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# Thermal ecology drives alternate responses to rising temperatures in Caribbean anoles

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**Rapidly rising temperatures threaten populations of ectothermic animals worldwide, with the greatest impacts predicted in the tropics—hotspots for biodiversity. Ectotherms can respond to warming through two primary compensatory responses: behavioral thermoregulation, which buffers exposure to extreme temperatures; and heat tolerance increases via plasticity, adaptation, or both. The relative contribution of these responses is predicted to depend on ecological context, but whether these principles can anticipate organismal responses to contemporary warming remains largely untested. Here, using a decadal resurvey of anole lizards from Hispaniola, Jamaica, and Puerto Rico, we show that simple principles of thermal ecology can reliably anticipate organismal responses to rising temperatures. Species occupying thermally heterogeneous open/edge habitats, such as dry forests, behaviorally thermoregulate and have shown little to no increase in heat tolerance over the past decade. By contrast, species from thermally homogeneous closed-canopy environments are poor thermoregulators and have increased their heat tolerance by 2 °C, on average, over the same period. Seasonal comparisons, acclimation experiments, and laboratory-rearing experiments indicate that contemporary increases in heat tolerance likely reflect contributions from rapid evolutionary change and physiological plasticity. Thermal ecology, not phylogenetic or spatial proximity, is the key factor driving responses to rising temperatures. Our results consistently link organismal responses to habitat complexity and thermoregulatory behavior; we suggest that these factors are key to predicting how ectotherms respond to climate warming.**

behavioral thermoregulation | global warming | heat tolerance | physiological plasticity

## Significance

Animals may respond to rising temperatures through behavioral thermoregulation, heat tolerance increases, or both, with the relative contribution of these responses predicted to differ among ecological contexts. We tested this prediction in a decadal resurvey of Caribbean *Anolis* lizards. In thermally variable open and edge habitats, lizards behaviorally buffered their body temperatures and showed little heat tolerance change. In thermally homogeneous closed-canopy forests, limited thermoregulation was accompanied by rising body temperatures and increased heat tolerance. The greatest increases in heat tolerance occurred where thermoregulation was constrained, not where habitats were warmest. The balance between behavioral buffering and physiological adaptation depends on the opportunities and costs of thermoregulation, helping anticipate how a wide diversity of animals will meet a warming world.

Anthropogenic climate change is one of the defining selective pressures of our time: human activities are increasing both environmental temperatures and the frequency of extreme climate events (e.g., heat waves and hurricanes), imposing stressful conditions on organisms across ecosystems (1–3). The impact of these changes is exacerbated in ectothermic animals (such as amphibians, insects, and reptiles) because their body temperature ($T_b$), performance, and Darwinian fitness are tightly coupled to environmental temperature (4–6). As the planet warms, body temperatures of ectotherms could exceed their thermal optima (temperatures at which physiological performance is maximized) or their critical thermal maxima ($CT_{max}$; the upper thermal tolerance limit), leading to thermal stress, mortality, demographic decline, and elevated extinction risk (7, 8). Behavioral thermoregulation represents a primary line of defense against stressful temperatures, allowing ectotherms to maintain field body temperatures within optimal ranges (8–11). Access to this strategy, however, varies widely among species, populations, and environments. Mobile ectotherms in thermally heterogeneous habitats can shuttle among microhabitats or exploit thermal refuges to avoid overheating (12, 13). By contrast, behavioral buffering is limited or unavailable to ectotherms with restricted mobility (e.g., corals) or those inhabiting spatially homogeneous thermal habitats, such as cloud forests (8, 14–16). For these thermoconforming ectotherms, increases in environmental temperature could greatly reduce activity time and elevate body temperatures beyond optimal temperatures or physiological limits, resulting in heat stress and mortality (17, 18).

Perhaps counterintuitively, the same thermoconformity that renders some ectotherms vulnerable to rising temperatures may also facilitate physiological adjustment through acclimatization and/or adaptive evolutionary change (8). Whereas thermoregulators could buffer themselves against thermal extremes (and thus from selection), thermoconformers experience direct exposure to warming, such that individuals with higher heat tolerance could have greater survivorship than those with lower heat tolerance (19–21). This contrast suggests alternative strategies for persistence in a warming world: whereas mobile ectotherms from thermally heterogeneous habitats are expected to rely more on

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thermoregulation than physiological adjustment, ectotherms with limited mobility and/or from thermally homogeneous habitats should rely more on physiological adaptation or acclimation than thermoregulation to keep pace with rising temperatures (8, 22, 23). If so, then straightforward principles of thermal ecology may provide a basis for broadly anticipating the compensatory responses ectotherms deploy as temperatures rise.

Empirical evidence for both strategies requires temporal comparisons in wild ectothermic populations from contrasting thermal habitats. Anole lizards from the Caribbean islands of Hispaniola, Jamaica, and Puerto Rico offer a powerful study system with which to investigate these responses (22). Across these tropical islands, anole lizards vary in the types of thermal habitats they occupy (24–29). Whereas some anole populations occur in clearings, forest edges, and relatively open-canopied forests (i.e., open/edge habitats) (27–31), others are restricted to the shaded interiors of closed-canopy forests (27–32). In open/edge habitats, operative temperatures (i.e., the equilibrium body temperatures available to lizards) are more spatiotemporally heterogeneous than in closed/shaded forests (12, 30, 32–34). Therefore, open/edge habitat anoles tend to maintain their field body temperature within their preferred thermal range (i.e., a preferred set-point range; $T_{set}$) with higher thermoregulatory effectiveness than their closed/shaded habitat relatives (27, 30, 31). Extensive historical data exist for Caribbean anoles. For five species (*Anolis cooki*, *Anolis cybotes*, *Anolis cristatellus*, *Anolis gundlachi*, and *Anolis shrevei*) thermoregulatory behavior was quantified more than a decade ago (27, 30, 31). For these species, plus 11 more (*Anolis cuvieri*, *Anolis evermanni*, *Anolis garmani*, *Anolis grahami*, *Anolis krugi, Anolis lineatopus*, *Anolis opalinus*, *Anolis poncensis*, *Anolis pulchellus*, *Anolis stratulus*, and *Anolis valencienni*), heat tolerance (critical thermal maximum; $CT_{max}$) was also estimated between 2011 and 2013 (26, 28). Together, this wealth of historical data on behavioral thermoregulation and heat tolerance affords a basis of temporal comparison with present-day populations on three islands that have been progressively warming during recent decades (35) (*SI Appendix*, Fig. S1).

Of the representative populations from the 16 anole species included in this study, five are from open/edge habitats and 11 from closed/shaded environments. Together, anoles from Hispaniola and Puerto Rico form five sister-species pairs (Fig. 1*A*), each comprised of one open/edge habitat species and one closed/shaded habitat species. The Jamaican populations all occupy closed canopy habitat and are phylogenetically independent from the other Caribbean anoles (Fig. 1*A*). This combination of phylogenetic lability and geographic replication of canopy use allows us to isolate the effect of thermal ecology on physiological responses to warming. From 2022 to 2025, we revisited the anole populations previously studied from 2011 to 2013 (*SI Appendix*, Table S1), and we quantified thermoregulatory behavior and/or heat tolerance to assess temporal change. To assess the contribution of physiological plasticity to observed heat tolerance shifts in several species, we performed seasonal comparisons in wild populations and laboratory acclimation experiments for a subset of taxa. Additionally, we reared offspring of contemporary *A. cybotes* from a closed/shaded habitat population under standardized laboratory conditions to evaluate whether elevated heat tolerance persisted across generations.

We hypothesized that anoles should exhibit contrasting responses depending on the thermal structure of their habitats and the opportunities available for behavioral thermoregulation (8, 23). Open/edge habitat anoles should rely on behavioral thermoregulation to maintain their body temperatures within their preferred thermal range, resulting in little change in heat tolerance over the past decade. By contrast, closed/shaded-habitat populations of anoles should thermoregulate less effectively and, if body temperatures exceed their preferred thermal range, exhibit increases in $CT_{max}$ through time. Alternatively, and independently of thermal habitat, anoles may exhibit concurrent changes in both behavioral thermoregulation and heat tolerance, highlighting the potential for multiple, interacting responses to climate warming.

## Results and Discussion

**Heat Tolerance Shifts When Behavioral Buffering Is Limited.** Air temperatures across Hispaniola, Jamaica, and Puerto Rico have risen significantly over the past two decades, increasing by ~1 °C from 2011 (when historical $CT_{max}$ was measured) to 2025 (*SI Appendix*, Fig. S1). Across the seven localities where we conducted field work, daily maximum air temperatures increased significantly in Boquerón, Los Patos, St. Mary Parish, and Valle Nuevo, tended to increase in Mata de Plátano, and remained relatively stable in Guánica and El Verde (*SI Appendix*, Figs. S2 and S3). Despite the absence of long-term trends in El Verde, air temperature increased abruptly by 2.8 °C relative to the previous 17 y immediately following Hurricane Maria in 2017 (*SI Appendix*, Fig. S3), likely due to canopy loss (36, 37). Because air temperatures are strongly associated with measured operative temperatures (*SI Appendix*, Fig. S4), warming conditions could increasingly expose closed-canopy anoles to body temperatures exceeding their preferred thermal range, potentially elevating thermal stress. Anoles could buffer these thermal challenges by behavioral and/or physiological adjustments (23). Among the five species for which historical data on thermoregulation were available, we did not observe any major behavioral shifts across time (*SI Appendix*, Fig. S5 and Table S2). *A. cooki* and *A. shrevei*—open/edge habitat species from low and high elevation, respectively, previously characterized as active thermoregulators (27, 30, 38) continue to thermoregulate today (*SI Appendix*, Figs. S5 and S6 *A* and *C*). Likewise, low elevation, closed-canopy populations of *A. cristatellus*, *A. cybotes*, and *A. gundlachi* previously observed to thermoconform or thermoregulate moderately (27, 30, 31) exhibit similar thermal behavior in contemporary populations (*SI Appendix*, Figs. S5 and S6 *B*, *D*, and *E*).

In contrast to the relative stability of thermoregulatory behavior across thermal contexts, heat tolerance responses differed strikingly among habitat types. Whereas four of five open/edge habitat species maintained similar heat tolerance across time, eight of 11 closed/shaded habitat anoles increased their $CT_{max}$ (Fig. 1*B* and *SI Appendix*, Figs. S7–S10 and Tables S3 and S4). These increases were especially pronounced in low-elevation populations from thermally homogeneous environments, which generally exhibited limited thermoregulatory behaviors. Two patterns nevertheless illustrate important departures from this broader trend. *A. shrevei* remained an active thermoregulator but also exhibited increased heat tolerance (Fig. 1*B* and *SI Appendix*, Fig. S9*A*), demonstrating that behavioral buffering and physiological adjustments can operate concurrently, as observed in flat rock spiders (39) and the mountain horned lizard (40). Conversely, *A. grahami, A. gundlachi,* and *A. valencienni* inhabit closed-canopy environments where behavioral buffering is limited (30), yet showed no detectable change in heat tolerance across time (Fig. 1*B* and *SI Appendix*, Figs. S7*D* and S10 *A* and *D*) despite rising air temperatures (*SI Appendix*, Figs. S2*E* and S3). This apparent stability could reflect limited physiological capacity for adjustment, as observed in some bee species (41). Because these species also appear constrained in their ability to behaviorally buffer warming

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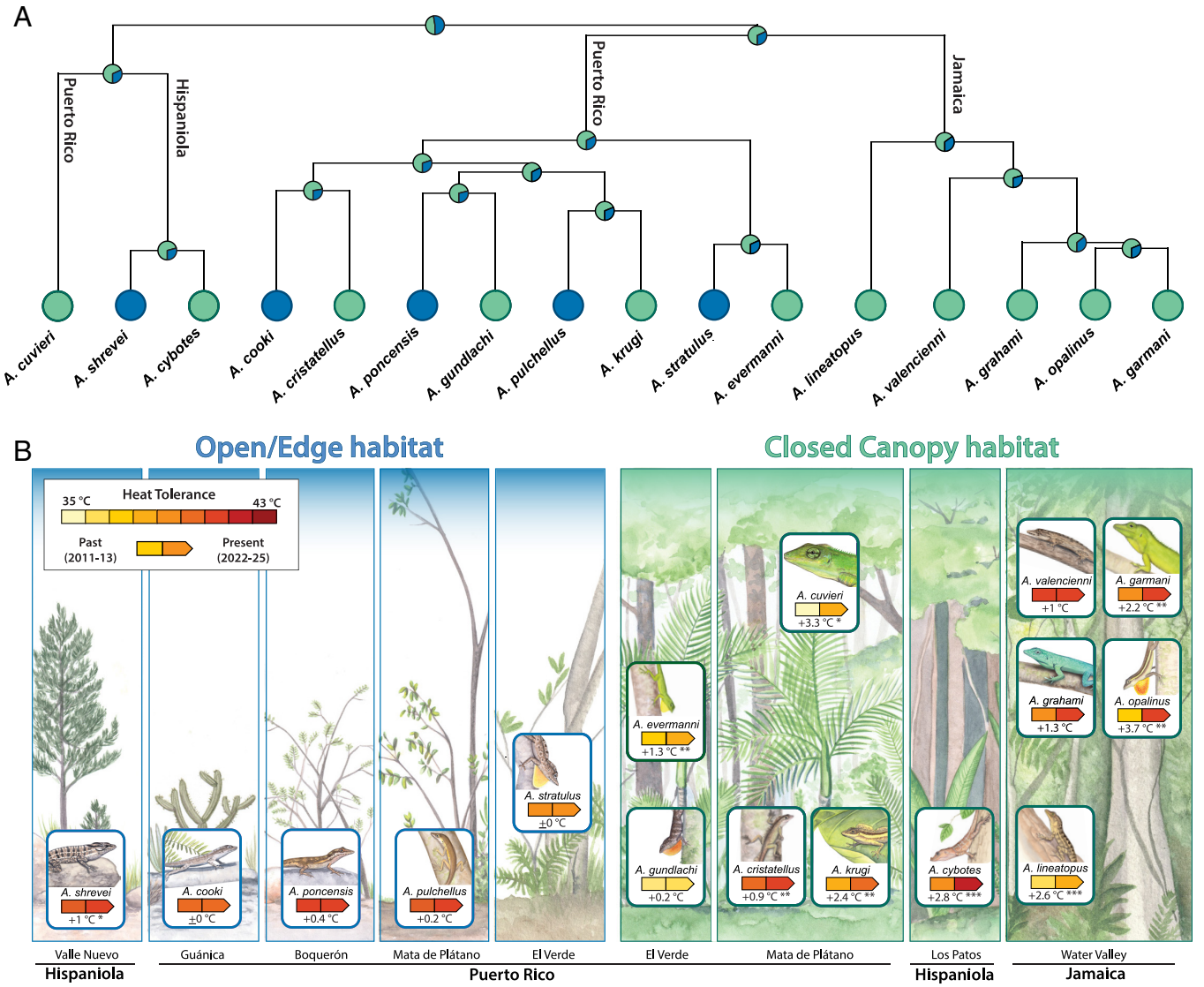


**Fig. 1.** Evolutionary relationships, thermal habitat distribution, and heat tolerance shifts among anole species from Hispaniola, Jamaica, and Puerto Rico. (*A*) Five parallel transitions between open/edge habitat (blue) and closed-canopy habitat (green) occurred in these Caribbean anoles. These transitions are supported by a stochastic character mapping of habitat use (500 simulations) across the MCC tree. Pie charts at nodes of the phylogeny indicate posterior probabilities of habitat use, and color denotes whether species are specialized for open/edge habitat (blue) or closed/shaded habitat (green). (*B*) For each species, the color ramp illustrates the shift in $CT_{max}$ from 2011–2013 (*Left*) to 2022–2024 (*Right*). Asterisks denote significant increases (*** indicates $P \leq 0.001$, ** indicates $P \leq 0.01$, and * indicates $P < 0.05$), and lack of asterisks denote no shifts ($P > 0.05$). Whereas open/edge habitat species (with the exception of *A. shrevei*) maintained a similar critical thermal maximum across time, most closed/shaded habitat anoles (with the exceptions of *A. grahami*, *A. gundlachi*, and *A. valencienni*) increased their heat tolerance (*SI Appendix*, Tables S3 and S4). Important to note is that historical heat tolerance was higher in open/edge habitat anoles, compared with their closed-canopy relatives. Graphic provided by J. Johnson (Life Science Studios).

temperatures, limited physiological change could place them at particular risk under continued climate warming.

**A Shielding Effect of Thermoregulation in Some Anoles.** Differences in physiological responses across habitat types were closely associated with variation in thermoregulatory behavior and exposure to thermal stress. Open/edge habitats provide higher and more spatially heterogeneous operative temperatures than closed, shaded environments (*SI Appendix*, Figs. S11 and S12). In these thermally variable settings, behavioral thermoregulation offers substantial protection against heat stress (9, 10). For example, during body-temperature sampling in the Puerto Rican dry forest of Guánica, 10% of the operative temperatures exceeded 40 °C—the $CT_{max}$ of *A. cooki* (*SI Appendix*, Fig. S6*A*)—yet lizard field body temperatures remained stable and well below heat stress levels, indicating a strong capacity for behavioral buffering (30). Although NicheMapR simulations suggest that body temperatures of open-edge habitat anoles have increased over the past 25 y, they rarely exceed the upper bounds of species-specific preferred temperature ranges (*SI Appendix*, Figs. S13–S17), even during warmer months (*SI Appendix*, Figs. S18–S20). Like open/edge habitat anoles (27, 42), other mobile ectotherms (such as littorinid snails) from thermally complex habitats avoid lethal operative temperatures by seeking cooler microclimates (43). Furthermore, behavioral thermoregulation in open/edge habitat anoles has remained highly effective through time (*SI Appendix*, Fig. S5), as has been observed in Algerian sand lizards (44).

Stability in heat tolerance among most open/edge habitat anoles likely reflects, at least in part, the continued effectiveness of behavioral thermoregulation. By behaviorally regulating body temperature within preferred ranges, organisms can avoid or attenuate exposure to heat stress, reducing the extent to which warming

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translates into physiologically stressful body temperatures (20, 45). This dynamic is a hallmark of the Bogert effect (42), the tendency for homeostatic behaviors (like behavioral thermoregulation) to buffer organisms from environmental variation and limit physiological divergence (20). Although thermoregulation likely contributes to the observed stasis in heat tolerance, other factors are also likely at play. One factor is climatic stability: the heat tolerance of *A. cooki* may not have changed simply because air temperatures in Guánica (*SI Appendix*, Fig. S2*B*) have remained relatively unchanged over recent decades, likely buffered by their proximity to the ocean. Likewise, if the energetic cost of thermoregulation to maintain relatively stable body temperature increases, it may limit the energy needed to increase or even maintain a stable heat tolerance (46, 47). In addition, open/edge habitat populations generally exhibit higher preferred body temperatures than their closed/shaded habitat relatives (*SI Appendix*, Figs. S13 and S14), which may limit thermal stress. For example, simulation-derived body temperatures exceeding the upper bounds of preferred thermal ranges became increasingly common in *A. krugi* and *A. evermanni* but remained comparatively rare in the more heat-tolerant *A. pulchellus* and *A. stratulus* from the same localities (*SI Appendix*, Figs. S13 and S15).

Yet, even this flexibility has limits as behavioral buffering is unlikely to be cost-free (12). Rising temperatures can increase the energetic demands of lizards while shortening their daily activity period and reducing food intake, decreasing survivorship and reproductive output and, if severe enough, precipitating demographic collapse (47, 48). Maintaining stable body temperatures may require increased movement among microsites, reduce time available for foraging or reproduction, and elevate exposure to predators or parasites (8). As warming intensifies and suitable thermal refuges become increasingly limited, these ecological and energetic costs may further constrain the effectiveness of behavioral thermoregulation. Moreover, thermal reaction norms are nonlinear: species with higher heat tolerance generally exhibit less capacity to further increase it (49, 50), although exceptions exist (51, 52). For instance, whereas porcelain crabs with high heat tolerance do not increase their $CT_{max}$ under experimental warming, their less heat-tolerant relatives do (53). Consistent with this pattern, anole species with the highest historical $CT_{max}$ tended to exhibit the smallest shifts over the last decade (Fig. 2*A*). For example, *A. pulchellus* and *A. stratulus* have not increased their heat tolerance whereas their sympatric, closed-canopy sister species (*A. krugi*, and *A. evermanni*, respectively) did (*SI Appendix*, Fig. S8). Alternatively, open/edge habitat anoles may not yet experience the need for further $CT_{max}$ shifts given higher thermal preferences (*SI Appendix*, Figs. S13 and S14) and higher historical heat tolerances (*SI Appendix*, Figs. S7–S9), compared with their closed-canopy habitat sister species. Open/edge-habitat anoles already exhibit some of the highest thermal limits observed in this clade (54, 55); their apparent physiological stability may also reflect an approaching evolutionary ceiling. When microclimatic refuges diminish and upper thermal limits are bounded by biochemical (2) and phylogenetic constraints (56), behavioral resilience will contract. It is at this intersection that thermal stress, selection on heat tolerance, and vulnerability to continued warming may all intensify simultaneously (8, 19).

**Warming Has Driven Physiological Convergence across Thermal Habitats.** In contrast to open/edge environments, closed-canopy forests offer limited opportunities for behavioral thermoregulation (12, 29). In shaded habitats beneath the canopy, operative temperatures are relatively homogeneous across space and time (*SI Appendix*, Figs. S11 and S12), making thermoregulation more challenging (30, 31). As a result, the field body temperatures of closed-canopy anoles often closely track operative temperatures, even when these exceed their preferred thermal range (*SI Appendix*, Fig. S6 *B* and *D–H*). Accordingly, simulation-derived body temperatures of closed/shaded habitat anoles increased at a rate of 0.06 °C per year, three times faster than their open/edge habitat relatives (*SI Appendix*, Figs. S13 and S14). From 2011–2013 (when $CT_{max}$ was first estimated) to 2022–2025 (contemporary estimations), the mean annual simulation-derived body temperatures have increased up to 1.2 °C

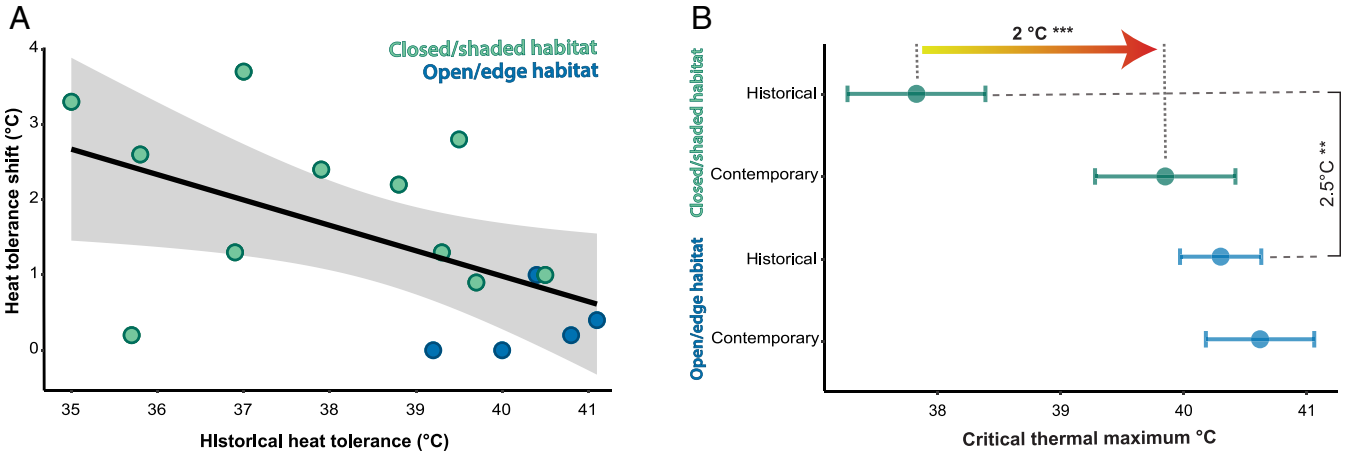


**Fig. 2.** Heat tolerance increased in the closed-canopy anoles from Hispaniola, Jamaica, and Puerto Rico between 2011–2013 and 2022–2024. (*A*) The magnitude of the observed heat tolerance shift tends to be negatively correlated with the historical heat tolerance in anole lizards (y = −0.14.41x + 52.48, two-sided $P = 0.076$). There are no significant differences in intercept (two-sided $P = 0.087$) or slope (two-sided $P = 0.642$) between habitats. Each point represents a different species and the gray shading shows the 95% confidence band. The regression slope was estimated using a phylogenetic regression (PGLS). (*B*) Closed-canopy anoles (green) increased their heat tolerance by 2 °C in the last decade [paired $t = -6.29$, two-sided $P < 0.001$, mean ± SE = 37.83 ± 0.56 °C in 2011–2013 ($n = 11$), and 39.85 ± 0.57 °C in 2022–2024 ($n = 11$)]. By contrast, open/edge habitat species (blue) maintained a similar $CT_{max}$ across years [paired $t = -1.73$, two-sided $P = 0.250$, mean = 40.3 ± 0.33 °C in 2011–2013 ($n = 5$), and 40.6 ± 0.44 °C in 2022–2024 ($n = 5$)]. Closed/shaded habitat anoles had a 2.5 °C lower heat tolerance than open/edge habitat anoles in 2011–2013 [$F_{1,14} = 7.97$, two-sided $P = 0.012$, mean = 37.83 ± 0.56 °C for closed/shaded habitat species ($n = 11$) and 40.3 ± 0.33 °C for open/edge habitat species ($n = 5$)], but species from both habitats exhibited a similar critical thermal maximum during 2022–2024 [$F_{1,14} = 0.89$, two-sided $P = 0.470$, mean = 39.78 ± 0.56 °C for closed-canopy species ($n = 11$), 40.62 ± 0.44 °C for open/edge habitat species ($n = 5$), and 40.04 ± 0.41 °C for all species]. Data are presented as mean values with SE bars. The comparison in heat tolerance between habitats (whether 2011–2013 or 2022–2024) was performed using phylogenetic ANOVA (500 replicates on the MCC tree). Asterisks denote significant differences (*** indicates $P \leq 0.001$ and ** indicates $P \leq 0.01$).

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(on average) in closed-canopy anole populations, twice that of their open/edge habitat counterparts (*SI Appendix*, Figs. S13 and S14). Because closed-canopy forests are cooler and more thermally homogeneous, ectotherms from these habitats often exhibit lower heat tolerance than their relatives from more open habitats (57). Butterflies, frogs, and skinks confined to living below canopy cover, for example, have lower $CT_{max}$ compared to relatives from sun-exposed or thermally variable habitats (58–60). This physiological specialization for cooler temperatures, coupled with limited behavioral buffering, means that even modest increases in air temperatures can elevate body temperatures in closed-canopy species, potentially pushing them above optimal ranges, increasing heat stress and mortality risk (8, 22). As simulation-derived body temperatures commonly exceeded thermal preferences of closed-canopy anoles (*SI Appendix*, Figs. S15–S21) but not their heat tolerance, it is possible that $CT_{max}$ was not directly under selection. Instead, warming may have imposed selection on preferred body temperatures, at which performance and fitness of lizards are typically maximized before declining as body temperatures approach $CT_{max}$ (8, 61). The observed increase in heat tolerance may therefore reflect a broader evolutionary shift in thermal physiology, potentially as a correlated response to selection on other components of thermal performance. Potential thermal stress may also vary across environmental gradients. Closed-canopy anoles from high elevations, where air temperatures are usually low, could instead benefit from warming if their body temperatures shift from below to within their preferred thermal range (8, 62).

One decade ago, anoles from closed-canopy habitats were, on average, 2.5 °C less heat tolerant than their relatives from open/edge habitats [$F_{1,14}$ = 7.97, two-sided $P$ = 0.012, mean ± SE = 37.83 ± 0.56 °C for closed/shaded habitat species ($n$ = 11) and 40.3 ± 0.33 °C for open/edge habitat species ($n$ = 5); Fig. 2*B* and *SI Appendix*, Table S5]. Under recent warming, however, this physiological distinction has largely collapsed. During 2022–2024 we detected no differences in $CT_{max}$ between closed/shaded habitat and open/edge habitat anoles [$F_{1,14}$ = 0.89, two-sided $P$ = 0.470, mean = 39.78 ± 0.56 °C for closed/shaded habitat species ($n$ = 11), 40.62 ± 0.44 °C for open/edge habitat species ($n$ = 5), and 40.04 ± 0.41 °C for all species; Fig. 2*B* and *SI Appendix*, Table S5]. This narrowing of the physiological gap reflects ~2 °C increases in $CT_{max}$ among closed-canopy anoles [paired $t$ = −5.83, two-sided $P$ < 0.001, mean = 37.83 ± 0.56 °C in 2011–2013 ($n$ = 11), and 39.78 ± 0.56 °C in 2022–2024 ($n$ = 11)], bringing their heat tolerance in line with that of their open/edge habitat counterparts (Fig. 2*B*).

We evaluated whether recent heat-wave exposure could have contributed $CT_{max}$ increases in closed-canopy anoles through heat hardening, an ephemeral increase in heat tolerance that typically occurs within 2 to 4 h after heat shock exposure that dissipates after approximately 24 h, or through other forms of plasticity induced by repeated exposure to acute heat (63, 64). The most recent heat waves occurred between 11 and 27 d before the capture of *A. cristatellus*, *A. evermanni*, *A. garmani*, *A. grahami*, *A. gundlachi, A. krugi, A. opalinus, and A. valencienni* (*SI Appendix*, Table S6). Because no lizards were captured during or shortly after (1 to 2 d) a heat wave, and because we held lizards at a constant 20 °C for 24 h before heat tolerance assays, $CT_{max}$ estimates are unlikely to reflect hardening. We also experimentally tested whether a short heat wave could induce a more persistent increase in heat tolerance. *A. cybotes* lizards exposed to 31.5 °C for 3 d and then returned to 28 °C for 11 d exhibited similar heat tolerance to their siblings maintained continuously at 28 °C ($t$ = −0.37, two-sided $P$ = 0.712; *SI Appendix*, Fig. S22). In addition, *A. gundlachi* from El Verde did not exhibit elevated heat tolerance (Fig. 1*B* and *SI Appendix*, Fig. S7*D*), as would be expected if heat waves had influenced measurements. Although these results argue against recent, short-term heat waves as the primary explanation for the observed $CT_{max}$ increases, we acknowledge the possibility that physiological plasticity associated with sustained or repeated exposure to stressful temperatures weeks before sampling could have contributed.

With physiological limits now converging across habitats, closed-canopy anoles are approaching the same ceiling that may constrain their open-habitat relatives. Yet, lacking the behavioral flexibility that buffers species in thermally heterogeneous environments, these forest populations face a narrowing safety margin; further warming could overwhelm physiological capacity and trigger widespread population decline (22).

**Assessing Evolutionary and Plastic Responses to Warming.** In addition to short-term heat waves, more gradual increases in air temperatures could also promote heat tolerance increases. To evaluate this possibility, we used three complementary approaches: seasonal comparisons in the field, laboratory acclimation experiments, and intergenerational laboratory rearing experiments. We first compared heat tolerance among seasons in wild populations of 11 species, five from Jamaica and six from Puerto Rico (*SI Appendix*, Figs. S7–S10 and Tables S3 and S4). Five species exhibited significant seasonal variation in $CT_{max}$: *A. cristatellus* (two-sided $P$ = 0.013), *A. cuvieri* (two-sided $P$ = 0.041), *A. evermanni* (two-sided $P$ = 0.010), *A. gundlachi* (two-sided $P$ < 0.001), and *A. lineatopus* (two-sided $P$ = 0.006). The magnitude of seasonal variation observed here (*SI Appendix*, Figs. S7–S10) is consistent with observations in other lizard species; shifts are typically modest, averaging 1 to 2 °C across species (65). In all five species, $CT_{max}$ was lowest in late winter/early spring (*SI Appendix*, Figs. S7–S10). Although historical and contemporary spring heat tolerance did not differ for *A. gundlachi*, this species nevertheless exhibited elevated $CT_{max}$ during the summer (*SI Appendix*, Fig. S7*D*).

We brought live individuals of the Dominican anoles (*A. shrevei* and *A. cybotes*) to the lab for intra- and intergenerational experiments. For *A. shrevei*, we conducted a series of sequential thermal exposure experiments to test whether contemporary increases in $CT_{max}$ could be experimentally reversed or reproduced through short-term thermal plasticity. Wild-caught adults were sequentially maintained at 28 °C, corresponding to the historical average field-active body temperature ($T_b$) (26), followed by a cooler but nonstressful 20 °C treatment, and finally at 31 °C, corresponding to the contemporary average field-measured $T_b$. Heat tolerance declined toward historical levels under the 28 °C treatment, showed no further reduction at 20 °C, and increased again after exposure to 31 °C, matching contemporary field estimates (*SI Appendix*, Fig. S23). These results indicate that short-term plasticity can largely reproduce the thermal tolerance shifts observed in the wild for this species.

For *A. cybotes*, which breeds readily in captivity (27), we also tested whether elevated heat tolerance persisted across generations under standardized laboratory conditions. Lizards reared at 28 °C already exhibited higher heat tolerance than wild-caught individuals in 2011 ($t$ = −7.1, two-sided $P$ < 0.001), but lower $CT_{max}$ than wild-caught individuals measured in 2023 ($t$ = 5.87, two-sided $P$ < 0.001) (Fig. 3). Exposure to 31 °C for 2 wk further increased heat tolerance by 1.6 °C ($t$ = −6.43, two-sided $P$ < 0.001), producing values indistinguishable from contemporary wild populations ($t$ = −1.05, two-sided $P$ = 0.830), and this elevated tolerance persisted after lizards were returned to 28 °C for a month ($t$ = 2.16, two-sided $P$ = 0.23) (Fig. 3). As lizards reared

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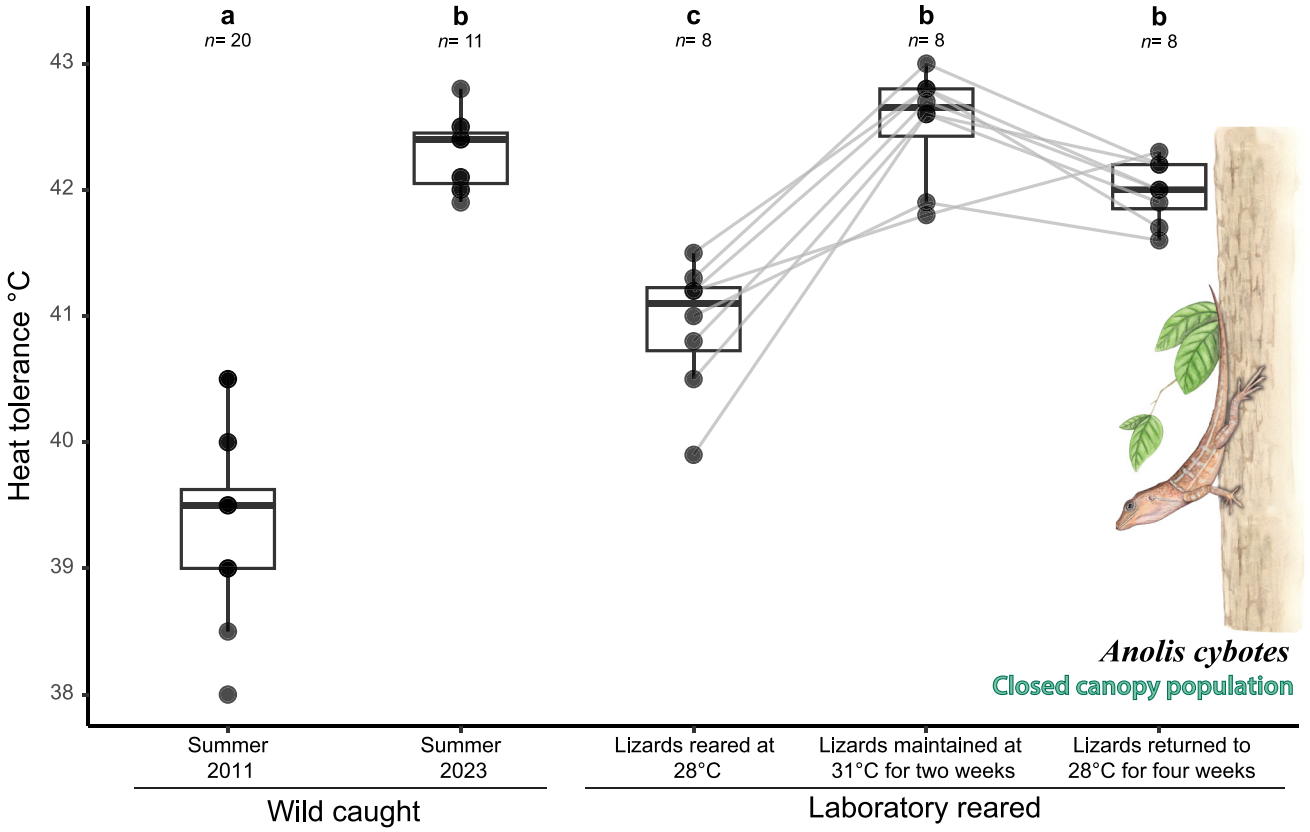


**Fig. 3.** Comparison of heat tolerance among *A. cybotes* lizards caught in the wild and reared in laboratory conditions. We found that in their natural habitat (Los Patos, DR), lizards were more heat tolerant in summer 2023 than in summer 2011 ($t = -15.2$, two-sided $P < 0.001$). Lizards from the same population reared at 28 °C, the historical average field body temperature, exhibit a higher heat tolerance than wild-caught lizards from summer 2011 ($t = -7.1$, two-sided $P < 0.001$) but lower than lizards from summer 2023 ($t = 5.87$, two-sided $P < 0.001$). When those individuals were then maintained at 31 °C their heat tolerance increased ($t = -6.4$, two-sided $P < 0.001$) to values equivalent to those observed in natural conditions during summer 2023 ($t = -1.05$, two-sided $P = 0.830$). Lizards maintained this increased heat tolerance even when returned to 28 °C ($t = 2.16$, two-sided $P = 0.230$). Groups with the same letter are not statistically different. Numbers in parentheses indicate the sample size. Graphic of *A. cybotes* provided by J. Johnson (Life Science Studios).

at 28 °C still exhibited higher $CT_{max}$ than individuals measured in 2011, contemporary increases in heat tolerance likely include an evolved component rather than reflecting acclimatization alone. Another nonmutually exclusive possibility is that parental or intergenerational plasticity contributed to the elevated baseline heat tolerance, as laboratory-reared offspring came from wild-caught parents (66, 67).

The elevated heat tolerance observed in laboratory-reared *A. cybotes* encourages a discussion of its potential mechanisms. One possibility is the evolution of proteins adapted to higher temperatures (55, 68), as warming can impose strong directional selection on heat tolerance and prompt rapid evolutionary shifts (69, 70). Although studies on anoles and skinks suggest that components of thermal performance may exhibit only modest heritability (71, 72), Caribbean anoles can reach sexual maturity within 7 to 12 mo, meaning that our temporal comparisons likely span ~12 to 20 generations, sufficient time for evolutionary responses to accumulate. Forward-genetic simulations support this view: SLiM-based models show that body temperature and proteins directly responsible for thermal performance can respond quickly to warming environments (73). Empirical studies mirror these predictions. Wild populations of *Daphnia* have increased their $CT_{max}$ over the past decades in parallel with rising pond temperatures (74). Similarly, in urban heat islands, *Anolis cristatellus* exhibits higher heat tolerance than conspecifics from nearby forests, a pattern attributed to physiological adaptation (55, 68). Comparisons between urban and forested populations serve as spatial analogues to temporal comparisons of lizards within the same locality, suggesting comparable processes are at play. In the Puerto Rican city of Arecibo, for example, *A. cristatellus* is ~1 °C more heat tolerant than individuals in forested areas outside the city (55). Analogously, across years we found that *A. cristatellus* from the shaded forest from Mata de Plátano (a forested area outside of Arecibo) increased their heat tolerance by ~1 °C (Fig. 1*B* and *SI Appendix*, Fig. S7*B*). Notably, rapid thermal trait shifts in anoles can also occur in the opposite direction: following extreme winter storms in the southern United States, populations of *Anolis carolinensis* rapidly evolved lower cold tolerance, accompanied by regulatory and genomic shifts consistent with strong contemporary selection (75). Together, these findings suggest that thermal limits in anoles can adapt rapidly to thermal stress.

**Behavior Shapes the Pace of Physiological Change under Warming.** The general principles linking thermal habitat complexity, behavioral thermoregulation, and the pace of heat tolerance adjustment observed here are broadly applicable across ectotherms. Mobile species active in thermally heterogeneous habitats are expected to rely more strongly on behavioral thermoregulation, often reducing exposure to the selective pressures that drive physiological change (23). For instance, ants in urban habitats behaviorally avoid lethal operative temperatures without exhibiting shifts in $CT_{max}$ (13). By contrast, species that are thermoconformers—whether because they are sessile or inhabit thermally homogeneous habitats—may experience stronger selection for physiological adjustment under thermal stress because they are less able to behaviorally buffer rising temperatures (23).

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When certain tabletop corals were experimentally transplanted to warm reef sites, for instance, their heat tolerance rapidly increased through a combination of physiological acclimatization and adaptation (76). Similar stage-specific patterns also occur within species: immobile metamorphic stages, such as insect pupae, may exhibit greater increases in heat tolerance than mobile, more behaviorally flexible stages (77). Likewise, nocturnal species could experience increasingly stressful temperatures within their diurnal retreats as the environment warms (78). Notably, however, increases in the upper thermal limits of ectotherms can only occur until certain intrinsic limits (2, 50), and given the rate of global warming, the potential for evolution to keep pace may be limited (79, 80). More generally, responses to stressful environments may themselves be asymmetric. Reciprocal transplant experiments in marine sponges showed that organisms rapidly adopted stress-tolerant morphologies under physically stressful conditions, whereas shifts toward less stress-tolerant forms occurred more slowly in benign environments (81). Such asymmetries suggest that exposure to chronic environmental stress can favor rapid compensatory responses, particularly when opportunities for behavioral buffering are limited.

Behavioral responses and physiological adjustments represent complementary strategies for contending with a rapidly warming world, but their relative contributions likely differ among ecological contexts (8, 22). The same environmental features that favor behavioral buffering may also dampen physiological change, whereas environments that constrain behavior may intensify selection on thermal physiology. The tactic upon which tropical anoles rely can be predicted from their general thermal ecology. Geographic proximity or phylogenetic relatedness alone may poorly predict vulnerability to climate change when species differ in how they experience and buffer climatic conditions; as temperatures rise, predicting biological vulnerability will require renewed attention to the ecological and behavioral details that shape how organisms actually experience climate (6). This insight helps to better anticipate what is in store for ectotherms in a warming world.

## Materials and Methods

**Data Collection.**

***Field work locations.*** We performed field work from June 2022 to July 2025 in seven localities in Hispaniola (the Dominican Republic, DR), Jamaica, and Puerto Rico (PR) where heat tolerance for 16 anole species was previously estimated (2011–2013) (26, 28). These localities are Los Patos DR (for *A. cybotes*), Valle Nuevo DR (for *A. shrevei*), St. Mary Parish, Jamaica (for *A. garmani*, *A. grahami*, *A. lineatopus*, *A. opalinus*, and *A. valencienni*), Bosque Estatal de Boquerón PR (for *A. poncensis*), Bosque Estatal de Guánica PR (for *A. cooki*), El Verde Field Station PR (for *A. evermanni*, *A. gundlachi,* and *A. stratulus*), and Mata de Plátano Field Station PR (for *A. cristatellus*, *A. cuvieri*, *A. krugi,* and *A. pulchellus*) (*SI Appendix*, Table S1). Los Patos, Valle Nuevo, Guánica, and Mata de Plátano are also the localities where the thermoregulatory behavior of *A. cybotes*, *A. shrevei*, *A. cooki*, and *A. cristatellus*, respectively, was previously estimated (27, 30, 31). Coordinates and elevations for all sites are provided in *SI Appendix*, Table S1. Categorizations of thermal habitat use for Caribbean anoles are given in *SI Appendix*, *Supplementary Methods*.

***Air temperatures and simulation-derived body temperatures.*** We were interested in evaluating whether temperatures at the macroscale (2-m open air temperature under well-ventilated and shaded conditions; $T_{air}$) and/or organismal level (body temperatures) increased from 2000 to 2025. We focused on this time period to compare trends between 2000–2010 (the decade preceding the historical $CT_{max}$ estimates) and 2013–2022 (the decade preceding our contemporary heat tolerance measurements). We downloaded ERA5 global reanalysis (82, 83) air temperatures for terrestrial grid cells for Jamaica, Hispaniola, and Puerto Rico, and averaged annually to estimate mean island-scale $T_{air}$. We also used hourly ERA5 reanalysis, queried and processed via the mcera5 package (83), to model hourly microclimates available to anole lizards via the NicheMapR microclimate model (84). We parameterized the NicheMapR microclimate model using estimates of canopy shading (minimum and maximum shading for each species; *SI Appendix*, Table S7), and 40% reduced windspeeds within shaded environments. Minimum and maximum shade were both needed, as these are used to provide the range of options available for a thermoregulating lizard (i.e., an anole lizard that is simulated to shuttle between min and max shade as it pleases) to maintain homeostasis. Hurricane Maria hit Puerto Rico on September 20, 2017, negatively affecting vegetation structure and reducing canopy cover by approximately 15% in both arid and shaded forests (e.g., Ponce and the Luquillo Mountains) (36, 37, 85). Canopy damage, in turn, affected environmental temperatures. For instance, air temperatures recorded in El Verde after Hurricane Maria were ~3 °C higher compared to the previous 17 y (*SI Appendix*, Fig. S3). We incorporated such potential effects of Hurricane Maria on modeled microclimates by running NicheMapR simulations incorporating a 15% reduction in shade beginning September 21, 2017, for all Puerto Rican localities, with canopy cover recovering by 2% annually (36) until reaching 100%. Other vegetation parameters required by NicheMapR's microclimate model (e.g., leaf area index) were estimated using built-in vegetation data from the microclimc package (86). Soil conditions were held constant across locations and time. As ERA5 macroclimate timeseries are derived from elevation estimates made from a 0.25° decimal degree grid, we performed lapse rate corrections to ERA5 according to a 100-m digital elevation model via the microclimc package (86). Slope and aspect were kept at 0 for all simulations. Then, we used NicheMapR microclimate data to model hourly body temperatures for each anole species at their corresponding location using the NicheMapR ectotherm model (87). Environmental change that was simulated in the NicheMapR microclimate modeling (e.g., effects of Hurricane Maria on vegetation) were therefore also represented in ectotherm modeling. Throughout the main text and Supplementary Information, we use the term "simulation-derived body temperatures" whenever referring to body temperature predictions from NicheMapR's ectotherm model. This mechanistic model produces a first-principles estimate of hourly body temperatures for each species, namely at the average height and distribution of levels of shading that each species can experience (87). Simulation-derived body temperatures were predicted at the spatial coordinates where we measured empirical field-measured body temperatures (*SI Appendix*, Table S1). Validation of NicheMapR simulations is given in *SI Appendix*, *Supplementary Methods*.

***Heat waves.*** We were interested in evaluating whether heat waves occurred in the days or weeks preceding our contemporary heat tolerance estimations. We used the air temperatures derived from the ERA5 reanalysis described above to estimate heat waves in each locality where we conducted field work. We first summarized hourly air temperature to daily averages, and then estimated the 95th percentile of the daily air temperature registered during 25 continuous years (2000–2025). When daily $T_{air}$ in each locality exceeded the 95th percentile during three or more consecutive days, we considered this event as a heat wave (88). Heat waves were considered independent events if they were separated by at least four consecutive days (88).

***Comparing thermal heterogeneity between closed and open sites.*** We compared operative temperatures ($T_e$) between one open environment and one shaded habitat to evaluate thermal heterogeneity. $T_e$ represents the equilibrium body temperature of a lizard in the absence of behavioral thermoregulation (89). We recorded $T_e$ using copper models of lizards during 14 consecutive months (July 25, 2021, to August 21, 2022) in the Guánica dry forest (17.96°N, −66.89°W; 135 m) and the humid forest of Mata de Plátano (18.41°N, −66.73°W; 150 m), Puerto Rico. In each habitat, we placed 50 copper models randomly distributed in microsites occupied by anoles, from the ground level up to 5 m in height; microsites were selected following (27). Of these, 47 were recovered from Guánica and 48 from Mata de Plátano. Inside each copper model we inserted one temperature data logger (Thermochron iButton® DS1925L-F5; accuracy ±0.5 °C), which recorded temperature every 30 min from 6:00 to 18:00 h. Because the data were not normally distributed, we used a Wilcoxon rank-sum test to compare operative temperatures between Guánica and Mata de Plátano (*SI Appendix*, Fig. S11).

***Thermoregulatory behavior.*** Active thermoregulation occurs when individuals use behavioral adjustments to maintain their field body temperature within a certain range (30). By contrast, thermoconformity occurs when individuals allow their body temperature to track the environment (30). We were interested in quantifying the

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thermoregulatory differences between open/edge habitat and closed/shaded habitat anoles and evaluating whether thermal behavior changed over time. To this end, we estimated the thermoregulatory effectiveness (*E*) of two open/edge habitat species (*A. cooki* and *A. shrevei*) and six closed/shaded habitat anoles (*A. cybotes*, *A. cristatellus*, *A. evermanni*, *A. gundlachi*, *A. krugi*, and *A. lineatopus*) (*SI Appendix*, Fig. S6 and Table S2) following the equation by ref. 30; 1) $E = 1-(\overline{db}/(\overline{de}))$, where *E* close to 1 indicates active thermoregulation, and *E* close to 0 indicate thermoconformity. $\overline{db}$ (accuracy of $T_b$) indicates the deviation (°C) of $T_b$ from a set-point temperature range ($T_{set}$, which describes the central 50% of body temperatures selected in a laboratory thermal gradient, with $T_{set25}$–$T_{set75}$ defining the boundaries of this range; experiment described in *SI Appendix*, *Supplementary Methods*), and $\overline{de}$ (thermal quality of the habitat) indicates the deviation (°C) of $T_e$ from $T_{set}$. Details to estimate thermoregulatory effectiveness are given in *SI Appendix*, *Supplementary Methods*.

***Heat tolerance.*** We compiled data for the critical thermal maximum [$CT_{max}$; which describes the upper thermal limit to locomotion (90)] measured in 2011–2013 for 16 Caribbean anole species (26, 28) (summarized in *SI Appendix*, Table S3). Between 2022 and 2025 we revisited the seven localities where heat tolerance was previously estimated to measure the $CT_{max}$ of the same species (*SI Appendix*, Table S3 and Dataset S1). The dates of historical and contemporary estimations are included in the *SI Appendix*, Table S6 and Dataset S1. For all 16 species, our field work was conducted during the same seasons in which $CT_{max}$ had previously been estimated (*SI Appendix*, Table S3). In addition, for 10 species we also conducted fieldwork during a different season to test for physiological plasticity in contemporary $CT_{max}$ estimates (*SI Appendix*, Tables S3 and S4). In each locality, between two and five people performed at least 2 d of field work with diurnal (6:00 to 18:00) and/or nocturnal sampling (20:00 to 2:00) and we captured lizards manually or by a lasso attached to an extensible panfish pole. On the same day of capture, we transported the lizards to a field laboratory (room with air conditioning at 20 °C), and we placed each lizard individually into a small, plastic Tupperware™ container with wet paper and water ad libitum.

On the next day, we estimated the $CT_{max}$ of lizards following our previous work with anoles (26). Briefly, we placed a fine-gauge Omega temperature probe (5SC-TT-T-40-36 [0.08-mm diameter]) ~1 cm into the cloaca of each lizard, and we secured the temperature probe to the base of the tail using a small piece of medical tape, without compromising lizard movement. Then, we connected the temperature probe to a digital thermometer (HH806AU, Omega) and placed each lizard into a small plastic container. We suspended a 100 W light bulb ~20 cm above the plastic container to increase the core temperature of each lizard at a rate of ~1 °C min. When we observed signals of heat evasion, we began flipping lizards onto their backs. If lizards righted themselves, we then raised the core temperature an additional 0.2 °C and flipped them again. When a lizard failed to right itself, we registered their body temperature as the critical thermal maximum. At the end of the experiment, we allowed lizards to return to the laboratory temperature (20 °C), and we hydrated them ad libitum. On the day after heat tolerance measurement, we released the lizards back to their capture sites.

For each species, we were interested in comparing heat tolerance among years (historical vs. contemporary) and seasons. Sample sizes varied among sampled periods, and the variance and distribution of heat tolerance usually departed from parametric assumptions for most species. Therefore, we used nonparametric Kruskal–Wallis tests to evaluate differences in $CT_{max}$ among years and seasons within each species. When significant differences were detected, we conducted pairwise comparisons using Wilcoxon rank-sum tests with Benjamini–Hochberg correction to control the false discovery rate associated with multiple comparisons (91). Additional experiments indicated that neither heating rate, observer identity, nor the temperature interval at which lizards were flipped onto their backs significantly affected contemporary $CT_{max}$ estimates (*SI Appendix*, *Supplementary Methods*). Last, we were interested in comparing heat tolerance across years and among species from different thermal environments. For these interspecific comparisons of $CT_{max}$, we employed a phylogenetic ANOVA as described below (*Phylogenetic Analyses* section).

***Experimental thermal exposure.*** In addition to seasonal comparisons in the wild, we conducted a series of sequential thermal exposure experiments on seven adult males of *A. shrevei* from Valle Nuevo to test whether contemporary shifts in $CT_{max}$ could be experimentally reversed or reproduced through short-term plasticity. Lizards were brought back to our facilities at Yale University where they were maintained in environmental chambers at a constant temperature of 28 °C (±1 °C), humidity of 70% (±5%), and a 12:12 D cycle of light for 2 mo (from August 5 to October 9, 2023). 28 °C corresponds to the mean $T_b$ of wild-caught lizards sampled a decade ago in the same locality (26, 27). After this period, we measured $CT_{max}$ using the procedure described above. We then maintained the same individuals at a constant temperature of 20 °C (±1 °C) for 4 wk (from October 10 to November 10, 2023), after which time we measured heat tolerance again. The 20 °C treatment was included as a cooler but nonstressful condition to test whether $CT_{max}$ could be further reduced below historical levels. This temperature approximates the average daytime $T_e$ of Valle Nuevo (*SI Appendix*, Fig. S6*C*). After this period, we returned lizards to 28 °C (from November 11, 2023, to April 29, 2024) and raised the chamber temperature to 31 °C (±1 °C) for 3 wk (from April 30 to May 20, 2024), after which we again measured heat tolerance. 31 °C reflects the contemporary average field-active body temperature of *A. shrevei* (*SI Appendix*, Fig. S6*C*). Each lizard was kept in an individual terrarium (38 cm L, 23 cm W, and cm 28 H) and provided of water ad libitum and fed with 0.5-inch banded crickets (*Gryllodes sigillatus* sprinkled with calcium and multivitamins) twice a week. To compare $CT_{max}$ values measured after the experimental treatments together with those obtained from wild-caught lizards, we used a linear mixed model (LMM), where heat tolerance was the dependent variable and lizard ID was included as a random effect to account for repeated measurements across experimental temperatures (*SI Appendix*, Fig. S23).

***Intergenerational laboratory-rearing experiment.*** In September 2024, we captured 14 females and 15 males of *A. cybotes* from Los Patos, DR. We brought these lizards back to our environmental chambers at Yale and maintained them at a constant temperature of 28 °C (±1 °C), humidity of 70% (±5%), and a 12:12 D cycle of light. Based on our previous work with anoles (27), each female–male pair was housed within a plastic container (38 cm L × 23 cm W × 28 cm H) in which we included a felt carpet, a small pot with moist soil for laying eggs, and a mesh hammock and a wood dowel for perching. Lizards were misted twice daily and fed with 0.5-inch banded crickets dusted with calcium and multivitamins twice a week. We checked the small pots daily for eggs. Each egg we found was placed individually within a Petri dish (14 cm in diameter) containing 20 g of vermiculite mixed with 20 mL of spring water. Those eggs were incubated in the same environmental chamber (at 28 °C) and each hatchling was housed individually within a plastic container (31 cm L, 20 cm W, and 20 cm H) in which we included a felt cage carpet, a small pot for refuge, and a mesh hammock and a wood stick for perching. Hatchlings were misted twice daily and fed daily with 0.25-inch banded crickets dusted with calcium and multivitamins. When hatchlings reached ~30 mm in SVL we switched to feeding them with 0.5-inch crickets twice a week. We reared lizards to adulthood (6 to 8 mo) and then estimated their heat tolerance. On July 3, 2025, we chose 8 lizards reared in the laboratory (39 to 46 mm SVL for females, $n = 3$ and 48 to 54 mm SVL for males, $n = 5$), with one representative from 8 female–male pairs. We estimated the heat tolerance of lizards reared at 28 °C and transferred them to another environmental chamber at a constant temperature of 31 °C (±1 °C), humidity of 70% (±5%), and a 12:12 light:dark cycle. After 2 wk, we remeasured the heat tolerance of the same individuals and returned them to 28 °C. After they spent a month at 28 °C, we measured the $CT_{max}$ of those same lizards once more. Temperatures of 28 and 31 °C represent the set-point temperature range measured in *A. cybotes* from Los Patos a decade ago (27). We compared heat tolerance values obtained after each experimental temperature with those measured from wild-caught lizards using an LMM, with heat tolerance as the dependent variable and lizard ID included as a random effect to account for repeated measurements across experimental temperatures (Fig. 3).

***Experimental heat wave.*** Because several of our $CT_{max}$ measurements for closed-canopy anoles were conducted within 2 wk of a heat wave (*SI Appendix*, Table S6), we tested whether short-term heat wave exposure could contribute to elevated heat tolerance. We transferred eight laboratory-reared *A. cybotes* lizards from 28 °C to 31.5 °C (the average $T_{air}$ experienced by this species during a heat wave preceding our contemporary measurements; *SI Appendix*, Table S6) for 3 d. We then returned the lizards to 28 °C for 11 d, reproducing the shortest interval between the end of the heat wave and our contemporary $CT_{max}$ measurements (*SI Appendix*, Table S6). We compared their $CT_{max}$ with that of their siblings, which were continuously reared at 28 °C and never exposed to higher temperatures. We tested for differences in heat tolerance among groups using an LMM with $CT_{max}$ as the dependent variable and maternal ID as a random effect.

**Phylogenetic Analyses.** All analyses were conducted using the R environment v4.2.0 (92), and using the maximum clade credibility (MCC) anole tree of ref. 93.

***Stochastic character mapping of habitat preference.*** We performed stochastic character mapping (94) of habitat use (open/edge or closed/shaded

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habitat) using the *make.simmap* function with 500 simulations across the MCC tree and a transition model of all rates different (ARD) in the phytools (v2.1.1) R package (95) to graphically illustrate independent transitions in thermal habitat use in Caribbean anoles. This is a probabilistic approach for reconstructing ancestral states and transitions across phylogenies; the ARD transition model permits asymmetric transition rates between habitat states.

***Phylogenetic generalized least squares (PGLS).*** We performed a PGLS regression using the *gls* function in the nlme (ver. 3.1.157) R package (96) to evaluate the relationship between the magnitude of the heat tolerance shift and historical heat tolerance. We included the thermal habitat categorization (open/edge vs. closed-canopy) in the analysis to account for potential differences in the intercept and/or slope between groups.

***Phylogenetic ANOVA.*** We performed phylogenetic ANOVAs using the *phylANOVA* function with 500 simulations across the MCC tree in the phytools (v2.1.1) R package (95) to test for differences in historical (2011–2013) heat tolerance between open/edge and closed/shaded habitat species. Subsequently, we reran the same analysis using the contemporary (2022–2024) heat tolerance data. As *A. stratulus* (considered an open/edge population in this study) can also inhabit shaded conditions in El Verde, we reran the two ANOVAs switching thermal habitat of this species and obtained similar results (*SI Appendix*, Table S5).

**Ethics Statement.** The field work and data collection were conducted in accordance with the collecting permits DRNA: 2022-IC-021 and 2025-IC-011, DJ-C-1-2023-00038, and NEPA: Ref.#18/27 approved by the Departamento de Recursos Naturales y Ambientales del Gobierno de Puerto Rico, the Ministerio de Medio Ambiente y Recursos Naturales de la República Dominicana, and the National Environment and Planning Agency of Jamaica, respectively. *A. cybotes* and *A. shrevei* were exported from the Dominican Republic to the United States of America in accordance with the permit VAPB-11787 provided by the Viceministerio de Areas Protegidas y Biodiversidad, Ministerio de Medio Ambiente y Recursos Naturales de la República Dominicana. All protocols, including animal care and experiments, were conducted in accordance with the Institutional Animal Care and Use Committee policies (Yale IACUC 2022-20297).

**Data, Materials, and Software Availability.** Raw data used to perform temporal comparisons of $CT_{max}$ (Dataset S1), to estimate thermoregulatory effectiveness (Dataset S2), and to generate all the figures (Dataset S3) are included as supplementary files. The estimated body temperatures (Dataset S4), and all code needed to reproduce the analyses are available on Dryad data have been deposited in Dryad (https://doi.org/10.5061/dryad.gmsbcc30z). Previously published data were used for this work (26, 28). All other data are included in the manuscript and/or supporting information.

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