially sensitive to even small increases in temperature (Deutsch et al., 2008; Sunday et al., 2011, 2019).

To date, tests of the climate variability hypothesis have focused on latitudinal patterns of variation in temperature tolerances, yet the same principles should also apply at smaller spatial scales. Within a given locality, temperature regimes can vary markedly within and among habitats (De Frenne et al., 2021; Scheffers et al., 2014). For example, temperatures differ among habitats and among vertical strata within forests, generally becoming hotter and more variable in open habitats and with increasing forest height (De Frenne et al., 2019; Scheffers et al., 2013, 2014). Correspondingly, a wide range of ectothermic taxa that inhabit more exposed habitats and forest canopy exhibit broader thermal tolerances and higher heat tolerances than their counterparts in the forest understory (Baudier et al., 2018; Huey et al., 2009; Kaspari et al., 2015; Leahy et al., 2021; Marshall et al., 2015; Muñoz et al., 2014; Pintanel et al., 2019; Tracy et al., 2010). Ultimately, these microclimate-driven differences in thermal physiology can impact fitness and underlie variation in susceptibility to climate change (Duffy et al., 2015; Huey, 1991; Huey et al., 2009, 2012;

Pincebourde & Woods, 2020). Therefore, understanding the links between microclimate, thermal physiology, and fitness will be a critical step toward predicting and mitigating the impacts of climate change.

Although evidence in endotherms is comparatively sparse, several recent studies have revealed associations between microclimate and thermal physiology in both birds and mammals. Desert rodents occupying drier, hotter, and more variable microclimates tended to have broader thermoneutral zones (TNZs) and higher heat tolerances than closely related species inhabiting cooler, less variable microclimates (van Jaarsveld et al., 2021; Wallace et al., 2021). Cave-roosting bats that rest in cooler, more stable microclimates had lower heat tolerances and evaporative cooling capacities than those from more thermally variable, open environments (Czenze et al., 2022). Finally, an open-country songbird, the horned lark (*Eremophila alpestris*), exhibited greater seasonal flexibility in metabolic rates than the house sparrow (*Passer domesticus*), a similarly sized species that occupies less thermally variable habitats (Oboikovitz & Swanson, 2022). Taken together, these studies suggest a link between microclimate variation and thermal physiology in endotherms as well. However, most of these studies involve species pairs inhabiting environmental extremes such as deserts and caves, where differences in thermal physiology are likely to be maximized. Furthermore, all studies are focused on environmental temperature, which is only one of many aspects of the microclimates that organisms experience and that can influence thermoregulation (Maclean et al., 2021). Thus, the generality of these conclusions as they pertain to less extreme climate differences, other aspects of microclimate such as humidity and solar radiation, and a greater diversity of species remains unclear. Understanding the relationships between microclimate and thermal physiology is of particular importance in the tropics, where the majority of biodiversity resides (Pillay et al., 2022) and vulnerability to environmental change is highest (Deutsch et al., 2008; Sunday et al., 2011).

Questions about how microclimate impacts thermal physiology are particularly relevant for tropical forest birds, which inhabit some of the most thermally buffered terrestrial climates on Earth (De Frenne et al., 2019). Evolution in such thermally stable environments is thought to select for narrow physiological tolerances (reviewed in Sherry, 2021), and this putative physiological sensitivity has been invoked for explaining the declines of

understory birds following forest fragmentation (Canaday, 1996; Stratford & Robinson, 2005). Specifically, the microclimate hypothesis proposes that understory birds cannot physiologically tolerate the abiotic changes associated with forest fragmentation such as reduced humidity, increased temperature, and increased solar radiation (Laurance et al., 2002), resulting in population declines in fragmented forests (reviewed in Robinson & Sherry, 2012; Sherry, 2021). Given the widespread sensitivity of tropical understory birds to forest fragmentation (Boyle & Sigel, 2015; reviewed in Powell et al., 2015) and the recent evidence of their population declines even in intact forests (Blake & Loiselle, 2015; Neate-Clegg et al., 2021; Pollock et al., 2022; Stouffer et al., 2021), it is a research priority to evaluate the potential role of thermal sensitivity as the mechanism for their declines.

To explore the links between microclimate, thermal physiology, and susceptibility to climate warming, we conducted the first community-wide, local-scale test of the climate variability hypothesis in endotherms. Our analyses focused on two particular aspects of environmental temperature—mean temperature and temperature variability. We acknowledge that focusing on mean temperature oversimplifies how animals respond to climate in two key ways. First, other aspects of climate can interact with temperature to influence the thermal physiology of endotherms, including humidity and solar radiation (McKechnie & Wolf, 2019; Wolf & Walsberg, 1996). Second, temperature extremes and chronic exposure to high temperatures can exacerbate the impacts of climate on thermal physiology and may not be captured by mean temperatures (Bailey & van de Pol, 2016). Nevertheless, our data provide an important first step toward understanding how variation in temperature regimes impacts the thermal physiology of endotherms. Specifically, we assessed the relationships between thermal physiology and daily temperature variability in an ecologically and taxonomically diverse suite of tropical bird species ($n = 89$) from central Panama. First, we employed 10 years of temperature data to empirically characterize daily temperature variation across local habitat types (forest vs. nonforest) and, within forests, vertical strata (understory vs. midstory vs. canopy). We then combined these temperature data with published information on heat tolerances (Pollock et al., 2021) and new data on TNZs to test for associations between thermal physiological traits (Appendix S1: Figure S1) and habitat type/ vertical stratum. Lastly, we calculated two metrics of temperature sensitivity, thermal safety margin and warming tolerance (following Pollock et al., 2021), to assess whether vulnerability to climate warming varied between species exposed to distinct environmental temperature regimes. Based on the climate variability hypothesis, we

predicted that species exposed to higher and more variable temperatures (i.e., species inhabiting open habitats or the forest canopy) would have (1) higher heat tolerances and broader TNZs and (2) lower thermal safety margins and warming tolerances than those inhabiting closed habitats and the forest understory.

METHODS

Study site

We conducted fieldwork and thermal physiology experiments in central Panama from 2013 to 2015. Rainfall in our study area varies seasonally, with a pronounced dry season occurring between December and April and a rainy season from May to November. In each year, we sampled birds across seasons (February–August) since these species do not exhibit strong seasonal variation in thermal physiological traits (Pollock et al., 2019). We captured birds in a variety of habitats to encompass the available range of temperature variation at our study site. "Open" habitats included fields and suburban gardens in and around the village of Gamboa (09°07′ N, 79°42′ W). In contrast, "forested" habitats included a ~25-ha forest fragment in Gamboa and continuous lowland moist forest ranging in age from young secondary forest (~40 years old) to tracts of primary growth (>300 years old) along Pipeline Road in Soberanía National Park.

Ecological correlates of temperature regime

To explore the potential influence of temperature on avian thermal physiology, we selected two well-established ecological sources of temperature variation—habitat type (Huey et al., 2009; Muñoz et al., 2014) and, for forest species only, vertical stratum (Scheffers et al., 2013, 2014). Specifically, temperature profiles vary predictably with degree of habitat openness and vertical stratum, generally becoming hotter and more variable with increasing exposure to sunlight (i.e., in open habitats and the forest canopy; De Frenne et al., 2019; Scheffers et al., 2013, 2014). We classified species-specific habitat associations and vertical strata based on capture locations supplemented with information on habitat use from Birds of the World species accounts (see https://birdsoftheworld.org/bow/home). We categorized species into one of four categories based on their preferred habitat type: open (inhabiting open habitats with the greatest direct sun exposure), second growth (inhabiting local gardens and young successional habitats), forest edge (inhabiting edges, gaps, or forest canopy), and

forest interior (inhabiting the understory or midstory of closed-canopy forest). We similarly categorized forest species into one of three vertical strata: understory (0–10 m above the ground), midstory (10 m–canopy), and canopy (remaining in or above the canopy). Generalist species that used multiple strata were aggregated into the midstory stratum.

To quantify variation in daily temperature regimes within and between (1) habitat types and (2) vertical forest strata, we used 10 years of temperature data (2010–2019) collected by the Smithsonian Tropical Research Institute's Physical Monitoring Program (https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado). Specifically, we synthesized data from four different temperature sensors on Barro Colorado Island (<10 km from our study sites): one from a clearing ("El Claro") and three vertically stratified sensors in nearby closed-canopy forest (understory [1 m], midstory [20 m], and canopy [42 m]). All four sensors recorded the average air temperature during 15-min intervals, with very few failures or data gaps (99.3%–99.9% of records were designated as "datum acceptable"). The understory sensor registered the least temperature variability (Figures 1 and 2), both in terms of the smallest mean daily variation (maximum−minimum = 4.0°C) and the least variation around those ranges (SD = 1.3°C). In contrast, the open clearing displayed the greatest variability (6.2°C and 1.6°C, respectively), whereas the midstory and

canopy were intermediate (Figures 1 and 2). This 2.2°C difference translates to a 55% increase in mean daily temperature variation from the forest understory to the open habitat. Increasing ranges were primarily due to divergent mean daily maxima (Figure 1): understory (28.2°C) < midstory (29.3°C) < canopy (29.5°C) < open (30.0°C). Mean daily minima were more consistent (Figure 1), with only a 0.5°C difference between the coolest (open; 23.7°C) and warmest (understory; 24.2°C) microhabitats. Because these data were collected <10 km away, we acknowledge that they only approximate the temperature profiles from sites where birds were captured. However, the close proximity to our study site and its similar forest structure (Leigh, 1999) suggest that similar patterns of temperature variation are likely across vertical strata and within habitat types.

Bird capture and handling

We captured birds in mist nets (12 × 2.6 m; 36-mm mesh) and banded them to ensure that no individual was sampled more than once. We also assessed individual breeding condition, releasing all individuals that exhibited signs of reproduction such as an active brood patch or obvious cloacal protuberance. We then transported focal birds to a temperature-controlled lab (27°C) and housed them in cloth-covered cages for 1–4 h
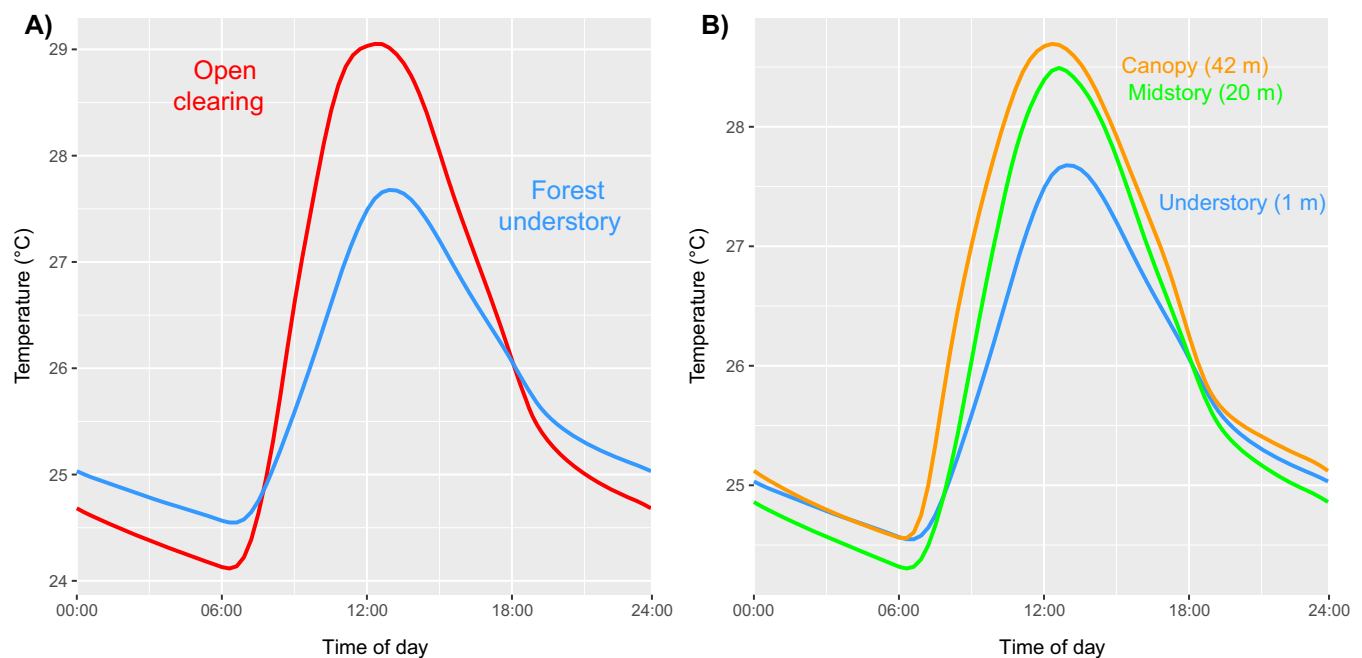
FIGURE 1 Differences in daily temperature regimes (A) between forest understory and an open clearing (both 1 m in height) and (B) across three vertical forest strata (understory [1 m], midstory [20 m], and canopy [42 m]) at Barro Colorado Island, Panama (<10 km from the study area). Temperature data were obtained from two long-term environmental monitoring stations ('El Claro' for the open clearing and the Lutz Meteorological Tower for forest data) as part of the Smithsonian Tropical Research Institute's Physical Monitoring Program. Habitat- and stratum-specific temperature profiles were generated by modeling average air temperatures recorded at 15-min intervals (2010–2019) using generalized additive models with cyclic cubic regression splines.
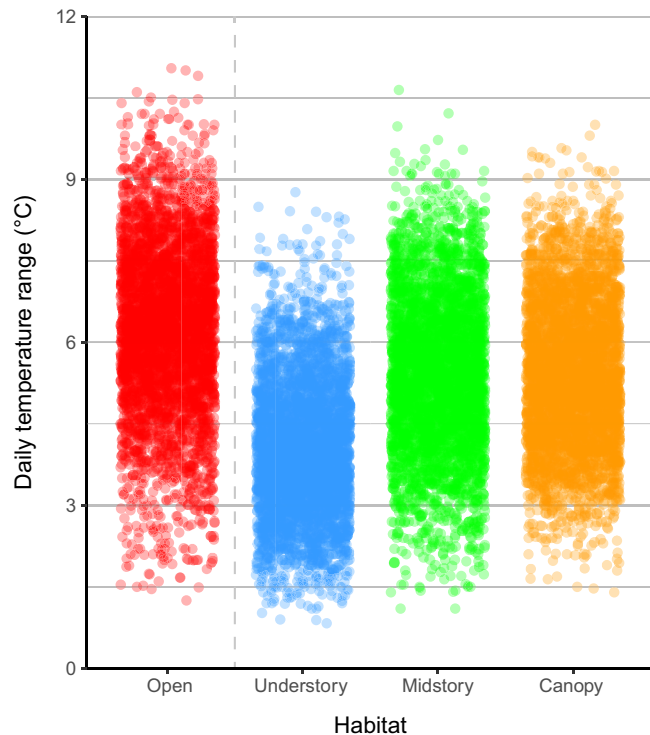
FIGURE 2 Daily temperature ranges (maximum daily temperature − minimum daily temperature) from the four environmental monitoring sensors at Barro Colorado Island, Panama, where temperature data were collected between 2010 and 2019. For each sensor, only days with complete temperature data were retained (3615–3649 individual days).

TABLE 1 Glossary of thermal physiological traits and temperature sensitivity metrics measured in present study.

Term	Definition	Source
Thermal physiological trait		
LCT	Lower limit of TNZ	McNab (2002)
UCT	Upper limit of TNZ	
TNZ breadth	Range of temperatures within which an endotherm lies at a basal metabolic rate and is not expending energy to maintain heat balance	
HTL	Maximum air temperature an endotherm can tolerate before onset of thermoregulatory failure	McKechnie & Wolf (2019)
Temperature sensitivity metric		
TSM	Difference between maximum air temperature and a species' mean UCT at given locality	Pollock et al. (2021)
WT	Difference between maximum air temperature and a species' mean HTL at given locality	

Abbreviations: HTL, heat tolerance limit; LCT, lower critical temperature; TNZ, thermoneutral zone; TSM, thermal safety margin; UCT, upper critical temperature; WT, warming tolerance.

with water provided *ad libitum* until temperature experiments began. Prior to the onset of experiments, we weighed all individuals using a digital scale (American Weigh Scales Model AWS-201, 200 ± 0.01 g).

Endotherm thermal physiology and temperature sensitivity metrics

The thermal physiology of endotherms can be conceptualized using a Scholander curve (Scholander et al., 1950; see Table 1 for thermal physiology definitions). Within the TNZ, endotherms maintain a basal metabolic rate (BMR), defined as the minimum metabolism required for existence measured during the rest phase (i.e., the time period in the diel cycle when birds are generally inactive) and after the animal is post-absorptive, or not expending metabolic energy on digestion (following McKechnie & Wolf, 2004). The TNZ is bounded by the lower critical temperature (LCT) and upper critical temperature (UCT). Below the LCT, endotherms must generate heat to maintain internal temperature homeostasis, thereby increasing metabolic rate. Similarly, above the UCT, endotherms must actively dissipate heat via evaporative water loss, which is also accompanied by a concomitant increase in metabolic rate (McNab, 2002). The maximum capacity to tolerate acute heat stress, or the heat tolerance limit (HTL), is defined by the air temperature at which an endotherm can no longer regulate its body temperature and uncontrolled hyperthermia begins (McKechnie & Wolf, 2019; Smith et al., 2015).

We also calculated two metrics of temperature sensitivity that have been previously employed as proxies for an organism's sensitivity to climate warming. To do so, we used estimates of UCT and HTL coupled with habitat- and stratum-specific average maximum temperatures derived from the aforementioned tower data. First, to determine the magnitude of temperature increase that an organism could tolerate prior to incurring energetic costs due to thermoregulation, we calculated the thermal safety margin (TSM), the difference between the UCT and the maximum air temperature (Khaliq et al., 2014). To determine the magnitude of temperature increase an organism could tolerate prior to reaching its thermoregulatory limit, we calculated the warming tolerance (WT), the difference between HTL and maximum air temperature (Diamond et al., 2012).

Temperature experiments

We performed two types of temperature experiments: (1) gradual thermal ramping to assess the breadth of the TNZ and (2) acute thermal ramping to assess heat tolerance. TNZ experiments were conducted at night, during which time we collected data on the LCT, UCT, and TNZ breadth. Heat stress experiments were conducted during the day, during which we measured HTL. All data on TNZ breadth are original, whereas the HTL data were collated from Pollock et al. (2021). Both data sets were collected using the same respirometry system (see Pollock et al. [2021] for more details on the methodology used in the heat stress experiments). In brief, we weighed and processed focal individuals, placed the birds in respirometry chambers held at 30°C, and then increased temperature by intervals of 3°C until the birds reached their HTL (i.e., exhibited uncontrolled hyperthermia or prolonged signs of distress behavior such as flight attempts, pecking the chamber walls, or loss of motor coordination). We monitored body temperature at 1-min intervals throughout both trials using temperature-sensitive Passive Integrated Transponder tags that were inserted into the cloaca (Pollock et al., 2021).

For the TNZ experiments, we transferred focal individuals at ~19:00 from cages to respirometry chambers (see *Respirometry system and gas analysis* below) situated inside a PTC-1 temperature cabinet (Sable Systems, Inc.) controlled by a Peltier device (Pelt-5, Sable Systems, Inc.). We let birds acclimate to the chambers at 30°C for ≥3 h to ensure that individuals were both post-absorptive and resting before initiating temperature experiments. Throughout the temperature experiments, we precisely regulated ambient temperature (T_a) in the cabinet and continuously monitored chamber temperatures using thermistor probes (Model SEN-TH, Sable Systems, Inc., ±0.2°C accuracy). We also used infrared cameras (Model WCM-6LNV, Sabrent) to continuously monitor bird behavior inside the chambers throughout the experiment. Because activity level can influence metabolic rate (Aschoff & Pohl, 1970) and confound the relationship between T_a and metabolic rate, we discarded data for focal birds that exhibited high levels of activity (i.e., individuals that were visibly agitated and attempting to fly inside the respirometry chamber) during the experiment.

After the initial 3-h acclimation period, we used thermal ramping protocols (sensu Mitchell & Hoffmann, 2010) to determine the relationship between T_a and metabolic rate and to characterize TNZ breadth (Appendix S1: Figure S1). Starting at 30°C, we either increased (UCT experiments) or decreased (LCT experiments) T_a in increments of 3°C, holding birds at each T_a for 1 h while measuring their O_2 consumption. We concluded the experiments when O_2 consumption had increased in three successive sampling intervals, thereby ensuring that the focal individual had exceeded the bounds of the TNZ. The morning after the temperature experiments, we weighed each individual again before releasing it at the site of capture, using the mean of its initial and final mass as its body mass.

Respirometry system and gas analysis

We employed push-mode flow-through respirometry (Withers, 2001) to measure the gas exchange of our focal bird species, which we then used to assess relationships between metabolic response to temperature. To minimize the impact of humidity on estimates of thermal physiological traits (Gerson et al., 2014), we scrubbed water vapor from the airstream prior to gas analysis. To remove water, we pumped incurrent air (PP2 pump; Sable Systems, Inc.) through a column of Drierite and into a mass-flow controller (Flowbar-8; Sable Systems, Inc.) that divided the air stream into four channels. Each channel was plumbed through Bevaline IV tubing (Cole-Parmer) and led to one of four separate Plexiglas metabolic chambers. To prevent leakage, each chamber was equipped with a rubber gasket in the lid and sealed with binder clips (ACCO Brands Corporation), and the system was tested regularly for leaks. One empty chamber served as a reference or baseline for the other three chambers, each of which was designed to hold a single bird. During the experiments, birds rested on perches made of wire mesh. To ensure that incurrent air flowed directly across the bird before exiting the chamber, the inlet (on the lid of the chamber) was situated opposite the outlet (on the side of the chamber). Flow rates (300–1500 mL min^{-1}) and chamber sizes (1.97 or 4.53 L) varied depending on the size of the focal species, with higher flow rates and larger chambers used for larger species. Excurrent air from each chamber was sequentially subsampled at 100–150 mL min^{-1} through barrel syringes, scrubbed of water vapor (Drierite) and CO_2 (Ascarite), and analyzed for $\%O_2$ (FoxBox; Sable Systems, Inc.). During each experiment, we measured flow rate, T_a, and $\%O_2$ at 1-s intervals using the program Expedata (Sable Systems, Inc.). We used a Catmull-Rom spline to correct for drift in the O_2 analyzer. Using the following equation, we then converted $\%O_2$ to $\dot{V}O_2$ (rate of O_2 consumption, measured in milliliters of O_2 per minute):

$$\dot{V}O_2 = FR \times (FiO_2 - FeO_2)/(1 - FeO_2),$$

where FR is the flow rate of the animal chamber (in milliliters per minute at standard temperature and pressure dry), FiO_2 is the incurrent fractional O_2

concentration (0.2095), and FeO_2 is the excurrent fractional O_2 concentration. We calculated BMR as the lowest stable 5-min average of $\dot{V}O_2$ measured during the experiment (Londoño et al., 2015). We used a coefficient of 20.08 J/mL O_2 to convert $\dot{V}O_2$ to metabolic rate (Schmidt-Nielsen, 1997). To determine the relationship between metabolic rate and T_a, we obtained 3-min rolling averages for metabolic rate and the corresponding T_a throughout the entire experiment, generating a series of paired T_a and metabolic rate measurements, which we then used to parameterize the TNZ of each focal individual. To estimate TNZ breadth for each individual, we identified inflection points in the relationship between T_a and metabolic rate using piecewise linear regression in the *segmented* package (Muggeo, 2008) in R (version 4.1.0; R Core Team, 2021). Due to the duration of thermal ramping protocols, we were only able to estimate either the UCT or the LCT of a given individual bird. To obtain species-level estimates of LCT and UCT, we pooled individual values and applied the mean as that species' LCT/UCT. From these values, we calculated species-level TNZ breadth as the difference between a species' UCT and LCT (Khaliq et al., 2014).

Statistical analysis

Prior to assessing the relationships between air temperature and thermal physiology, we generated a phylogeny that we used to account for the influence of nonindependence among taxa on thermal traits. Using the TreeAnnotator tool in BEAST (Drummond & Rambaut, 2007), we first built a maximum clade credibility tree, which we pruned down to our 89 focal species (Appendix S1: Figure S2). We then tested whether phylogenetic relatedness predicted variation in thermal physiological traits using phylogenetic generalized least-squares (PGLS) models with the "pgls" function in the *caper* R package (Orme et al., 2013). We optimized branch length transformations using maximum likelihood and employed Pagel's λ (a metric of phylogenetic signal ranging from 0 to 1, with 0 indicating trait evolution independent of phylogeny and 1 indicating that traits are evolving according to Brownian motion on the given phylogeny; Pagel, 1999) to estimate phylogenetic signal for each thermal trait. PGLS models revealed strong phylogenetic effects on HTL (λ = 0.7), whereas we found no evidence of phylogenetic signal for UCT, LCT, or TNZ breadth (all λ = 0). However, given the strong phylogenetic signal for HTL, we opted to use PGLS models for our subsequent analyses, and we present those results in what follows.

We tested for associations between avian thermal physiological traits and correlates of microclimate variation with phylogenetically controlled analysis of variance, a simulation-based test derived from Garland et al. (1993), using the "phylANOVA" function in the *phytools* package (Revell, 2012). Because this was a simulation-based test, which does not calculate degrees of freedom or Pagel's λ (nor provide effect sizes or R^2 values), we report the F-statistic and p-value for each phylogenetic ANOVA.

For each ANOVA, we included habitat type or vertical forest stratum as the predictor variable and the trait of interest (i.e., thermal physiological trait or temperature sensitivity metric) as the response variable. To correct for multiple comparisons, we then conducted Holm's sequential Bonferroni post hoc tests on each ANOVA. We report the t-statistic and p-value for each of the significant pairwise post hoc comparisons (α = 0.05).

Because we had small sample sizes (<3 individuals) for 47% (42/89) and 55% (30/55) of focal species whose TNZs and heat tolerances were measured, respectively, we conducted analyses in two ways: (1) on the entire complement of focal species and (2) on focal species with sample sizes of $n \geq 3$ individuals (following recommendations for minimum sample sizes for physiological analyses in McKechnie & Wolf, 2004). We found qualitatively similar results between analyses for all traits (Appendix S1: Tables S1 and S2), and therefore we report results from the analysis of the entire complement of focal species. Similarly, because we had small sample sizes for species from canopy ($n = 3$) and open habitats ($n = 6$), we combined canopy and midstory species and combined forest edge/interior species and edge/open species and reran the vertical stratum analyses. We found qualitatively similar results between analyses for all traits (Appendix S1: Table S2), and therefore we opted to retain the original stratum and habitat classifications in the analyses presented below.

RESULTS

We estimated thermal physiological traits and temperature sensitivity metrics in 478 individuals representing 89 bird species sampled from 27 avian families (henRyPollock, 2023). We found no evidence that sources of temperature variability (i.e., habitat type and vertical forest stratum) explained interspecific variation in avian thermal physiology (Figures 3 and 4). None of the four thermal physiological traits was significantly associated with either habitat type or vertical stratum (Table 2), and we found broad overlap in mean trait values across habitats and strata (Appendix S1: Tables S3 and S4).
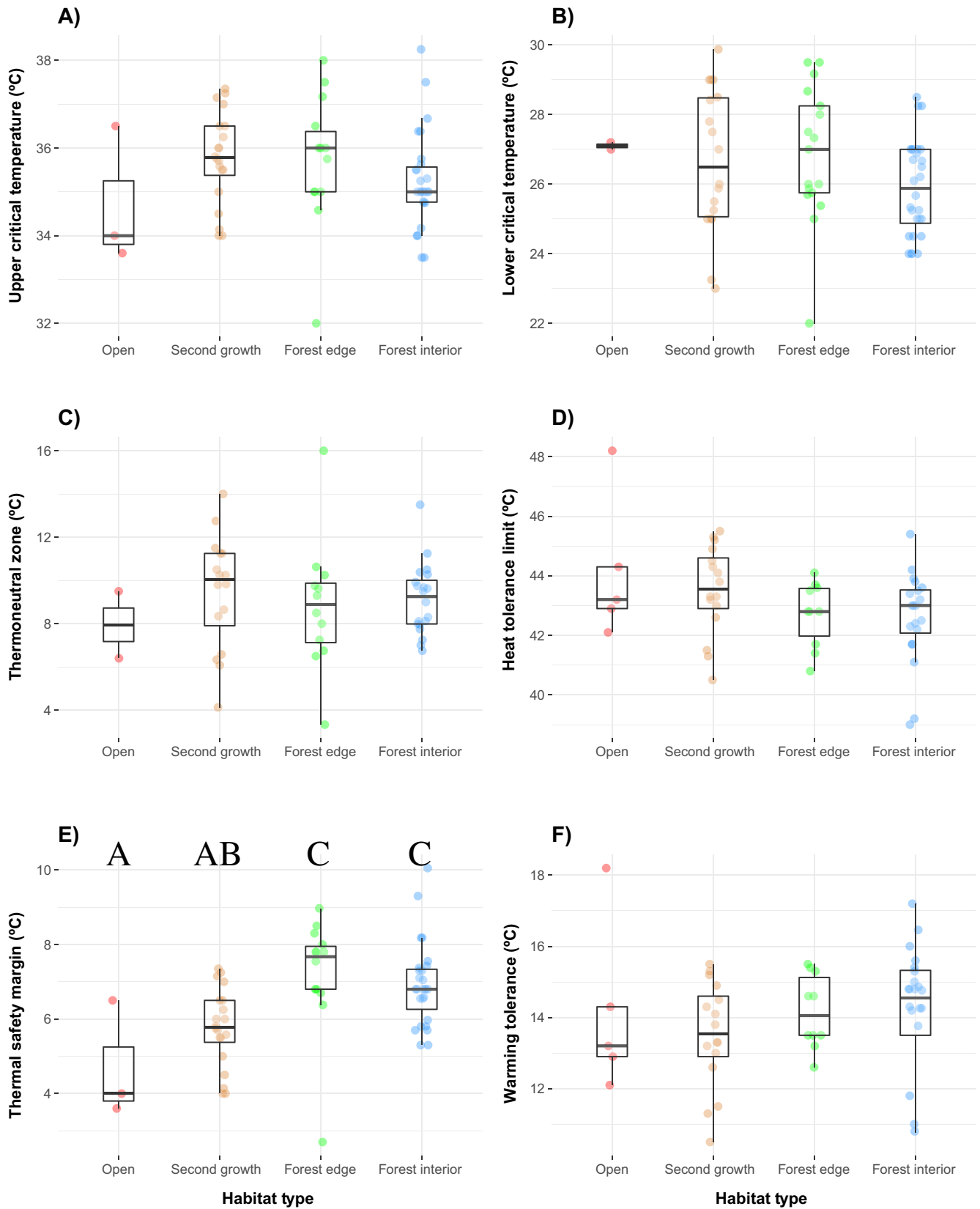
FIGURE 3 Box plots of thermal physiological traits (A: upper critical temperature; B: lower critical temperature; C: thermoneutral zone; D: heat tolerance limit) and temperature sensitivity metrics (E: thermal safety margin; F: warming tolerance) in relation to habitat type for 89 species of tropical birds from central Panama. See Table 1 for trait and metric definitions.
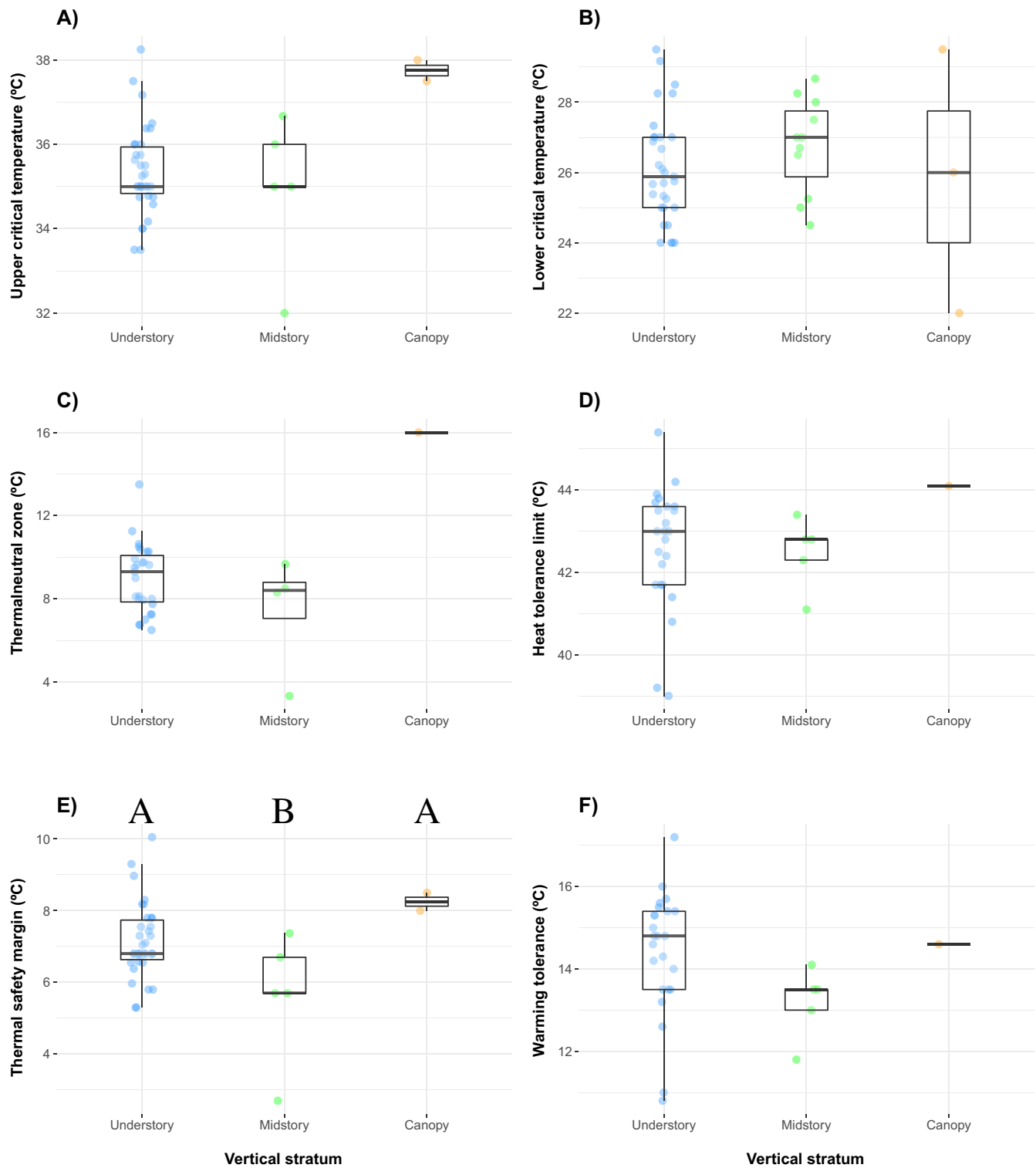
FIGURE 4 Box plots of thermal physiological traits (A: upper critical temperature; B: lower critical temperature; C: thermoneutral zone; D: heat tolerance limit) and temperature sensitivity metrics (E: thermal safety margin; F: warming tolerance) in relation to vertical forest stratum for 89 species of tropical birds from central Panama. See Table 1 for trait and metric definitions.

In contrast to thermal physiological traits, we found differences in temperature sensitivity metrics across habitat types and vertical forest strata. TSM, the difference between UCT and maximum air temperature, was significantly associated with both habitat type and vertical stratum (Table 2, Figures 3 and 4). Specifically, TSM was significantly higher in forest edge species compared to second growth ($t = 3.41$, $p = 0.006$) and open habitat

TABLE 2 Phylogenetic analysis of variance (ANOVA) model results testing for associations between avian thermoregulatory responses and two correlates of temperature variation for 89 species of tropical birds from central Panama.

Temperature correlate	Trait	F-statistic	p-value
Habitat type	Thermal physiological trait		
	UCT	1.44	0.32
	LCT	1.43	0.24
	TNZ	0.34	0.81
	HTL	2.02	0.18
	Temperature sensitivity metric		
	TSM	7.34	**0.002****
	WT	0.70	0.65
Vertical forest stratum	Thermal physiological trait		
	UCT	0.57	0.43
	LCT	0.70	0.66
	TNZ	2.52	0.08
	HTL	0.04	0.85
	Temperature sensitivity metric		
	TSM	5.12	**0.02***
	WT	3.16	0.11

Note: For each model, the *F*-statistic and *p*-value are shown. Note that the degrees of freedom are not provided because the *p*-values were obtained from phylogenetic simulation. (1) Associations between habitat type and thermal physiological traits or temperature sensitivity metrics. (2) Associations between vertical forest stratum and thermal physiological traits or temperature sensitivity metrics. Bold font indicates a significant association.
Abbreviations: HTL, heat tolerance limit; LCT, lower critical temperature; TNZ, thermoneutral zone; TSM, thermal safety margin; UCT, upper critical temperature; WT, warming tolerance.
*p < 0.05; **p < 0.01.

species ($t = 3.27$, $p = 0.006$) and significantly higher in forest interior species compared to open habitat species ($t = 3.03$, $p = 0.008$). With respect to vertical stratum, TSM was significantly higher in understory species ($t = 2.79$, $p = 0.009$) and canopy species ($t = 2.75$, $p = 0.02$) than midstory species. However, WT, the difference between HTL and maximum air temperature, was not significantly associated with either habitat type or vertical stratum (Table 2, Figures 3 and 4). Similar to thermal traits, we found broad overlap in mean values of TSM and WT across habitats and strata (Appendix S1: Tables S3 and S4).

DISCUSSION

We coupled thermal physiology data from 89 Neotropical bird species with in situ temperature data across habitats and forest strata to provide the first community-wide assessment of associations between local temperature variation, thermal physiology, and temperature sensitivity in endotherms. Contrary to the predictions of the climate variability hypothesis, we found no evidence that site-specific temperature variation influenced avian thermal physiology. None of the four thermal physiological traits (LCT, UCT, TNZ breadth, or HTL) was associated with either habitat type or vertical stratum. Similarly, we found no support for the prediction that species exposed to less variable temperature regimes (i.e., forested habitats and lower vertical strata) would have narrower TSMs and WTs. In fact, we found the exact opposite—species from open habitats and the forest canopy had narrower TSMs than species from forest habitats and the forest understory, respectively. Our results therefore stand in sharp contrast to numerous studies in ectotherms that document strong associations between local-scale temperature, thermal physiology, and sensitivity to climate warming (Baudier et al., 2018; Deutsch et al., 2008; Huey et al., 2009, 2012; Kaspari et al., 2015). Furthermore, our results do not support the longstanding but untested microclimate hypothesis, which posits that the constrained thermal physiology of tropical understory birds is the mechanism for their sensitivity to environmental change (Stratford & Robinson, 2005). Instead, our findings echo the evidence summary by Sherry (2021), which asserts that recent empirical studies of tropical birds have largely failed to find support for this putative physiological sensitivity.

From a purely physiological perspective, our findings suggest that tropical endotherms may be fundamentally less impacted by variation in environmental temperature than tropical ectotherms. Whereas ectotherm thermal physiology and fitness are directly tied to the environmental temperatures they experience (Huey et al., 2012), the links between temperature, thermal physiology, and fitness in endotherms are less clear (Levesque & Marshall, 2021). This is primarily because endotherms are thermoregulators and can more effectively buffer body temperature from fluctuations in environmental temperature (Buckley et al., 2012; Levesque & Marshall, 2021; McKechnie & Wolf, 2019). Therefore, a taxonomically diverse group of tropical ectotherms exhibits reliable and consistent relationships between microclimate and thermal physiology (Baudier et al., 2018; Huey et al., 2009; Kaspari et al., 2015; Leahy et al., 2021; Marshall et al., 2015; Muñoz et al., 2014; Pintanel et al., 2019) and, with few exceptions, is more susceptible to climate warming than temperate counterparts (Deutsch et al., 2008; Huey et al., 2009; Somero, 2010). In endotherms, analogous evidence is largely lacking, and in fact, a recent study found that although tropical birds experienced different temperature regimes in shaded and

unshaded coffee farms in Costa Rica, they did not differ in resting metabolic rates or dehydration risk (Monge et al., 2022). Consistent with this study, our results suggest that within a tropical bird community, variation in local temperature regime and thermal physiology are largely decoupled and that tropical birds may be physiologically less sensitive to temperature than their ectothermic counterparts (Pollock et al., 2021).

The lack of relationships that we found between temperature variation and thermal physiological traits also contrasts with some recent findings in other endotherms. For example, desert rodents were more heat tolerant than their mesic counterparts (van Jaarsveld et al., 2021; Wallace et al., 2021), and cave- and crevice-roosting bats had reduced heat tolerances, lower capacities for evaporative cooling, and employed torpor less often than species that roosted in open habitats (Czenze et al., 2022; Reher et al., 2022). The apparent disparity between our findings and these results may be due to differences in the absolute magnitude of local temperature variability. Our study site in the thermally stable tropics had smaller temperature extremes and less variability than the other four studies, which took place predominantly in the temperate zone and often in extremely stable (i.e., caves, crevices) or variable (i.e., deserts) thermal environments. Thus, the tropical birds we measured may not experience sufficient temperature variability to exhibit differences in thermal physiology. However, because there are so few thermal physiology datasets available from tropical birds, we cannot presently evaluate this hypothesis. More comparative data sets will be necessary before we can determine whether the lack of signal we found between temperature and thermal physiology is the norm or the exception.

Our study provides the first direct test of the "microclimate hypothesis," an influential explanation for the disproportionate sensitivity of tropical understory birds to environmental change. The hypothesis posits that narrow thermal tolerances and limited physiological flexibility in this group induce high susceptibility to environmental perturbations such as forest fragmentation and climate change (Powell et al., 2015; Şekercioğlu et al., 2002; Stratford & Robinson, 2005). We found no evidence to support the microclimate hypothesis—understory forest species presented TNZs and HTLs similar to those of canopy and open-habitat species, both of which experience more variable and extreme temperatures (Figure 1). Additionally, and counter to the predictions of both the climate variability and microclimate hypotheses, species from forest habitats and the understory stratum actually had broader TSMs than those from open habitats and the forest canopy, respectively. Our findings are largely consistent with previous indirect tests of the microclimate

hypothesis that have failed to find relationships between microclimate variation and tropical bird abundance and behavior (Jirinec et al., 2022; Patten & Smith-Patten, 2012; Pollock et al., 2015). Taken together, these findings suggest that other factors may be responsible for the declines of understory birds in both fragmented (Şekercioğlu et al., 2002; reviewed in Powell et al., 2015) and intact Neotropical forests (Blake & Loiselle, 2015; Pollock et al., 2022; Stouffer et al., 2021). For example, the widespread loss of arthropods could explain population declines of insectivorous birds (Sherry, 2021; Tallamy & Shriver, 2021). It has also been hypothesized that body size could mediate sensitivity to environmental change. For example, smaller-bodied species at La Selva Biological Station in Costa Rica showed steeper population declines than larger-bodied species over a ~20-year study period from 1989 to 2011 (Boyle & Sigel, 2015), and understory forest birds have been decreasing in body mass in intact lowland forests of the Brazilian Amazon in recent decades (Jirinec et al., 2021). Nevertheless, counter to this hypothesis, Pollock et al. (2021) found no associations between body mass and thermal physiological traits or metrics of temperature sensitivity among our focal species. Furthermore, to our knowledge, no previous studies of tropical birds linked thermal physiology with population trends. This will be an important future step toward understanding whether thermal physiology affects individual fitness and scales up to impact population dynamics.

Although tropical birds appear less likely to conform to expectations of the climate variability hypothesis than ectotherms, at least within a given locality, the limited scope of our study cautions against overgeneralization. First, birds were measured in a controlled laboratory setting where experiments focused on a single environmental variable—air temperature. In the wild, other factors can influence thermal physiological responses, such as wind (Wolf & Walsberg, 1996), humidity (Gerson et al., 2014), and solar radiation (Wolf & Walsberg, 1996), all of which must be considered in order to provide a holistic picture of an organism's response to microclimate. Humidity in particular is extremely high in the tropical forest understory and at our study site specifically (e.g., Pollock et al., 2015), which reduces the potential for heat dissipation via evaporative water loss (Gerson et al., 2014; McKechnie & Wolf, 2019). Thus, our experimental protocol of measuring birds in dry air maximizes the humidity gradient between the animal and the environment and could result in overestimates of heat tolerance capabilities. Future studies that characterize the joint effects of humidity and temperature (e.g., James, 1970) will be necessary to quantify how they interact to influence thermal physiology. Second, our metrics of sensitivity to climate warming (WT and TSM) are purely

physiological and belie the complex ways in which climate change can interact to influence organisms and populations. For example, climate change can act synergistically with other factors such as land-use change to negatively affect wildlife populations (e.g., Srinivasan & Wilcove, 2021) and impact birds indirectly by depressing arthropod prey populations (Møller, 2019; Tallamy & Shriver, 2021). Finally, we did not account for extreme climatic events such as heat waves (e.g., McKechnie & Wolf, 2010) or seasonal drought (Boyle et al., 2020), which can undoubtedly exacerbate the thermal physiological responses of endotherms. Future studies that encompass greater variation in temperature regime by incorporating data from multiple geographic locations and across environmental gradients will be necessary to evaluate the generality of our findings.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
All data and statistical code (henRyPollock, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8419552.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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