Bigger is not better: Larger bees face greater risks from climate change

by

Theresa Wolff

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Approved by

Dr. Clint Penick, Chair, Assistant Professor, Department of Entomology and Plant Pathology
Dr. Anthony Abbate, Assistant Professor, Department of Entomology and Plant Pathology
Dr. Alana Jacobson, Associate Professor, Department of Entomology and Plant Pathology

Abstract

Body size plays a fundamental role in how animals respond to their environment. Smaller animals are more vulnerable to heat loss and desiccation due to their high surface-area-to-volume ratio. I investigated the relationship between bee body size and climate response by measuring physiological tolerance in the lab and physiological resistance in the field. I found that small bees are cooler while foraging than larger bees, but body size does not significantly affect thermal tolerance. I found that smaller bees are drier but have a greater desiccation tolerance, which evolved due to regular exposure to high desiccation risk. For all results except for desiccation tolerance, relationships are independent of phylogenetic relatedness. Finally, larger bees are closer to their absolute physiological limits and therefore may be at increased risk to the effects of climate change. If we see declines in large bees, we may see changes in pollination services and plant communities.

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Table of Contents

List of Tables

List of Figures

List of Abbreviations

AIC	Akaike's information criterion
CT_{max}	Critical thermal maximum
CWC	Critical water content
E	Actual vapor pressure
E_s	Saturated vapor pressure
GLMM	Generalized linear mixed effects model
GLM	Generalized linear model
ITD	Intertegular distance
kPa	kilo Pascal
PGLS	Phylogenetic generalized least squares
RH	Relative humidity
SA	Surface area
SA/V	Surface-area-to-volume ratio
T	Actual air temperature
T_b	Body temperature
T_{amb}	Ambient temperature
V	Volume
VPD	Vapor pressure deficit

Chapter 1. Literature Review

Introduction

Body size is a fundamental trait influencing an animal's response to climatic conditions (Bishop & Armbruster, 1999; Claunch et al., 2021; Kaspari et al., 2015; Pincebourde et al., 2021). Smaller animals have a higher surface-area-to-volume ratio, which means they lose heat and water faster (Bujan et al., 2016; Claunch et al., 2021). Therefore, smaller animals are expected to face higher risks of desiccation and death during heat waves and droughts, both of which are expected to increase as a result of climate change (Dai, 2013a; Gonzalez et al., 2024; Prugh et al., 2018). As Haldane states in "On Being the Right Size," simply scaling up a body plan with no modifications is impossible. An increase or decrease in size is limited by physical rules (Haldane, 1927). Larger animals have a higher volume, allowing more efficient thermal regulation as they have greater thermal inertia. Larger animals also have a lower surface area and thicker boundary layers which reduce the amount of heat they lose to the ambient air due convective cooling (Bogert, 1949; Clusella Trullas et al., 2007). As with all other aspects of an organism's life history, changes in body size are associated with survival trade-offs. For example, longer wings increase foraging distances but also increase energy expenditure from heat loss over an increased surface area (Peat et al., 2005; Peters et al., 2016). The effect of body size on heat gain and water loss may highly influence habitat selection, especially for small ectotherms.

While relatively small when compared to vertebrates, insects comprise the bulk of animal diversity (Müller et al., 2023). Insects range in size from a fairy fly (0.5mm long, *Mymaridae*) to a giant Chinese walking stick (0.5m long, *Phryganistria*), which represents a 1,200-fold difference in body size. Therefore, it is likely that variation in body size could drive differences in vulnerability to climate change. If there is a strong relationship between body size and thermal or hygric tolerances, body size could even be used as a tool to predict which insects will be affected by climate change. Further, variation in body size globally may even be able to predict which geographic areas will face greater insect loss due to climate change.

Global size trends

Some groups of animals follow latitudinal clines in body size — as latitude increases their body size increases or decreases. One of these clines is defined in Bergmann's rule, which states that larger individuals will be found in colder environments at higher latitudes and elevations (Geraghty et al., 2007). Organisms at high latitudes and altitudes are exposed to both colder temperatures and a wider range of temperatures than organisms in more temperate areas. This means that larger individuals should be more tolerant of colder temperatures as larger animals are able to maintain their internal temperature for longer due to higher thermal inertia (Perez & Aron, 2020; Rubalcaba et al., 2019). This rule is supported across endotherms with increases in body size both within and among taxa associated with higher latitudes and elevations, but there is no wide consensus if this rule is applicable across all taxa (Perez & Aron, 2020).

Most studies on Bergmann's rule have been focused on endotherms even though poikilotherms comprise up to 99% of diversity globally (Gérard et al., 2018). Ectotherms have been found to follow the converse of Bergmann's rule, with body size decreasing towards the poles (Chown & Gaston, 2010). However, this pattern differs across ectotherm taxa, especially among insect groups that can thermoregulate using facultative endothermy, like bees. Gérard et al. investigated this hypothesis in bee genera (Hymenoptera:Anthophila) across the European continent and found that mean assemblage body size increases with increasing latitudes, meaning that least some bees follow Bergmann’s rule (Gérard et al., 2018). Another study looking at the effect of body size on minimum and maximum temperatures in bumble bees (*Bombus spp*.), found a significant relationship between body size, elevation and critical limits (Oyen et al., 2016). These studies provide further support that larger-bodied insects are better able to regulate their internal temperatures across both cool and warm climates (J. A. Bishop & Armbruster, 1999).

Other studies on bees have found a positive correlation between body size and cold tolerance across species, though it does not hold true for every species (Peters et al., 2016), but see (Oyen et al., 2016). Body size in bumble bees has been linked to both latitude and elevational range (Oyen et al., 2016). Larger bees are found across colder climates and in tropical climates, with temperate bumble bees being intermediate in size (Peat et al., 2005). This study found that the largest bumble bees are present in the tropics, though they postulate this could be due to other factors like decreased seasonality and more abundant floral resources (Peat et al., 2005). Altogether, these studies point to variation in body size trends by taxa and no clear consensus across the insect kingdom (Chown & Gaston, 2010).

Thermoregulation

The challenge of thermoregulation, or efficiently maintaining a survivable internal body temperature, is ubiquitous across the animal kingdom. Ectotherms control their body temperature through the use of microclimates (Tattersall et al., 2012). This is achieved, for example, by seeking shade to escape high temperatures or basking in sunlight to increase internal temperatures. In contrast, endotherms can generate their own heat through metabolic heat production. While endothermy and ectothermy are commonly characterized as dichotomous, these represent the extremes of a thermoregulatory spectrum (Bogert, 1949). Moreover, animals may exhibit homeothermy, whereby their internal body temperature is maintained at a consistent temperature, or poikilothermy, whereby the body temperature fluctuates with that of the external environment. Within insects, individuals have three options to deal with variable environmental temperatures: they can change their behavior, adapt their physiology, or evolve morphological traits to withstand extreme temperatures. With respect to behavior, honeybees and bumble bees, achieve a consistent, elevated internal temperature by shivering flight muscles at rest (Heinrich, 1974). Other examples include short cooling flights taken by small bees while foraging (Corbet & Huang, 2016), or a butterfly basking with wings spread in the sun (De Keyser et al., 2015). These behaviors work in concert with physiological and morphological adaptations. Physiological adaptations, such as restructuring the cuticle by adding more hydrocarbons to protect against freezing or the creation of heat shock proteins, have been shown to directly relate to thermal limits (Helms Cahan et al., 2017; Miller & Stillman, 2012). Less work has been done to correlate morphology with these thermal limits, though there is evidence to support that morphology does have an impact on thermal tolerance. Thermal limits have been shown to vary globally for insects, with little variation in global thermal maximums (Addo-Bediako et al., 2000). This minimal variation in upper lethal limits is a problem, particularly for tropical species that are already close to their limits especially as temperatures globally are predicted to increase (Tewksbury et al., 2008). Morphological adaptations may provide a buffer to developing energetically costly physiological or behavioral adaptations for ectotherms to tolerate increasing temperatures. Thus far the literature relating the impact of body size on thermal tolerances has not disentangled the effect of body size from behavioral adaptations and other selective pressures.

Body size and climate response

Factors that influence body size and environmental tolerances vary. Factors that influence both body size and tolerance include ambient temperature, phylogeny, and metabolic rate (Bosch & Vicens, 2002; Riemer et al., 2018; Terblanche et al., 2007). Life history traits like emergence time, nesting habits and sociality can also impact both body size as well as effecting tolerance to climatic extremes (Gérard et al., 2020; Hamblin et al., 2017; Maebe et al., 2021). Finally, environmental factors including water availability, food quality, food availability, and additional pressures like competition, pesticides and disease can influence both body size and tolerance (Brant et al., 2022; Goulson et al., 2015; Hamblin et al., 2017; Maebe et al., 2021; O'Donnell, 2022). Even if we only consider body temperature, small insects are influenced by a multitude of environmental factors. Microclimatic conditions experienced by small ectotherms are influenced by radiative heat gain from the sun, evaporative cooling at the body surface, heat gain by metabolic heat produced in flight, and rapid cooling in shaded niches (Kaspari et al., 2015; Pincebourde et al., 2021). These microclimatic effects on body temperature are complex and not well replicated in controlled lab conditions. Even within studies specifically interested in thermal limits, laboratory methods control for ambient conditions to isolate specific components influencing climatic response (Bujan et al., 2016). For example, to study the effect of the boundary layer —which been shown to be highly influence on the body temperature of small organisms —insects were housed in individual vials in the lab isolated from natural conditions (Corley et al., 2023; Kaspari et al., 2015; Pincebourde et al., 2021). Laboratory studies change the observed results regardless of the effects being controlled for, because there are so many variables impacting body temperature and hydration. As such, a field-based approach may better reflect body conditions experienced in the field, especially body temperature (Bishop &

Armbruster, 1999). Body size is also related to thermoregulation through muscular heat production. One well-known example is the use of thoracic muscles to warm up flight muscles in bumble bees; larger muscles are a direct result of larger body size, so larger-bodied bumble bees warm up and fly at lower temperatures than smaller bees (Heinrich, 1974). Another way body size is related to thermoregulation is the scale of microclimates an organism can use. An example is the boundary layer, which encapsulates smaller insects sitting on a leaf's surface keeping them cooler than larger insects on the same leaf (Pincebourde et al., 2021).

Most insects are several orders of magnitude smaller than the smallest vertebrates, and it is unclear if differences in body size among insects could have a biologically significant impact on heat absorption and water loss rates, as insects operate on such a small scale. Insects are an extremely diverse group that occupy a huge range of niches and may have evolved unique physiological, morphological, and behavioral mechanisms to buffer against environmental extremes that may mask body size effects (Barrett & O'Donnell, 2022; Baudier et al., 2015). For example, solar radiation reflected by hairs found on Saharan silver ants (*Cataglyphis bombycina)* living in the Sahara Desert, as well as on *Centris pallida* living in the Sonoran Desert, potentially mask any effects of body size variation (Barrett & O'Donnell, 2022; Shi et al., 2015). Additionally, this physical protection presumably allows activity at higher temperatures than internal adaptations alone. In other taxa like bumblebees, hair over thoracic flight muscles insulates them and allows flight at lower temperatures with or without the sun warming them (Peters et al., 2016; Roquer-Beni et al., 2020; Stone & Willmer, 1989). This allows insects to heat up more quickly and fly at lower temperatures, outcompeting less insulated insects regardless of body size (Stone & Willmer, 1989). Variations in physiology, morphological adaptations and behavior help insects survive dangerous environments though the extent of these effect vary by taxa. These adaptations work together with body size to allow organisms to persist even as climate conditions get hotter and drier.

Bee climate responses

Bees are essential pollinators facing global declines due, in part, to the effects of climate change. Native pollinators provide an estimated $3.06 billion in free crop pollination services in the United States alone (Meiners et al., 2019), and assist in crop production worth nearly $215 billion worldwide (Goulson & Nicholls, 2016). Changing precipitation patterns and temperature fluctuations are affecting bees with an array of impacts, occurring across all stages of development. Warmer temperatures lead to bees reaching maturity faster, earlier adult emergence, smaller adult body size, temporal and morphological mismatches between bees and flowers, and even range shifts as bees move into new niches with changing temperatures (Forrest & Thomson, 2011; Gérard et al., 2020; Imbach et al., 2017; Kjøhl et al., 2011; Oyen & Dillon, 2018; Parmesan & Yohe, 2003; Rittschof & Denny, 2023). Developmental time and temperature are closely linked—increased temperatures lead to shorter development time and decreased adult size consistent with the temperature-size rule (Gérard et al., 2020; Kingsolver & Huey, 2008; Rittschof & Denny, 2023). Bumble bees—larger bees well-adapted to cooler climates—are an example of a group already affected by declining body size due to climate change, which is in line with body size declines observed globally across taxa (Fitzgerald et al., 2022; Gardner et al., 2011). This decrease in body size may result in lower pollination efficiency by decoupling bee morphology from the flowers they pollinate, along with a decreased likelihood for efficient pollination, as larger bees are more efficient pollinators likely due to their increased surface area (Fitzgerald et al., 2022; Gérard et al., 2020; Kazenel et al., 2024). Many flowers requiring high morphological specificity are likely to be the most impacted by changes in bee body size, negatively impacting pollination success (Gérard et al., 2020). Additionally, faster development time could lead to bees emerging before the flowers bloom, negatively impacting both pollinator and plant populations (Gérard et al., 2020). Reduced adult body size could affect the distance bees travel for floral resources, which in turn could impact pollination efficiency for agricultural crops as native bees contribute to pollinating agricultural crops within their daily forage distance (Greenleaf et al., 2007). Smaller adult body size means greatly reduced foraging distance and smaller range for pollination services (Greenleaf et al., 2007). Reduction in pollination services could lead to lower crop yield and declines or extinctions for native plants that rely on wild bees for pollination (Goulson et al., 2015; Potts et al., 2010). Finally, the impact of the loss of native bees species will likely have ripple effect on larger taxa across ecosystems as plants are knocked out (González-Tokman et al., 2020; Potts et al., 2010).

Conclusion

Insects are highly susceptible to climate change due to their small size, high surface-area-to-volume ratios, and reliance on external conditions to thermoregulate. Body size plays a critical role in influencing how insects interact with their physical environment, with larger individuals generally exhibiting greater resistance to temperature extremes and desiccation (Bujan et al., 2016; Claunch et al., 2021; Gonzalez et al., 2024; Jones et al., 2024; Kaspari et al., 2015; Oyen et al., 2016). While behavioral and physiological adaptations contribute to thermal tolerance, morphological traits, particularly body size, may offer advantages in coping with changing climates. However, it remains unclear whether body size alone is a reliable predictor of limits across taxa, as insects have a variety of mechanisms potentially masking these effects.

Understanding the interplay between body size and climate resilience is especially important for bees, which are already experiencing declines in both body size and total abundance due to rising temperatures (Cameron et al., 2011; Fitzgerald et al., 2022; Kerr et al., 2015). Identifying how body size influences and interacts with climate responses can help predict which species are most vulnerable and guide conservation efforts in a warming world.

Chapter 2. Bigger is not better: Larger bees face greater risks from climate change

Introduction

Body size is a fundamental trait that shapes how animals interact with their environment (Bishop & Armbruster, 1999; Claunch et al., 2021; Kaspari et al., 2015; Pincebourde et al., 2021). As climate change increases the frequency of heat waves and droughts, body size is expected to influence which species persist and which decline (Dai, 2013b; Gonzalez et al., 2024; Prugh et al., 2018; Ummenhofer & Meehl, 2017). Smaller animals have a higher surface-area-to-volume ratio, which increases the rate that they exchange heat and moisture with their environment (Bujan et al., 2016; Claunch et al., 2021). This is expected to make small animals more vulnerable to overheating and desiccating in hot, dry conditions. In contrast, larger animals, with a lower surface-area-to-volume ratio, absorb heat more slowly and retain water more effectively due to their greater internal volume and relatively smaller surface area (**Fig 1A**). As a result, larger animals are often assumed to be better buffered against extreme temperatures and aridity (Bujan et al., 2016; Gonzalez et al., 2024). Despite these predictions, empirical studies linking body size to physiological tolerance of heat and desiccation have produced mixed results (Bujan et al., 2016; Claunch et al., 2021; Gonzalez et al., 2024; Jones et al., 2024; Kaspari et al., 2015; Oyen & Dillon, 2018; **Table S1**). A key challenge in interpreting these findings is that physiological assays do not always reflect how animals respond under natural conditions, and they often fail to distinguish between two important but distinct responses to environmental stress: resistance and tolerance. Clarifying the role of body size in climate vulnerability requires separating these components and understanding how each contributes to performance and survival in the field.

Resistance vs. tolerance

Although often used interchangeably, "resistance" and "tolerance" refer to different aspects of an organism's response to environmental extremes (Chown et al., 2011). Resistance is the ability to buffer internal conditions from external variation—for instance, maintaining a stable body temperature or internal water balance despite changes in the surrounding environment. Larger animals, for example, absorb heat more slowly due to their lower surface-area-to-volume ratio, causing their body temperature (T_b) to lag behind ambient temperature (T_{amb}) (Bishop & Armbruster, 1999; Bujan et al., 2016; Oyen & Dillon, 2018; Rubalcaba & Olalla-Tárraga, 2020). In contrast, smaller animals experience more rapid internal changes, with body temperature more closely tracking environmental conditions (Corbet & Huang, 2016). Thermal resistance can be approximated as the rate of internal change relative to ambient conditions over time ($[T_b – T_{amb}]/\text{time}$), with greater resistance indicated by a slower rate of change. An animal with greater thermal resistance will therefore take longer to reach thermal equilibrium with its environment, which will delay the physiological stress associated with extreme conditions.

Tolerance, on the other hand, is the ability to withstand extreme conditions once they are reached (Chown et al., 2011). Tolerance is typically quantified as an organism's critical limits, which can refer to thermal or desiccation limits. For example, thermal tolerance defines the range of temperatures within which an animal can remain active (Baudier et al., 2015; Huey et al., 2012). This range is bounded by an animal's critical thermal limits, CT_{max} and CT_{min}, which represent the maximum and minimum temperatures an animal can withstand before losing motor control (Baudier et al., 2015; Bishop & Armbruster, 1999; Bujan et al., 2016). For water balance, tolerance is bounded by the amount of water required for an animal to survive, estimated as the amount of water remaining in an animal's body after it dies due to desiccation, or their critical water content (CWC; M. G. Johnson, Alvarez, et al., 2023; Schilman et al., 2007). Animals with a lower CWC can survive with lower volumes of water in their bodies and are therefore more tolerant to desiccation.

While resistance and tolerance are both crucial for coping with environmental stress, their relationships to body size differ in predictability. Resistance is more easily linked to differences in body size. Smaller animals typically exchange heat and water more rapidly due to their higher surface-area-to-volume ratio, leading to lower thermal and desiccation resistance in most contexts, though convective cooling during flight may enhance heat loss in small flying insects (Benoit et al., 2023; Corbet & Huang, 2016; Pincebourde et al., 2021). In contrast, predictions for how body size influences tolerance—the ability to endure extreme conditions once internal limits are reached—are less straightforward. There is no direct mechanistic link, but size may influence selection on tolerance traits indirectly: small animals with lower resistance may evolve higher thermal limits or tolerate lower body water content, while larger insects may evolve greater thermal tolerance to offset internal heat buildup. These compensatory dynamics suggest that both small and large species may converge on similar tolerance traits via different physiological routes. Yet, it remains unclear how body size systematically predicts both resistance and tolerance to heat and desiccation, which represents a key gap in our understanding of physiological responses to climate stress.

Predicting climate responses

The physiological traits outlined above—particularly critical thermal limits (e.g., CT_{max}) and desiccation tolerance thresholds (e.g., critical water content or CWC)—have become central tools for predicting how animals will respond to ongoing and future climate change (Burdine &

McCluney, 2019; Deutsch et al., 2008; Diamond et al., 2012; Schilman et al., 2007). These traits define the boundaries of environmental conditions that individuals can tolerate and thus help estimate a species' capacity to survive extreme heat and drought events. Across taxa, from ectothermic vertebrates to invertebrates, upper thermal limits (CT_{max}) have been shown to predict warming tolerance, defined as the difference between CT_{max} and the highest temperatures experienced in a species' habitat (Deutsch et al., 2008; Sunday et al., 2014). Physiological limits can be used to calculate thermal and desiccation safety margins—metrics that quantify how close animals live to the edge of their physiological capacity. A thermal safety margin is typically calculated as the difference between an organism's CT_{max} and its operative body temperature, while a desiccation safety margin reflects the difference between an animal's tolerance to water loss (e.g., CWC) and its estimated water content under water stress (Burdine & McCluney, 2019; Clusella-Trullas et al., 2021; Sunday et al., 2014). Narrow safety margins indicate populations that are living dangerously close to their physiological limits and are therefore more likely to experience declines as climate extremes intensify.

Safety margins offer valuable predictive power for conservation and ecological forecasting. For example, species or populations with small safety margins are more vulnerable to heat waves, prolonged droughts, and other climate-related stressors. Recent empirical studies have confirmed that both thermal and desiccation tolerances—and their respective safety margins—are closely linked to population trajectories. In a large-scale study across hundreds of bee populations, increased thermal and desiccation tolerance were strong predictors of population persistence and even growth under conditions of increasing aridity and temperature extremes (Kazenel et al., 2024). Importantly, these physiological traits and safety margins are not independent of body size — which can influence heat and water exchange with the environment.

However, the extent to which body size drives variation in resistance and tolerance to climate extremes remains unresolved. This knowledge gap limits our ability to accurately incorporate body size into models predicting species' responses to climate change.

Climate responses in bees

Here, we focus on determining the role of body size in shaping bee responses to climate change. Bees are experiencing widespread declines across continents, with important consequences for ecosystem function and agricultural production (Cameron et al., 2011; Jackson et al., 2022; Kammerer et al., 2021; Kerr et al., 2015; Soroye et al., 2020). These losses extend beyond reductions in abundance or diversity to include range contractions, particularly at the warmer, southern edges of species distributions (Kerr et al., 2015). While multiple factors contribute to these declines—including habitat loss, pesticide exposure, pathogen pressure, and disruption of plant-pollinator interactions (Gérard et al., 2020; Goulson & Nicholls, 2016; Potts et al., 2010)—climate change is increasingly recognized as a major driver (Jackson et al., 2022; Kammerer et al., 2021), and bee responses have been found to correlate with their physiological limits (Hamblin et al., 2017; Burdine & McCluney, 2019; Kazenel et al., 2024). These findings underscore the importance of physiological constraints in shaping ecological responses and suggest that variation in traits such as thermal tolerance and water balance may help explain species-specific patterns of vulnerability or resilience under a changing climate.

We used field-caught bees to estimate physiological traits related to the resistance and tolerance of environmental extremes. We collected bee across more than 30 bee genera sampled from 60 urban gardens in 10 U.S. cities spanning broad temperature and humidity gradients (**Fig S1**). We captured bees in the field and measured thoracic body temperature, then assessed CT_{max}

and CWC through standardized lab assays. Percent body water was calculated gravimetrically, and body size was quantified using either dry mass or intertegular distance (ITD). We paired these measurements with fine-scale environmental data to estimate thermal and desiccation safety margins—defined as the difference between physiological limits (CT_{max} or CWC) and field-measured stress exposure (T_b or body water content). We predicted that body size would influence both resistance and tolerance traits (**Fig 1**). For thermal resistance, we expected that either larger bees would heat more slowly due to thermal inertia or smaller bees would exhibit greater convective cooling during flight, depending on which mechanism is dominant (**Fig 1B**). For thermal tolerance, larger bees may evolve higher CT_{max} to cope with greater heat retention, but smaller bees could also evolve higher CT_{max} to compensate for faster heat gain—making a null relationship equally plausible (**Fig 1C**). For desiccation resistance, we predicted that larger bees would retain more body water due to their lower surface-area-to-volume ratio (**Fig 1D**), while smaller bees may compensate through greater desiccation tolerance, reflected in lower CWC values (**Fig 1E**). By linking physiological traits to body size across environmental gradients, this study provides a mechanistic framework for identifying which bee species are most vulnerable to climate change.

Methods

Sample sites and environmental variables

We sampled bees from 60 community gardens across 10 U.S. cities over three summers (2021–2023; **Fig S1**, **Table S2**). The cities were selected to span a gradient in temperature and humidity, with high and low latitude cities selected within eastern (humid) and western (dry) regions. To confirm temperature and humidity gradients at each site, we measured temperature and humidity every four hours using iButton® data-loggers (DS1923, Maxim Integrated, Wilmington, MA, USA) from June 2021 –August 2023. We placed data-loggers inside an AcuRite solar radiation shield (Lake Geneva, WI, USA), suspended ~120 cm above the ground on a shepherd's hook (**Fig S2A**) to prevent direct sun exposure and ensure proper airflow around the sensors, which follows best practices for measuring air temperature at biologically relevant scales (Terando et al., 2017). We increased the measurement frequency to 10-minute intervals on days bees were sampled to capture fine-grain temperature and humidity to use in our calculations of thermal and desiccation resistance. We used vapor pressure deficit (VPD) as our metric for water stress, which we calculated using field measurements of temperature and humidity (see **Supplement**).

Body temperature (T_b)

To measure bee body temperature, we captured individuals using either a net or a custom-built "bee squeezer"—a modified 25 mL conical centrifuge tube with a mesh cap and sponge plunger (**Fig S2B**). The bee squeezer allowed for rapid capture and secure restraint, positioning the bee with its ventral thorax pressed against the mesh for efficient temperature measurement. We recorded thoracic temperature within 10 seconds of capture using a fine hypodermic thermal probe (~0.2 mm diameter; HYP0-33-1-K-G-24-SMPW-M, Omega Engineering Inc., Norwalk, CT, USA) connected to a handheld thermocouple reader (HH-25U, Omega Engineering Inc., Norwalk, CT, USA). After recording temperature, bees were anesthetized with CO_2 gas, cleaned of pollen and debris using forceps and a fine brush, and placed into pre-weighed vials for water content analysis (*n*= 6,802).

Critical thermal maximum (CT_{max})

We measured critical thermal maximum (CT_{max}) using a standard dynamic temperature ramping assay (Lutterschmidt & Hutchison, 1997). Bees were captured in the field and placed individually into 25mL conical centrifuge tubes with mesh lids for transport. To prevent starvation or desiccation during transport, each tube contained a sucrose-soaked cotton ball (1M concentration) taped to the mesh, providing access to both food and water. Tubes were transported to the lab in coolers with ice packs to induce chill coma (Mean±SD: 14.9°C ±6.13°C), and temperature was verified using iButton® data loggers (DS1923, Maxim Integrated, Wilmington, MA, USA). Upon arrival at the lab, bees were acclimated to room temperature (~20°C) for at least one hour and then transferred into individual 7mL glass vials before beginning trials. Trials were conducted using a digitally controlled dry heat block (Model IC25XT, Torrey Pines Scientific, Carlsbad, CA, USA) fitted with a custom aluminum insert containing 12 milled wells to securely hold each vial (**Fig S2C**). Vials were sealed with either plastic lids or aluminum foil lids with perforations for ventilation, and the inner rims of all lids were coated with Fluon (polytetrafluoroethylene, MSE Supply, Tucson, AZ, USA) to prevent bees from climbing into the lid to escape heat exposure. Preliminary tests showed no significant difference in CT_{max} based on lid type, so data from both lid types were pooled (see **Supplement**). The heat block was initially set to 36°C and held at that temperature for eight minutes to allow bees to acclimate. Following this period, the temperature was increased at a target rate of 1°C every four minutes (0.25°C/min). The actual ramp rate averaged 0.2°C/min (±3.55°C SD) based on internal vial temperature recorded with a temperature probe inserted through the lid of an empty vial in each run (HYP0-33-1-K-G-24-SMPW-M probe with a HH-25U thermocouple reader, Omega Engineering Inc., Norwalk, CT, USA). Bees were checked at four-minute intervals, and CT_{max} was considered the temperature at which individuals exhibited either spasming or loss of righting response, consistent with established protocols (*n* =2,977; Lutterschmidt & Hutchison, 1997). Due to minor variation in vial temperature among heat blocks, we corrected CT_{max} vials by determining slope of vial to block temperature at each block temperature within our dataset, then standardizing all CT_{max} values by block used (see **Supplement**). Control bees were held in identical vials at room temperature for the duration of each trial to account for potential handling effects.

Body water content

To determine the body water content of field-caught bees, we placed each bee into a pre-weighed vial immediately after measuring body temperature. Vials were weighed using an XPE56/A microbalance with a precision of 10 µg (Mettler Toledo, Columbus, OH, USA). To avoid contamination from skin oil that could alter weight measurements, we wore gloves while handling all vials. Bees collected for body temperature analysis were placed into vials in the field, which were then frozen and stored at −20°C. In the lab, we weighed each vial containing a bee along with any water vapor condensed inside. The vials were then opened and placed into a drying oven at 50°C for at least 48 hours to ensure complete water loss (McCluney et al., 2017). After drying, vials were re-weighed to obtain dry mass. Percent body water content was calculated as the difference between wet and dry weight, divided by the wet weight, following established methods (*n* = 3,272; Burdine & McCluney, 2019; Schilman et al., 2007).

Critical water content (CWC)

We calculated critical water content (CWC) as the percentage of body water remaining at the time of death due to desiccation, following Burdine & McCluney (2019). Bees were captured in the field and transported to the lab using the same procedures described for measuring critical thermal limits. In the lab, bees were placed into desiccation chambers (**Fig S2D**) maintained low relative humidity (Mean±SD: 14.34% ± 8.73%), which was verified using iButton® data loggers (DS1923, Maxim Integrated, Wilmington, MA, USA). Each chamber consisted of a 25 mL centrifuge tube connected to a second 25 mL tube containing either fresh or spent calcium sulfate desiccant (Drierite™, W. A. Hammond DRIERITE Co., Xenia, OH, USA). Chambers with spent desiccant served as controls, and control bees were provided with an additional piece of wet sponge to maintain moisture. We monitored bees for survival every two hours between 6:00 AM and 10:00 PM. Bees that died overnight, when monitoring was not possible, were excluded from the study. Upon death—indicated by a complete loss of responsiveness—we recorded the time of death and then transferred the bee to a pre-weighed vial for storage at -20°C. We then used the same procedures described for measuring body water content to calculate the percentage of water remaining in desiccated bees (*n* = 1,499). Lower CWC values indicated that a bee was able to survive with less body water and therefore had greater desiccation tolerance.

Body size

We quantified body size using one of two methods depending on the specimens used for each comparison. For bees used in comparisons of body temperature, water content, and CWC, we assessed body size was measured as dry mass following the same procedures used for calculating percent body water content. For bees used for CT_{max} comparisons, we assessed body size using intertegular distance (ITD), a metric shown to correlate strongly with body mass across bee taxa

(Cane, 1987; Kendall et al., 2019). We measured ITD by imaging each bee using a Nikon Z6 digital camera (Melville, NY, USA) mounted on a StackShot Macro Rail (Cognisys, Traverse City, MI, USA), with one of two interchangeable macro lenses (Venus 60mm f/2.8 and 25mm f/2.8, LAOWA, Hefei, China). Lighting was provided by a speedlight (Model TT685II N, Godox, GODOX Photo Equipment Co. Ltd, Shenzen, China) connected to DC power, along with two LED stand lights to ensure even illumination. Bees were positioned with the dorsal thorax in focus, including the tegulae at the wing bases. For hairy specimens, a pin dipped in 70% ethanol was used to gently move setae away from the tegulae to ensure measurement accuracy. Each image included a 10 mm reference scale, and ITD was measured to the nearest micrometer (range: 0.567–8.086 mm) using ImageJ software (Schneider et al., 2012; n =1,262).

Statistical analyses

We conducted all statistical analyses using R version 4.4.2 (R Core Team, 2024). To account for phylogenetic relatedness, we used phylogenetic generalized least squares (PGLS) analyses to examine how physiological traits varied with body size, including thermal resistance (temperature differential), thermal tolerance (CT_{max}), desiccation resistance (water differential), and desiccation tolerance (critical water content, CWC). We based our phylogenetic framework on the tree developed by Henríquez-Piskulich et al. (2024), using 1,001 bootstrap iterations to construct a maximum clade credibility tree. Analyses were performed at the genus level, where we summarized trait values as follows: median for thermal resistance, mean for desiccation resistance, 90th percentile for CT_{max}, and 10th percentile for CWC. These metrics were chosen to reduce the influence of extreme outliers while capturing biologically relevant trait extremes. Pagel's lambda was calculated to assess phylogenetic signal for each trait (Pagel, 1999). We evaluated five alternative tree models for each trait, varying tree structure and branch length criteria, and selected the model with the lowest Akaike Information Criterion (AIC). Final PGLS models were run across 1,001 bootstrap iterations to generate a distribution of *p*-values assessing the relationship between each trait and body size while accounting for phylogeny. All phylogenetic analyses were conducted using the packages ape v.5.8, caper v.1.0.3, and nlme v.3.1.166 (Orme et al., 2023; Paradis et al., 2002; Pinheiro et al., 1999). To complement our PGLS results, we also used generalized linear mixed-effects models (GLMMs) to evaluate individual-level trait variation, incorporating genus and species as nested random effects to account for taxonomic non-independence. These models allowed us to test for size effects using all individuals rather than solely genus-level summaries.

To conserve power within our analyses bees were grouped into three size classes based on log-transformed dry mass (range: 0.203–408.3 mg, n = 2,516). These size bins divided all bees for which we measure mass solely on the basis of dry weight, not by genus or species identity. For example, the genus *Bombus* was included across "large" and "medium" size bins based on individual dry mass. Other genera within the "large" size bin are big bees like *Xylocopa* and *Bombus*. The "medium" size bin includes *Apis*, *Halictus* and *Megachile*. Finally the "small" bin includes particularly minute bees like *Lasioglossum* and *Hylaeus*. To assess the relationship between body size and thermal resistance, we used a GLMM that included body size bin, ambient air temperature (T_{amb}), and a nested random effect for taxonomy (**Table 1;** n= 2,496, 10 to 655 individuals per taxon). We also conducted multiple comparisons among body size bins. We analyzed thermal tolerance primarily using PGLS to account for phylogenetic structure, with additional support from GLMMs. The GLMM included log-transformed intertegular distance (ITD), region, and a nested random effect for taxonomy (**Table 1;** n =

1,262; 1 to 227 individuals per taxon). For desiccation resistance, we used a GLMM with predictors including body size group, vapor pressure deficit (VPD), region, and nested taxonomic random effects. We also conducted multiple comparisons based on the same three body size bins described above (**Table 1;** *n* = 2,408; 13 to 653 individuals per taxon). To examine desiccation tolerance, we used both PGLS and GLMM approaches. The GLMM included log-transformed dry mass, region, and nested random effects for taxonomy. To minimize bias from weighing very small-bodied taxa, we restricted this analysis to genera with more than 10 individuals and excluded observations with CWC below 25% (**Table 1;** *n* = 1,352; 10 to 347 individuals per taxon).

To integrate resistance and tolerance metrics, we also calculated thermal safety margins as the difference between CT_{max} and field body temperature (T_b), and hygric safety margins as the difference between body water content and CWC (Burdine & McCluney, 2019; Deutsch et al., 2008; Sunday et al., 2014). For these calculations, we used genus-level estimates of CT_{max} and CWC, specifically 90th percentile for CT_{max} and 10th percentile for CWC, as these values best reflect the upper physiological limits for heat and desiccation tolerance, respectively. This approach allowed us to estimate conservative thresholds while minimizing the influence of extreme outliers. We calculated thermal safety margins for all individuals with both CT_{max} and T_b data (*n* = 2,457, 21 genera), and hygric safety margins for those with both body water and CWC data (*n* = 1,891, 16 genera). For both, we grouped individuals into three body size bins as described above and three environmental bins (T_{amb} for thermal margins, VPD for hygric margins). These environmental bins were based on the range of the most common ambient temperatures and entire range of VPD, respectively. Ambient temperature bins encompassed the majority of all bees measured including 2,457 bees out of 2,516 total bees measured. VPD bins included the full range of all bees measured (0.0468- 9.185 kPa VPD; 2,408 bees).

Results

Phylogenetic signal

We tested phylogenetic signal and body size relationships for four physiological traits across 31 bee genera (5 families), representing ~37% of U.S. genera (**Fig 2**). All traits except critical water content (CWC) exhibited strong phylogenetic signal consistent with Brownian motion (Pagel's $\lambda \approx 1.0$). CWC showed weak signal (Pagel's $\lambda = 0.46$). Because we observed a strong phylogenetic signal across most traits, we included a nested random effect of genus within family to account for shared evolutionary history and non-independence among observations for subsequent comparisons (**Table 2**).

Thermal physiology: resistance, tolerance, and safety margins

We predicted that body size could influence thermal resistance depending on whether smaller bees lose heat more effectively through convective cooling or larger bees absorb heat more slowly. Our results supported the former: smaller bees maintained significantly lower body temperatures than larger bees at high ambient temperatures, indicating enhanced convective heat loss during flight (**Fig 3A**). This was confirmed by a significant effect of body size on the relationship between body temperature (T_b) and ambient temperature (T_{amb}), where body size was approximated by size bin as defined in the Methods section (n=2,496, GLM, $p < 0.0001$; **Table 1**). However, when we included region and a nested random effect for taxonomy, the relationship between body temperature and body size was non-significant (p=0.2378, GLMM;

Table 1), although region was significant ($p < 0.0001$, GLMM; **Table 1**). At the highest ambient temperature recorded (45°C), small bees averaged 3.3°C cooler than large bees. At cooler ambient temperatures, all bees maintained body temperatures above ambient, consistent with thermoregulatory heat production during flight (Bishop & Armbruster, 1999). Because body temperature is significantly influenced by air temperature, we binned ambient temperature into three air temperature ranges and compared size groups within each range to minimize the impact of air temperature. We compared the temperature differential ($T_b - T_{amb}$) as our proxy for thermal resistance to size group. We found significant differences in thermal resistance across size groups for all temperature ranges. For the lowest temperature range, we found that large and small bees differed significantly from each other ($p<0.05$, Dunn's test with Bonferroni correction, **Table 3**). At the lowest temperature range, larger bees were 1.8ºC closer to ambient temperature than smaller bees. We found at the two upper temperature ranges that all size groups differed significantly from each other (**Table 3**). At the hottest temperatures, large bees were 2.4ºC closer to ambient than smaller bees (Kruskal-Wallis, $p<0.0001$, $\chi^2= 23.473$, df=2). Larger bees consistently had a smaller difference between their body temperature and ambient across air temperatures.

We further hypothesized that if larger bees operate at higher body temperatures, they might compensate by evolving higher thermal tolerances. However, this prediction was not supported. Thermal tolerance (CT_{max}) showed no significant relationship with body size. PGLS analysis revealed no association between 90th percentile CT_{max} and body size across 18 genera (**Table 2**; $p = 0.07365 – 0.09213$), despite strong phylogenetic signal in both traits (**Fig 2**). Similarly, GLMMs using individual-level data ($n = 1{,}262$ bees) found no significant relationship between CT_{max} and body size (GLMM, $p = 0.659$; see **Table 1**). Within-species analyses using

GLMs for four common taxa (*Apis mellifera*, *Bombus griseocollis*, *Bombus impatiens*, and *Xylocopa virginica*) also found no significant effects of body size on thermal tolerance for most species (**Fig S3; Table S4**). *Apis mellifera* was the only species with a significant relationship between size and CT_{max}. However, testing a second model which included region found no significance for body size.

Integrating results for thermal resistance and tolerance, body size was strongly related to safety margins, with larger bees consistently closer to their thermal limits (**Fig 3C**). Because body temperature is closely tied to ambient temperature, we binned data into three temperature ranges. In all bins, safety margins differed significantly among size groups (**Table 3**), with small bees consistently maintaining the largest margins. The only groups that did not differ significantly from each other were small and medium bees in the coolest bin (p= 0.1412, Dunn's test with Bonferroni correction). For the warmest temperature range, the largest bees had mean safety margins that were 1.3°C less than medium bees and 3.2°C less than the smallest bees.

Hygric physiology: resistance, tolerance, and safety margins

We predicted that body size would be positively correlated with desiccation resistance, with larger bees maintaining higher body water content due to a lower surface-area-to-volume ratio. Our results supported this prediction, as larger bees had significantly higher body water content compared to smaller bees across all vapor pressure deficit (VPD) values (**Table 1; Fig 3D**). Because percent body water is significantly influenced by air temperature and relative humidity, we binned VPD into three VPD ranges and compared size groups within each range to minimize the effects (**Table 3**). Under relatively humid conditions, large bees had 5.7% more body water than small bees, and this difference increased to 10.1% under the driest conditions.

We further hypothesized that if smaller bees lost more water due to having a higher surface-area-to-volume ratio, they might compensate by evolving higher desiccation tolerance. This prediction was supported by PGLS that showed a significant relationship between body size and critical water content (CWC) at the genus level across 14 genera (*p*=0.0012 – 0.0014; **Table 2**). Small bees could tolerate 6.8% less body water than the largest bees in our study (**Fig 3E**). These results remained significant when testing it in a GLMM framework that included region as an interaction effect. The inclusion of a nested random effect for taxonomy removed significance (n=1,352; **Table 1)**. Within-species analyses using GLMs for three common taxa (*Bombus griseocollis*, *Bombus impatiens*, and *Xylocopa virginica*) only found significant relationships between body size and CWC for *X. virginica*, though the trend was opposite to the intraspecific trend (**Fig S4, Table S6**). This demonstrates that at least within some species, larger bees have a lower CWC and are thus more tolerant of desiccation.

Integrating results for desiccation resistance and tolerance, we found that overall small bees had larger hygric safety margins compared to large bees (**Fig 3F**). Body size was negatively correlated with hygric safety margins, defined as the difference between body water content and the 10th percentile CWC by genus. Across all VPD bins (0-3, 3–6, 6-9 kPa), safety margins differed significantly among all three size classes (Kruskal-Wallis, $\chi^2 = 758.48$, df = 2, $p < 0.0001$; Dunn's post hoc tests, all $p < 0.0001$). In all cases, larger bees maintained the smallest hygric safety margins, indicating they operate closer to their desiccation limits, while smaller bees retained the largest buffers against critical water loss (**Table 3**).

Discussion

While larger animals are often thought to be better buffered against climate change, our results challenge this assumption. Although larger bees were expected to have higher thermal resistance due to slower heat absorption at rest, we found that smaller bees maintained cooler body temperatures at high ambient temperatures—likely due to greater convective heat loss during flight. Despite experiencing higher body temperatures, larger bees did not exhibit higher thermal tolerance (CT_{max}), and they ultimately had smaller thermal safety margins, indicating greater vulnerability to heat stress. For desiccation, larger bees had higher body water content as predicted, but smaller bees had lower critical water content, suggesting greater tolerance. As a result, smaller bees also had larger hygric safety margins. Together, these findings suggest that larger bees may be more susceptible to both heat and drought, aligning with observed declines in large-bodied taxa, such as bumble bees (Cameron et al., 2011; Kazenel et al., 2024; Kerr et al., 2015). These results underscore the necessity of accounting for body size when predicting the impact of climate change on bees and other ectothermic organisms.

Our results on thermal resistance differ from predictions that larger ectotherms should be more resistant to heat gain due to their lower surface-area-volume ratio (Clusella Trullas et al., 2007; Rubalcaba & Olalla-Tárraga, 2020; Stevenson, 1985). While this pattern has been supported in stationary lizards (Claunch et al., 2021), bees fly and our results indicate that smaller bees may have lower active body temperatures due to convective cooling (Corbet & Huang, 2016; Johnson et al., 2023). However, we do acknowledge that the relative effects of convective cooling may only be applicable to actively foraging bees, with differing impacts across species based on the microclimatic conditions they experience most. While we did not directly measure thermal resistance, our comparisons of field body temperature to ambient temperature across many thermal conditions account for variation in the roles of heat absorption, convective cooling, and thermoregulatory behavior. Additional laboratory studies are needed to test whether the lower body temperature of smaller bees is truly due to convective cooling, though our results provide strong support for this hypothesis. Larger bees are also expected to generate more internal heat via their flight muscles which is better retained due to their lower surface-area-to-volume ratio (Heinrich, 1974; Stone & Willmer, 1989). We found that body temperature of large bees at the lowest temperatures was on average about 4.5ºC (± 5.24ºC SD) warmer than ambient air temperatures, which is in line with predictions that bees generate and maintain higher body temperatures during flight, a key adaptation for flight at cooler temperatures (Bishop & Armbruster, 1999; Stone & Willmer, 1989). These results highlight the importance of testing thermal predictions in the field, where multiple aspects of thermal biology must be integrated to understand real world impacts.

With respect to thermal tolerance, we found no effect of body size either across genera or within several key species, which suggests that larger bees have not evolved a higher thermal tolerance. These findings support past studies in bees which found no relationship between body size and thermal tolerance (Hamblin et al., 2017; Kazenel et al., 2024; Maebe et al., 2021; Oyen & Dillon, 2018; Sánchez-Echeverría et al., 2019), although there have been conflicting conclusions from CT_{max} studies in bees (**Table S1;** see also Gonzalez et al., 2024; Jones et al., 2024; Oyen et al., 2016). Based on our conclusions, the conflation of resistance and tolerance as well as the inclusion of very large, heat tolerant species may be partially responsible for this discrepancy. Additionally, differences in start temperature and ramp rate have been well-discussed (Terblanche et al., 2007) and could lead to conflicting conclusions about the relationship between thermal tolerance and body size. Within three of the most common bee taxa (*Bombus griseocollis, Bombus impatiens, Xylocopa virginica*) we found no significant relationship between CT_{max} and body size. We did find intraspecific significance for *Apis mellifera*, but this was likely due to variation by region across the study, as we tested a second model including region and found no significance for body size. Overall, our results show that thermal tolerance is unrelated to body size, with taxonomic, phylogenetic and even within species comparisons being largely non-significant.

In contrast with our results on thermal tolerance, we did find that larger bees are more resistant to desiccation. Again, this is likely due the fact that smaller animals have a higher surface-area-to-volume ratio which increases water loss rates especially while in flight (Addo-Bediako et al., 2001; Benoit et al., 2023; Chown & Gaston, 2010; Kühsel et al., 2017; O'Donnell, 2022). Larger bees also have a larger total body water volume and a smaller surface area over which to lose their body water (O'Donnell, 2022). Cuticular water loss is the primary pathway through which insects lose water, so this result is consistent with predictions based solely on morphology (Bujan et al., 2016; Chown et al., 2011). Thus surface-area-to-volume ratio may be the main mechanism for higher resistance in larger bees, but desiccation resistance may have influenced evolution of size-differential desiccation tolerance.

Although smaller bees tend to be less resistant to desiccation, our results provide evidence that they have evolved higher desiccation tolerance. This supports the idea that low resistance may act as an evolutionary force driving the development of increased tolerance. Unlike desiccation resistance which is strongly linked to morphology, desiccation tolerance is largely determined by physiological processes, like modification of cuticular hydrocarbons or respiratory strategy (Chown et al., 2011; O'Donnell, 2022). Because of this reliance on physiology, changes in body size through phenotypic plasticity driven by desiccation resistance may have complex effects that extend beyond simply increasing desiccation tolerance. As a result, decreases in body size are unlikely to provide bees with biologically significant protection from the effects of climate change.

Combining all our results, we predict that larger bees will face greater challenges in response to future climate change. This is consistent with global population declines observed in bumble bees, which rank among the largest bees. Climate change is already having a demonstrable impact on bumble bees which are cold-adapted bees that are responsive to changes in temperature (Cameron et al., 2011; Jackson et al., 2022; Kammerer et al., 2021; Kerr et al., 2015; Soroye et al., 2020). Recent work has found that climate is driving bumble bee declines more than landscape-scale factors like floral abundance and land use (Jackson et al., 2022; Kammerer et al., 2021; Soroye et al., 2020). Additionally, bumble bees across Europe and North America are constricting their southern ranges without corresponding expansions at the northern edges of their ranges (Kerr et al., 2015). A confounding factor is that bumble bees are both large and cold adapted, although our results suggest that body size could play a role in these negative climate responses. In addition to declines in bumble bees, a large-scale comparison of climate responses of bee communities in the southwestern United States found that body size at the community level increased under historic climate change conditions but also predicted that future trends in body size will likely vary across ecosystems (Kazenel et al., 2024). They also predict that under future climatic extremes, larger bees may be disproportionately impacted due to their greater absolute metabolic needs which could negate any benefits conferred by their larger body size (Kazenel et al., 2024).

If larger bees are indeed more susceptible to climate change, we may expect that future bee populations will have smaller bodies, due to either developmental plasticity or evolution. Insect body size is plastic, as exemplified by the temperature-size rule (Kingsolver & Huey, 2008). A shift in community composition to smaller bees would be consistent with larger trends of body size declines across taxa in response to climate change (Gardner et al., 2011; Sheridan &

Bickford, 2011; but see Siepielski et al., 2019), as well as documented decreases in bumble bee body size (Fitzgerald et al., 2022). While smaller body size may offer adaptive advantages under increasingly hot and dry conditions, it also poses many challenges. Smaller bees have greatly reduced foraging distance which reduces their pollination range (Greenleaf et al., 2007). Reduced adult body size may also lower reproductive output and increase susceptibility to disease (Kingsolver & Huey, 2008; Van Wyk et al., 2021). There is also evidence to suggest that body size will not be able to change fast enough to efficiently buffer bees from shifting environmental conditions. Finally, these shifts in bee body size are likely to have cascading ecological effects, affecting plant-pollinator networks and wider scale interactions across landscapes.

Declines in large-bodied bees could drive widespread changes for pollinator communities globally, with compounding effects on pollination services across ecosystems. Smaller adult body size limits the distance bees can travel for floral resources, which may negatively impact pollination efficiency especially in agricultural systems where native bees pollinate crops within their foraging paths (Greenleaf et al., 2007). Decreasing body size may also reduce pollination efficiency, not only by decoupling bee morphology from flowers, but because larger bees are generally more efficient pollinators because of their higher surface area (Fitzgerald et al., 2022; Gérard et al., 2020; Kazenel et al., 2024). As body size largely determines tongue length in bees, and tongue length determines flowers visited, declines in large bees will differentially affect flowers depending on their size and structure (Cariveau et al., 2016) . Flowers that rely on a close match between pollinator and flower are likely to be the most vulnerable to these effects, which could negatively impact sensitive native plants, crop yields and overall ecosystem resilience as important players decline or drop out (Gérard et al., 2020; González-Tokman et al., 2020). Body size is a critical trait impacting climate response with wide-spread implications for bee survival, pollination services and ecosystems. Including body size could help identify which groups of bees are most vulnerable to climate change, which in turn could tell us which plants and crops may be at the greatest risk of a reduction in pollination. Including body size in future predictive models is essential to fully anticipate coming ecological and agricultural shifts as a consequence of climate change.

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Tables

Table 1. GLM and GLMM – Results from generalized linear mixed effects models.

Model	Terms	p-value
Thermal resistance		
Log10(body temp)~log10(air temp)+group		
	Group	**<0.0001***
Log10(body temp)~log10(air temp)+group +(1| Genus/species)		
	Group	0.2376
CT_{max}		
Log10(CTmax)~log10(ITD)+(1|Genus/species)	Log10(ITD)	0.659
Log10(CTmax)~log10(ITD)*region	Log10(ITD)	0.4838
	Region	**<0.0001***
	Log10(ITD)* Region	**<0.0001***
Log10(CTmax)~log10(ITD)*region+(1|Genus/species)	Log10(ITD)	0.5998
	Region	**<0.0001***
	Log10(ITD)* Region	**0.00047***
Desiccation resistance		
Log10(percent body water)~VPD+group		
	Group	**<0.0001***
Log10(percent body water)~VPD+group+(1| Genus/species)		
	Group	**0.00095***
CWC		
Log10(CWC)~log10(dry mass)+(1|Genus/species)	Log10(dry mass)	0.5245
Log10(CWC)~log10(dry mass)*region	Log10(dry mass)	**<0.0001***
	Region	**<0.0001***
	Log10(dry mass) * Region	**<0.0001***
Log10(CWC)~log10(dry mass)*region+(1|Genus/species)	Log10(dry mass)	0.3722
	Region	**<0.0001***
	Log10(dry mass) * Region	**<0.0001***

Table 2. PGLS - Results from PGLS model across 1,001 bootstrap phylogenies. Values in model are genus-level median (thermal resistance), 90th percentile (CT_{max}) or mean (desiccation resistance), or 10th percentile (CWC).

Model	Terms	p-value range
Thermal resistance		
Thermal differential~log10(dry mass)		
	Log10(dry mass)	**0.0039 – 0.0051***
Thermal tolerance		
Log10(CTmax)~log10(ITD)		
	Log10(ITD)	0.07365 – 0.09213
Desiccation resistance		
Slope of body water percent to VPD~log10(dry mass)		
	Log10(dry mass)	0.7243 – 0.9309
Desiccation tolerance		
Log10(CWC)~log10(dry mass)		
	Log10(dry mass)	**0.00125 – 0.00149***

Table 3. Multiple comparisons – Results for multiple comparisons for resistance and safety limits across temperature and humidity ranges. Initial Kruskal-Wallis tests all came back as significant. Multiple comparisons done using Dunn's test with Bonferroni correction, significance indicated with asterisk. Significance shown graphically in **Figure 3**.

Thermal resistance	**Comparison**	**p-value**
18 – 26ºC, Kruskal- Wallis: **p=0.007***		
	Small - Medium	0.09
	Medium - Large	0.2890
	Large - Small	**0.0089***
26 - 34 ºC, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**0.0021***
	Medium - Large	**<0.0001***
	Large - Small	**<0.0001***
34 - 42 ºC, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**0.006***
	Medium - Large	**0.0046***
	Large - Small	**<0.0001***

Thermal safety limits	**Comparison**	**p-value**
18 – 26ºC, Kruskal- Wallis: **p<0.005***		
	Small - Medium	0.1412
	Medium - Large	**0.0129***
	Large - Small	**0.002***
26 - 34 ºC, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**0.0043***
	Medium - Large	**<0.0001***
	Large - Small	**<0.0001***
34 - 42 ºC, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**0.014***
	Medium - Large	**0.00011***
	Large - Small	**<0.0001***

Desiccation resistance	**Comparison**	**p-value**
VPD <3, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**<0.0001***
	Medium - Large	1
	Large - Small	**<0.0001***
VPD 3-6, Kruskal- Wallis: **p<0.0001***		
	Small – Medium	**<0.0001***
	Medium - Large	**0.0016***
	Large - Small	**0.0099***
VPD 6+, Kruskal- Wallis: **p=0.039***		
	Small - Medium	1
	Medium - Large	0.13
	Large - Small	**0.033***
	Small - Medium	**<0.0001***

Hygric safety limits	**Comparison**	**p-value**
VPD <3, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	**<0.0001***
	Medium - Large	**<0.0001***

	Large - Small	**<0.0001***
VPD 3-6, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	0.8957
	Medium - Large	**<0.0001***
	Large - Small	**<0.0001***
VPD 6+, Kruskal- Wallis: **p<0.0001***		
	Small - Medium	1
	Medium - Large	**0.0021***
	Large - Small	**0.0018***

Figures

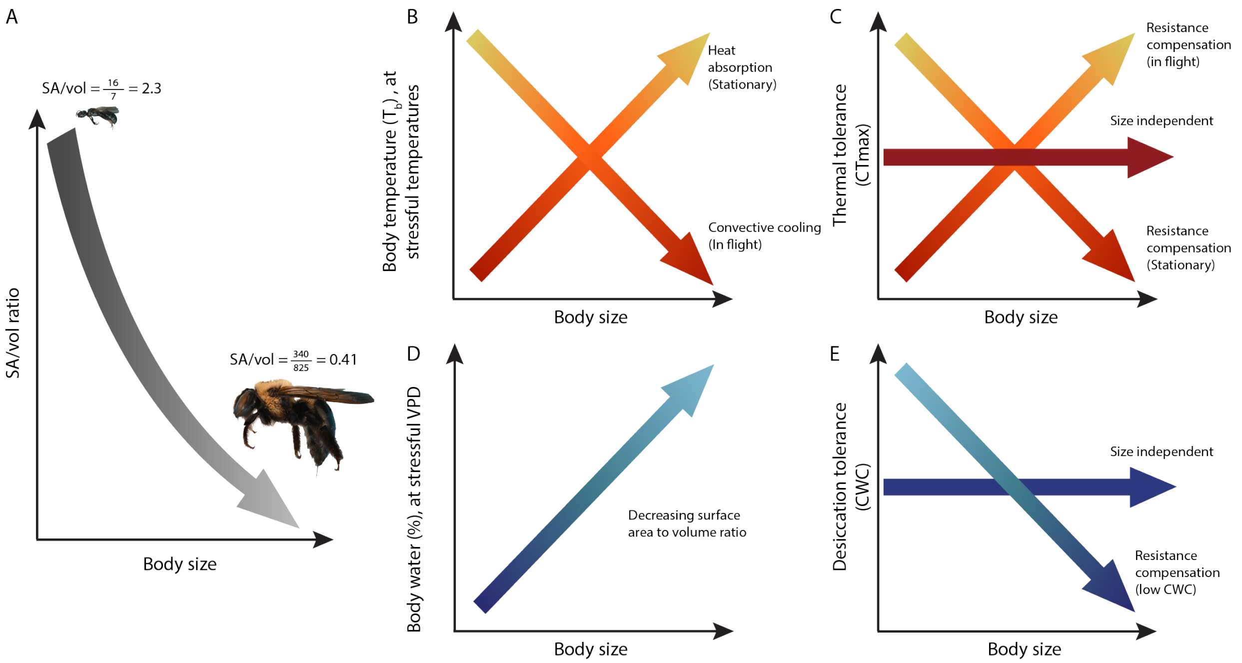

Figure 1. **Predicted relationships between body size and physiological metrics**. **(A)** Surface-area-to-volume ratio is expected to decrease logistically with increasing body size, measured by intertegular distance (ITD) or dry mass. **(B)** Predicted directional relationships between thermal resistance and body size. A positive relationship is expected if the effect of heat absorption while stationary is more important than the effect of convective cooling while in flight. **(C)** Predicted directional relationship between thermal tolerance and body size. Depending on how thermal resistance interacts with tolerance, we predict a positive or negative relationship to body size. We also predict a size independent relationship since tolerance is largely independent body geometry. **(D)** Predicted positive relationship between desiccation resistance and body size, driven solely by surface-area-to-volume ratio. **(E)** Predicted directional relationship between desiccation tolerance and body size. We predict either a negative relationship to compensate for decreased resistance, or a size independent relationship.

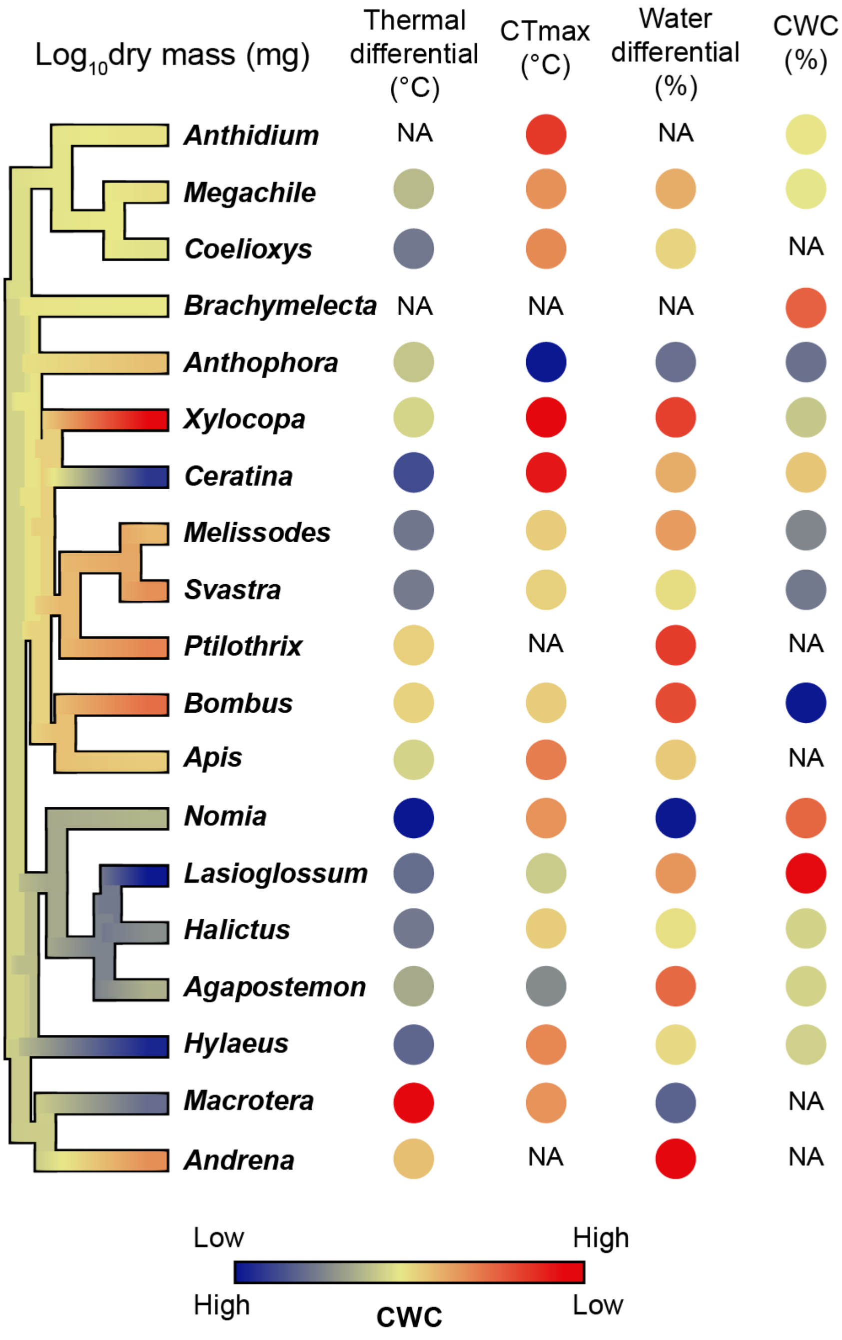

Figure 2. Mass and physiological responses mapped to bee phylogeny. Phylogeny was determined as described using phylogeny by Henríquez-Piskulich et al. (see **Methods**). Each trait was summarized at the genus level for all genera with more than 10 individuals. Genera with NA were not present across all methods. The color scale from low (blue) to high (red) is consistent across metrics (thermal resistance, CT$_{max}$, and desiccation resistance) with higher values indicating increased resistance or tolerance to hotter and drier conditions. The color scale for CWC is reversed, ranging from low (red) to high (blue), to reflect that lower CWC values indicate higher tolerance. Trait mapping visualized with R package phytools.

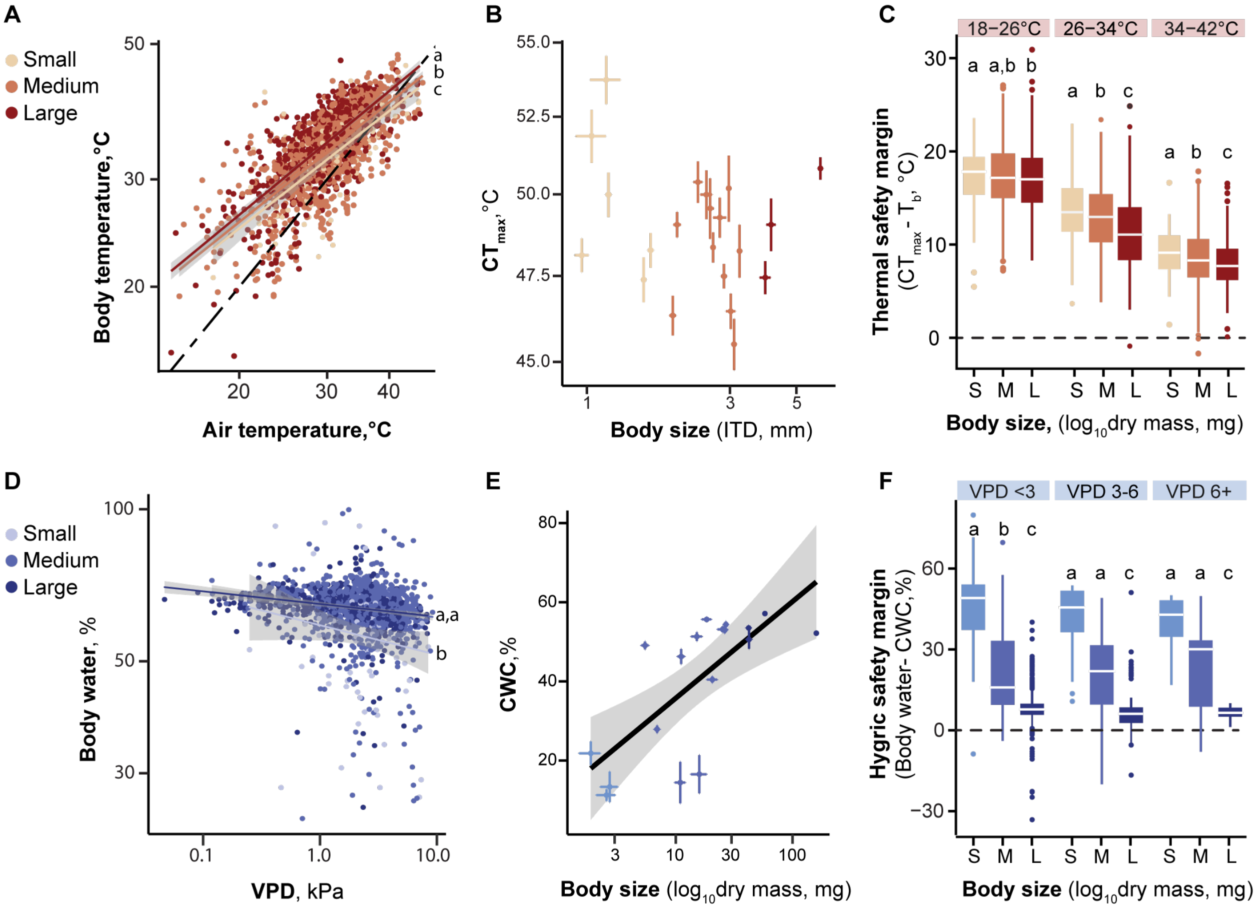

Figure 3. Relationship of body size to thermal and desiccation resistance and tolerance (A1) Ambient temperature to body temperature (ºC) for all bees (n=2,517). Size groups are based on log-transformed mass with three equal width body size bins (GLM, **Table 1**). **(B)** CT_{max} to intertegular distance (ITD) at the genus level, plotted on a log-scale for both axes (n=17 genera). **(C)** Thermal safety margins (ºC) by body size bin and air temperature range, with a dashed line at 0 ºC. Thermal safety margins were calculated by subtracting the active body temperature in the field from the 90th percentile CT_{max} value by genus (CT_{max} -T_b, n=21 genera; see **Table 3**). **(D)** Vapor pressure deficit (VPD) to percent body water (%) for all bees with body water percent greater than 24% and 10 or more individuals per genus (n=2,434; **Table 3**). **(E)** Critical water content (CWC) to mass at the genus level for bees with a CWC greater than 25% and with 10 or more individuals (n=17 genera), mass plotted on a log-scale (y=56.845x+0.0204, **p<0.001**, R^2=0.015). **(F)** Hygric safety margin by size, for all bees with body water greater than 25%. Hygric safety margins (%) were calculated by subtracting the 10th percentile CWC value by genus from percent body water in the field (CWC- percent water, n=14 genera; **Table 3**).

Appendix 1. Supplement
Supplementary methods

Vapor pressure calculations

We used vapor pressure deficit (VPD) as our metric for water stress, which we calculated using field measurements of temperature and humidity as follows:

$$\mathrm{VPD} = E_s - E$$

where E_s is the saturated vapor pressure and E is the actual vapor pressure, as calculated below.

$$E_s = 6.11\ x\ 10\left(\frac{7.5 * T_d}{237.3 * T_d}\right)$$

This is the Tetens equation for saturation vapor pressure, where T_d is the dewpoint temperature. For actual vapor pressure E:

$$E = 6.11\ x\ 10\left(\frac{7.5 * T}{237.3 * T}\right)$$

where T is the actual air temperature. We approximated dewpoint temperature from relative humidity and ambient temperature using the Magnus equation as follows:

$$T_d = \frac{243.04 * \ln\left(\frac{RH}{100}\right) + \left(\frac{17.27 * T}{243.04 + T}\right)}{17.27 - \ln\left(\frac{RH}{100}\right) + \left(\frac{17.27 * T}{243.04 + T}\right)}$$

where RH is the relative humidity. Finally, we converted our VPD from millibars to kilopascals (kPa).

CT_{max} heat block standardization

To account for methodological variation in our CT_{max} assays, we corrected for differences between the three heat blocks used in the study. Although all heat blocks were the same model (IC25XT, Torrey Pines Scientific, Carlsbad, CA, USA), they consistently produced different probe temperature readings at the same programmed block settings. To standardize CT_{max} values across blocks, we applied a temperature-specific correction based on linear regression. For each block (1–3) and region (Southeast, Atlantic, Great Lakes, Southwest, Rocky Mountain), we fit a linear model using programmed block temperature as the predictor and recorded probe temperature as the response (**Fig. S4**). We removed outliers using Cook's distance in R, selecting a threshold of 3/n (where n is the sample size) to exclude highly influential values while retaining meaningful variation. From the cleaned data, we extracted the slope and intercept to define a regression equation for each block-region pair. We then calculated the expected probe temperature for each integer block temperature from 35 to 59 °C. The difference between the expected probe temperature and the nominal block setting at each degree was used as a correction factor. This process generated a unique, degree-specific correction table for each block-region combination (**Table S7)**, which we used to adjust CT_{max} values across all blocks.

Supplementary Tables & Figures

Table S1. Summary of studies examining the relationship between body size and CT_{max}

Citation	Group	Number of taxa	Number of individuals	Effect
(Kazenel et al., 2024)	Bees	12 genera	133	None
(Gonzalez et al., 2024)	Bees	6 species	342	Positive
(Hamblin et al., 2017)	Bees	15 species	1,732	None
(Oyen et al., 2016)	Bees	3 species	72	Positive
(Jones et al., 2024)	Bees	1 species	418	Positive
(Maebe et al., 2021)	Bees	1 species	153	None
(Sánchez-Echeverría et al., 2019)	Bees	1 species	107	None
(Oyen & Dillon, 2018)	Bees	1 species	219	None
(Claunch et al., 2021)	Lizards	4 species	272	Positive
(Baudier et al., 2015)	Ants	9 species	972	Positive
(Kaspari et al., 2014)	Ants	88 species	800-1000	Positive

Table S2. CT_{max} sampling locations by region and date

City	Region	Number of sites	Years	Months
Atlanta, GA	Southeast	8	2021, 2022, 2023	June, July
Athens, GA	Southeast	4	2022, 2023	June, July
Raleigh, NC	Atlantic	8	2021, 2022, 2023	June, July
Durham, NC	Atlantic	4	2022, 2023	June, July
Detroit, MI	Great Lakes	8	2021, 2022, 2023	June, July, August
Toledo, OH	Great Lakes	5	2022, 2023	July
Phoenix, AZ	Southwest	8	2021, 2022, 2023	May, June
Tucson, AZ	Southwest	6	2022, 2023	May, June
Denver, CO	Rocky Mountain	8	2021, 2023	July
Fort Collins, CO	Rocky Mountain	4	2023	July, August

Table S3. Results from pairwise comparisons of body size effects on field body temperature differential (field body temperature – air temperature) across three ambient temperature ranges. Results are based on a linear model followed by Tukey-adjusted post hoc tests.

Temperature range bins	**Comparison**	**estimate**	**SE**	**df**	***t***	***p*-value**
18–26 °C	Small – Medium	-0.01956	0.00970	2465	-2.016	0.1086
	Small – Large	-0.02653	0.00974	2465	-2.724	0.0178 *
	Medium – Large	-0.00698	0.00482	2465	-1.448	0.3164
26–34 °C	Small – Medium	-0.01932	0.00566	2465	-3.412	0.0019 **
	Small – Large	-0.03774	0.00580	2465	-6.502	<0.0001 ***
	Medium – Large	-0.01842	0.00296	2465	-6.216	<0.0001 ***
34–42 °C	Small – Medium	-0.01883	0.00841	2465	-2.238	0.0652
	Small – Large	-0.02443	0.00899	2465	-2.718	0.0182 *
	Medium – Large	-0.00560	0.00494	2465	-1.135	0.4926

Table S4. Results of linear models testing the relationship between thermal tolerance (CT_{max}) and body size (intertegular distance, ITD) within species with ≥20 records. Both variables were log_{10} transformed.

Species	***n***	**estimate**	**adjusted *R*^{2}**	**AIC**	***t***	***p*-value**
Bombus impatiens	45	0.0748	0.00712	-188	1.15	0.2580
Bombus griseocollis	84	-0.00933	-0.00988	-447	-0.434	0.6660
Apis mellifera	227	0.44	0.0625	-745	4.01	< 0.0001***
Bombus bimaculatus	57	-0.0657	0.0492	-303	-1.97	0.0534 •
Xylocopa virginica	49	0.0506	0.0113	-329	1.24	0.2200

Table S5. Results from pairwise comparisons of body size effects on thermal safety margins (field body temperature – CT_{max}) across three ambient temperature ranges. Results are based on a linear model followed by Tukey-adjusted post hoc tests.

Temperature range bins	**Comparison**	**estimate**	**SE**	**df**	***t***	***p*-value**
18-26 °C	Small - Medium	1.49	0.739	2449	2.023	0.1069
	Small - Large	2.58	0.742	2449	3.48	0.0015 **
	Medium - Large	1.08	0.368	2449	2.947	0.0091 **
26-34 °C	Small - Medium	1.41	0.432	2449	3.275	0.0031 **
	Small - Large	3.76	0.442	2449	8.521	< 0.0001 ***
	Medium - Large	2.35	0.226	2449	10.402	< 0.0001 ***
34-42 °C	Small - Medium	1.91	0.641	2449	2.979	0.0082 **
	Small - Large	3.18	0.685	2449	4.657	< 0.0001 ***
	Medium - Large	1.28	0.376	2449	3.396	0.002 **

Table S6. Results of linear models testing the relationship between desiccation tolerance (inverse CWC) and body size (dry mass) within species with ≥20 records. Both variables were $\log_{10}$ transformed.

Species	***n***	**estimate**	**adjusted *R*²**	**AIC**	***t***	***p*-value**
Bombus bimaculatus	69	-0.00145	0.0351	-732	-1.86	0.0669 •
Bombus griseocollis	27	0.000901	-0.0121	-325	0.83	0.414
Bombus huntii	107	0.00104	0.0209	-1172	1.81	0.0735 •
Bombus impatiens	89	0.000199	-0.0103	-899	0.325	0.746
Bombus pennsylvanicus	30	0.000915	-0.031	-292	0.357	0.723
Xylocopa virginica	46	0.00402	0.0754	-464	2.16	0.0362 *

Table S7. Correction for CT_{max} values by region and block.

Block	Region	Initial block	Slope	Intercept	Corrected block value
1	Southeast	35	0.991006	-2.25881	32.4264
		36	0.991006	-2.25881	33.41741
		37	0.991006	-2.25881	34.40842
		38	0.991006	-2.25881	35.39942
		39	0.991006	-2.25881	36.39043
		40	0.991006	-2.25881	37.38143
		41	0.991006	-2.25881	38.37244
		42	0.991006	-2.25881	39.36345
		43	0.991006	-2.25881	40.35445
		44	0.991006	-2.25881	41.34546
		45	0.991006	-2.25881	42.33646
		46	0.991006	-2.25881	43.32747
		47	0.991006	-2.25881	44.31848
		48	0.991006	-2.25881	45.30948
		49	0.991006	-2.25881	46.30049
		50	0.991006	-2.25881	47.29149
		51	0.991006	-2.25881	48.2825
		52	0.991006	-2.25881	49.27351
		53	0.991006	-2.25881	50.26451
		54	0.991006	-2.25881	51.25552
		55	0.991006	-2.25881	52.24652
		56	0.991006	-2.25881	53.23753
		57	0.991006	-2.25881	54.22854
		58	0.991006	-2.25881	55.21954
		59	0.991006	-2.25881	56.21055
2	Atlantic	35	0.96598	2.85065	36.65995
		36	0.96598	2.85065	37.62593
		37	0.96598	2.85065	38.59191
		38	0.96598	2.85065	39.55789
		39	0.96598	2.85065	40.52387
		40	0.96598	2.85065	41.48985
		41	0.96598	2.85065	42.45583
		42	0.96598	2.85065	43.42181
		43	0.96598	2.85065	44.38779
		44	0.96598	2.85065	45.35377
		45	0.96598	2.85065	46.31975
		46	0.96598	2.85065	47.28573
		47	0.96598	2.85065	48.25171
		48	0.96598	2.85065	49.21769
		49	0.96598	2.85065	50.18367
		50	0.96598	2.85065	51.14965
		51	0.96598	2.85065	52.11563

		52	0.96598	2.85065	53.08161
		53	0.96598	2.85065	54.04759
		54	0.96598	2.85065	55.01357
		55	0.96598	2.85065	55.97955
		56	0.96598	2.85065	56.94553
		57	0.96598	2.85065	57.91151
		58	0.96598	2.85065	58.87749
		59	0.96598	2.85065	59.84347
3	Great Lakes	35	1.034316	-3.19073	33.01033
		36	1.034316	-3.19073	34.04464
		37	1.034316	-3.19073	35.07896
		38	1.034316	-3.19073	36.11328
		39	1.034316	-3.19073	37.14759
		40	1.034316	-3.19073	38.18191
		41	1.034316	-3.19073	39.21622
		42	1.034316	-3.19073	40.25054
		43	1.034316	-3.19073	41.28486
		44	1.034316	-3.19073	42.31917
		45	1.034316	-3.19073	43.35349
		46	1.034316	-3.19073	44.3878
		47	1.034316	-3.19073	45.42212
		48	1.034316	-3.19073	46.45644
		49	1.034316	-3.19073	47.49075
		50	1.034316	-3.19073	48.52507
		51	1.034316	-3.19073	49.55938
		52	1.034316	-3.19073	50.5937
		53	1.034316	-3.19073	51.62802
		54	1.034316	-3.19073	52.66233
		55	1.034316	-3.19073	53.69665
		56	1.034316	-3.19073	54.73096
		57	1.034316	-3.19073	55.76528
		58	1.034316	-3.19073	56.7996
		59	1.034316	-3.19073	57.83391
1 & 2	Southwest	35	0.93201	1.50999	34.13034
		36	0.93201	1.50999	35.06235
		37	0.93201	1.50999	35.99436
		38	0.93201	1.50999	36.92637
		39	0.93201	1.50999	37.85838
		40	0.93201	1.50999	38.79039
		41	0.93201	1.50999	39.7224
		42	0.93201	1.50999	40.65441
		43	0.93201	1.50999	41.58642
		44	0.93201	1.50999	42.51843
		45	0.93201	1.50999	43.45044
		46	0.93201	1.50999	44.38245

		47	0.93201	1.50999	45.31446
		48	0.93201	1.50999	46.24647
		49	0.93201	1.50999	47.17848
		50	0.93201	1.50999	48.11049
		51	0.93201	1.50999	49.0425
		52	0.93201	1.50999	49.97451
		53	0.93201	1.50999	50.90652
		54	0.93201	1.50999	51.83853
		55	0.93201	1.50999	52.77054
		56	0.93201	1.50999	53.70255
		57	0.93201	1.50999	54.63456
		58	0.93201	1.50999	55.56657
		59	0.93201	1.50999	56.49858
1	Rocky Mountains	35	1.02288	-3.11946	32.68135
		36	1.02288	-3.11946	33.70423
		37	1.02288	-3.11946	34.72711
		38	1.02288	-3.11946	35.74999
		39	1.02288	-3.11946	36.77287
		40	1.02288	-3.11946	37.79575
		41	1.02288	-3.11946	38.81863
		42	1.02288	-3.11946	39.84151
		43	1.02288	-3.11946	40.86439
		44	1.02288	-3.11946	41.88727
		45	1.02288	-3.11946	42.91015
		46	1.02288	-3.11946	43.93303
		47	1.02288	-3.11946	44.95591
		48	1.02288	-3.11946	45.97879
		49	1.02288	-3.11946	47.00167
		50	1.02288	-3.11946	48.02455
		51	1.02288	-3.11946	49.04743
		52	1.02288	-3.11946	50.07031
		53	1.02288	-3.11946	51.09319
		54	1.02288	-3.11946	52.11607
		55	1.02288	-3.11946	53.13895
		56	1.02288	-3.11946	54.16183
		57	1.02288	-3.11946	55.18471
		58	1.02288	-3.11946	56.20759
		59	1.02288	-3.11946	57.23047
2	Rocky Mountains	35	0.98023	2.161	36.46905
		36	0.98023	2.161	37.44928
		37	0.98023	2.161	38.42951
		38	0.98023	2.161	39.40974
		39	0.98023	2.161	40.38997
		40	0.98023	2.161	41.3702
		41	0.98023	2.161	42.35043

42	0.98023	2.161	43.33066
43	0.98023	2.161	44.31089
44	0.98023	2.161	45.29112
45	0.98023	2.161	46.27135
46	0.98023	2.161	47.25158
47	0.98023	2.161	48.23181
48	0.98023	2.161	49.21204
49	0.98023	2.161	50.19227
50	0.98023	2.161	51.1725
51	0.98023	2.161	52.15273
52	0.98023	2.161	53.13296
53	0.98023	2.161	54.11319
54	0.98023	2.161	55.09342
55	0.98023	2.161	56.07365
56	0.98023	2.161	57.05388
57	0.98023	2.161	58.03411
58	0.98023	2.161	59.01434
59	0.98023	2.161	59.99457

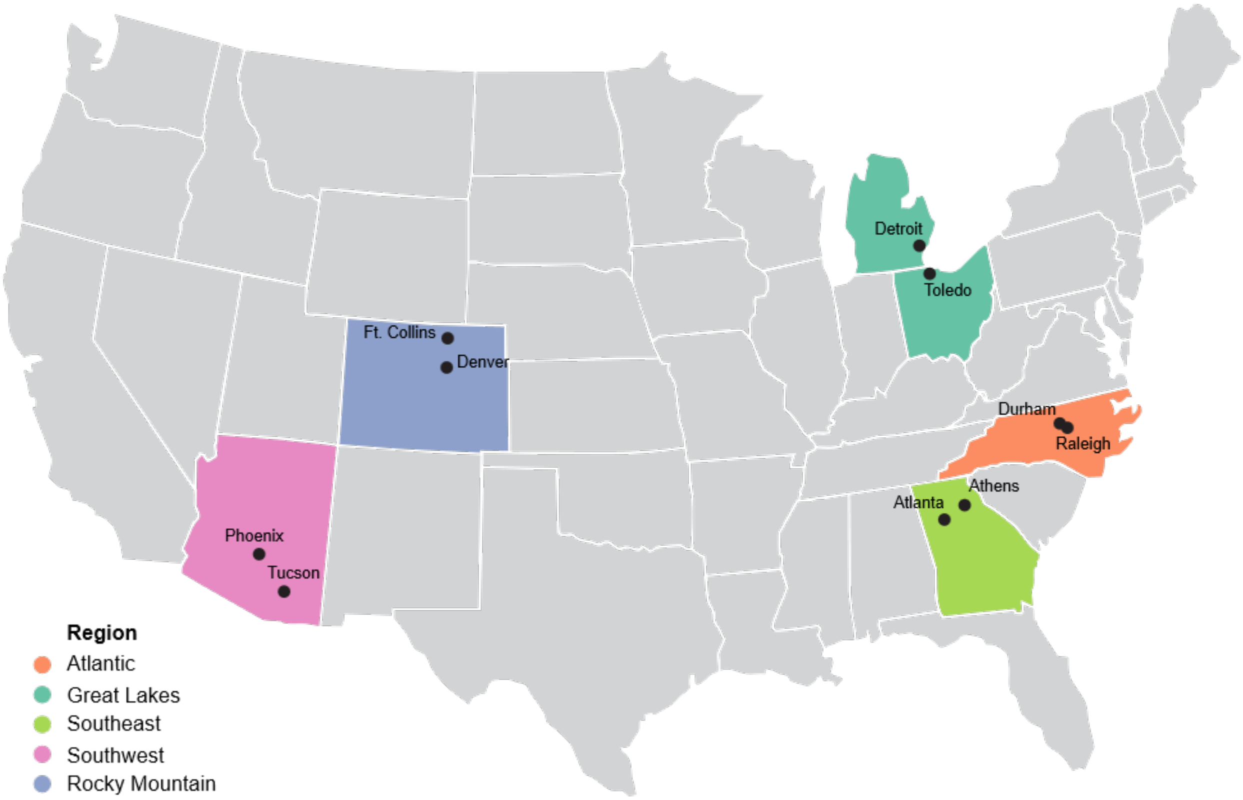

Figure S1. Geographic Distribution of Sampling Sites by Region

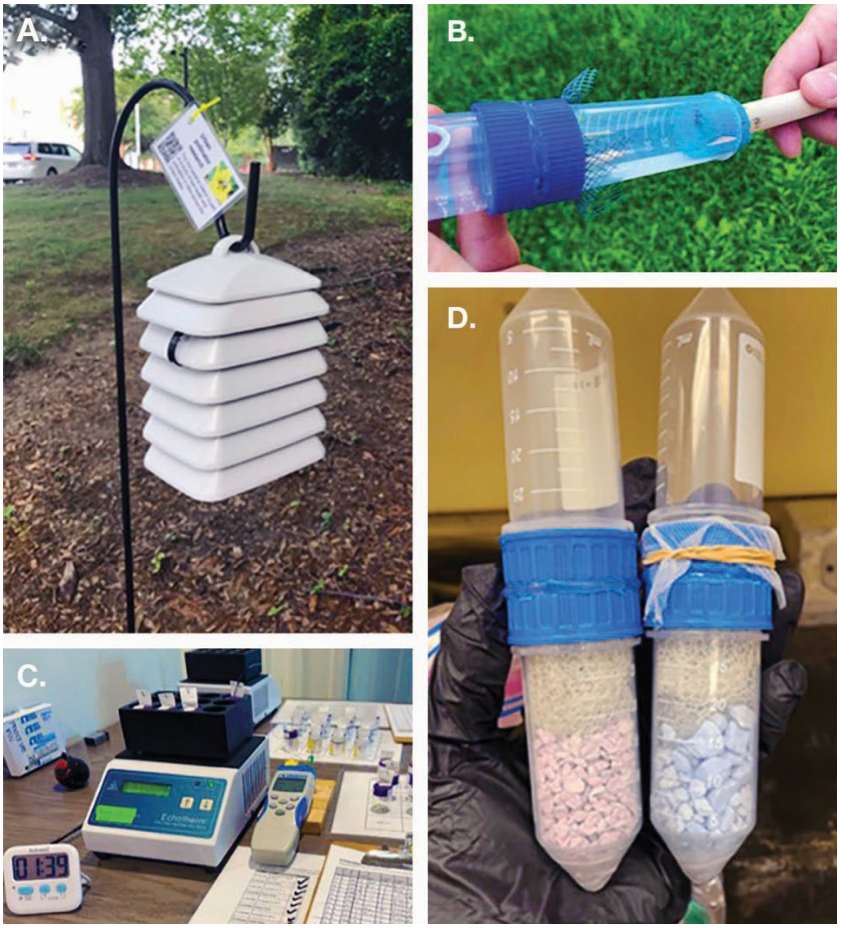

Figure S2. Field and laboratory equipment used for thermal tolerance and water balance assays. **(A)** Heat shield encasing an iButton® datalogger for measuring temperature and humidity at each site. **(B)** "Bee squeezer" used to capture bees for field body temperature measurements. **(C)** Heat block with vials and temperature probe for CT_{max} assays. **(D)** Desiccation chambers used in CWC trials, with fresh (blue) and spent (pink) desiccant for treatment and control trials; bees were placed in the empty vial along with a dry sponge.

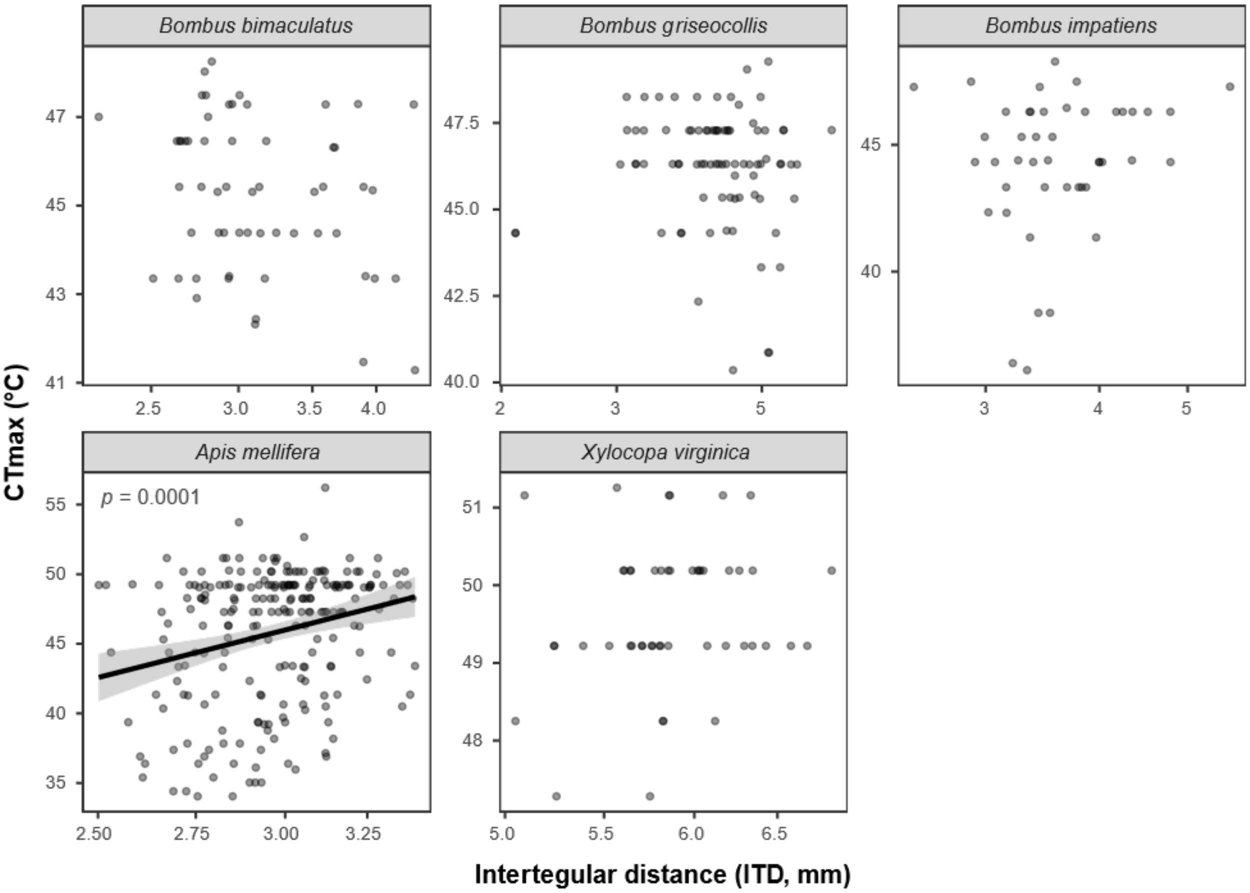

Figure S3. Within-species comparisons of thermal tolerance (CT_{max}). No significant relationship was found between body size (ITD) and CT_{max} for any species, except *Apis mellifera* ($y = 3.95x + 43$, $R^2 = 0.061$).

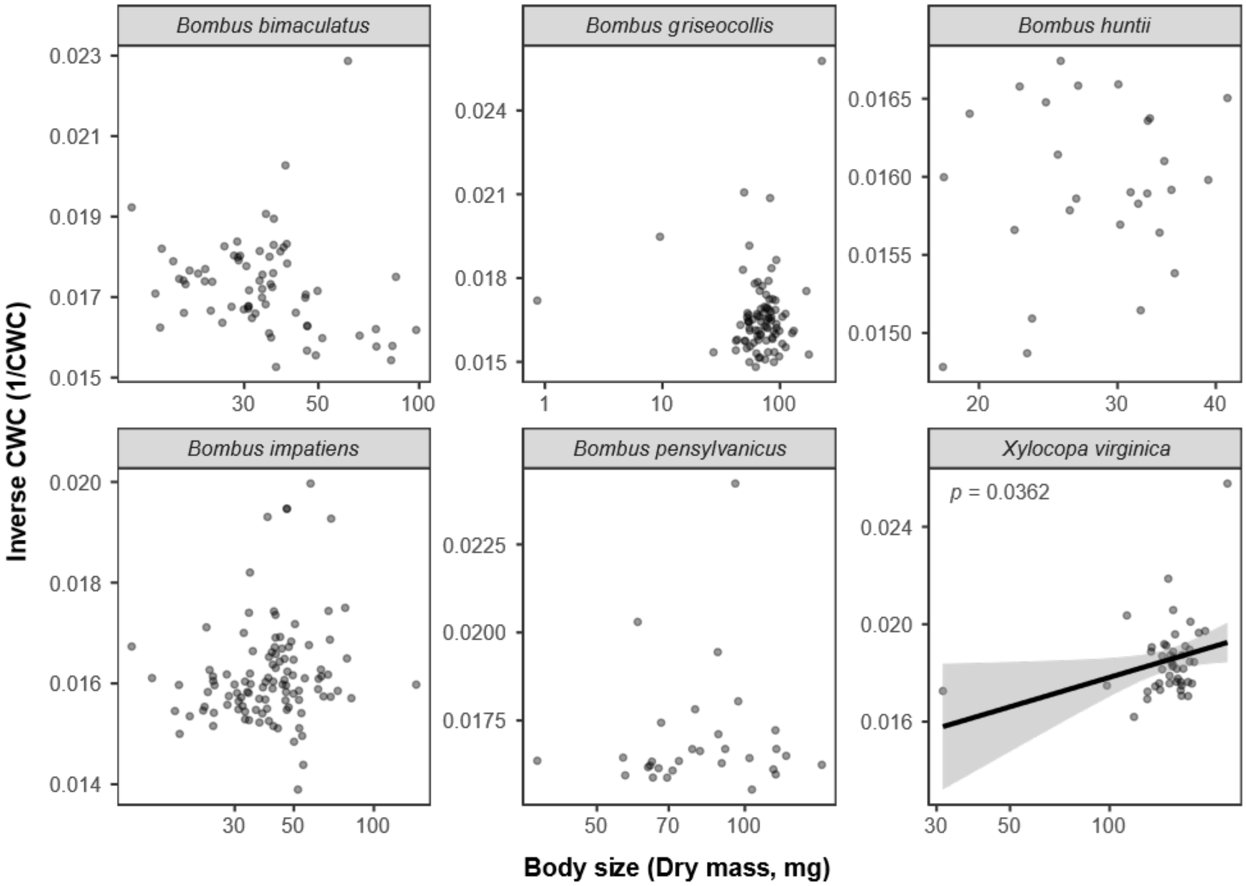

Figure S4. Within-species comparisons of desiccation tolerance (inverse CWC). No significant relationship was found between body size (dry mass) and inverse CWC for any species, except *Xylocopa virginica* ($y = 2.16x + 0.004$. $R^2 = 0.075$).

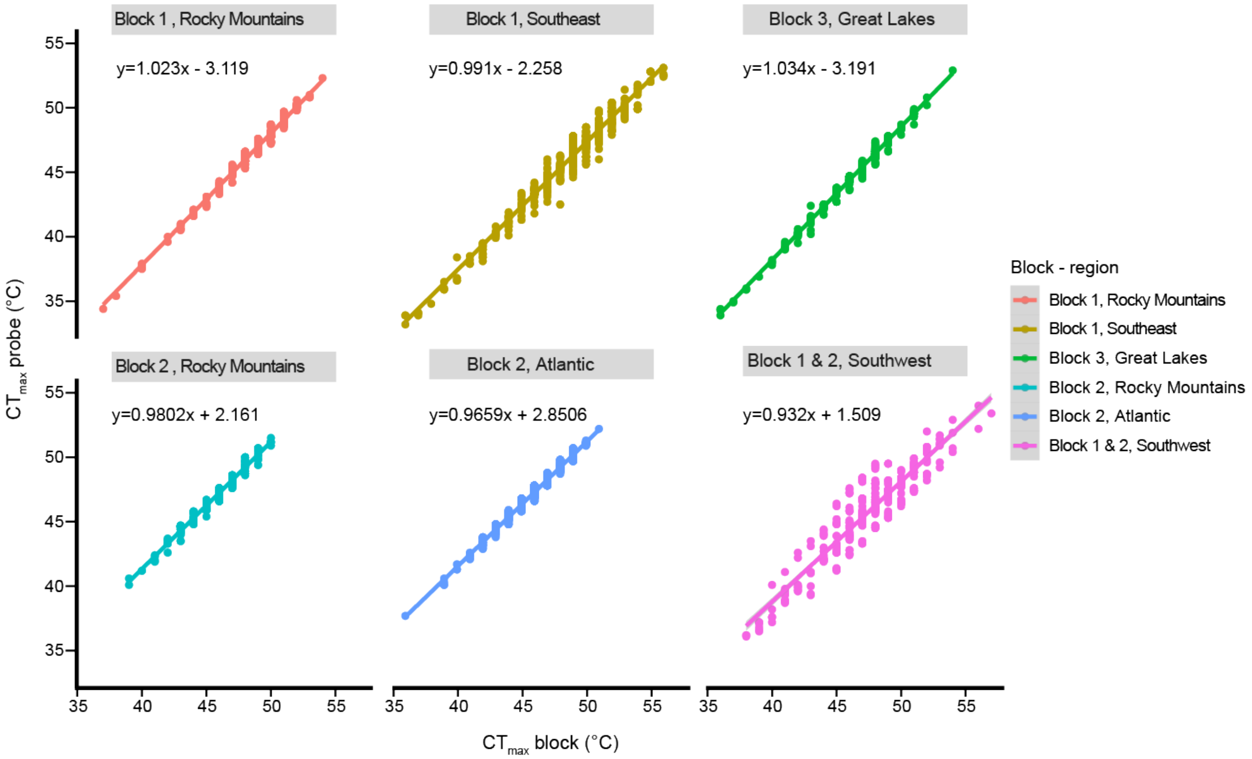

Figure S4. Linear regressions of vial probe temperature against set block temperature, shown after removing outliers using Cook's distance.