Heat tolerance in bees: a meta-analysis of ecological, evolutionary, and methodological drivers

Running title: Heat tolerance in bees

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ABSTRACT

Climate change poses a growing threat to bees, which provide essential pollination services in natural and agricultural ecosystems. Although the critical thermal maximum (CT_{max}) is widely used to assess the vulnerability of pollinators to climate change, we lack a comprehensive understanding of the factors shaping heat tolerance across bee species globally. We conducted a systematic review and meta-analysis of experimental CT_{max} measurements, extracting 339 effect sizes from 35 studies spanning 198 bee species. Across all moderator variables tested, we found that only three variables were significantly associated with variation in heat tolerance: nesting behaviour, climate zone, and ramping rate. On average, the CT_{max} of below-ground nesting bees was 1.3°C lower than that of above-ground nesters. This difference was most pronounced in solitary species and weaker in eusocial species, which may benefit from colony-level behavioural thermoregulation. Tropical species had slightly lower CT_{max} than temperate species, while species distributed across both tropical and temperate regions had the highest thermal tolerance. We also found that CT_{max} increased strongly with ramping rate, consistent with predictions of heat injury accumulation during dynamic assays. However, sex, body size, and five other methodological factors were not significantly associated with variation in CT_{max}, which may reflect species-specific responses differing in direction and magnitude, obscuring any overall pattern. We also found that variation in heat tolerance is strongly phylogenetically structured (43% of explained heterogeneity), suggesting that evolutionary adaptation to historical environmental conditions has shaped present-day thermal limits. Our synthesis identified substantial geographic and taxonomic biases, highlighting key priorities for future experimental research. By identifying important ecological drivers of heat tolerance evolution, our study provides a foundation for predicting bee heat tolerance and potential vulnerability to climate change.

Key words: critical thermal maxima; global warming; nesting ecology; quantitative synthesis; thermal plasticity; thermal tolerance

INTRODUCTION

Climate change is a major threat to global biodiversity, altering habitat suitability, disrupting ecosystem functioning, and increasing extinction risks (Bellard et al., 2012; Arneth et al. 2020). Rising temperatures and more frequent extreme weather events are already affecting bees, raising concerns about the future stability of pollination services (Soroye et al., 2020; Zapata-Hernández et al., 2024). These impacts are expected to intensify as species are pushed increasingly close to their upper thermal limits (Deutsch et al., 2008; Sunday et al., 2014). Understanding thermal limits is particularly important for ectotherms because their body temperatures and physiological performance are directly influenced by environmental conditions (Angilletta, 2009). Previous work has shown that heat tolerance in ectotherms is often evolutionarily constrained (Araújo et al., 2013; Hoffmann et al., 2013; Kellermann et al., 2012), but it is also shaped by species ecology, leading to variation in thermal tolerance among species (Diamond et al., 2012; da Silva et al., 2026). Consequently, investigating the ecological drivers of heat tolerance across phylogenetically related taxa can advance our understanding of how life-history traits shape the evolution of thermal limits and improve predictions of species vulnerability to climate change (Bennett et al., 2021; da Silva et al., 2026; Kellermann et al., 2012).

Bees are a useful model for investigating the evolution of heat tolerance because of their broad taxonomic, ecological, and geographic diversity (Michener, 2007). They occur on every continent except Antarctica, and exhibit remarkable variation in nesting ecology, sociality, body size, and climatic distribution (Michener, 2007). This diversity suggests that different bee lineages have experienced distinct selective pressures, which could drive the evolution of thermal limits (Bennett et al., 2021). For example, tropical bee species may exhibit higher heat tolerance than temperate species because they have evolved under warmer environmental conditions (Duarte et al., 2012; Sunday et al., 2019). Nesting ecology is also known to influence thermal tolerance, as below-ground nests typically provide cooler and more thermally stable microclimates than above-ground nests (da Silva et al., 2026; Mullan et al., 2026). Likewise, sociality may affect the evolution of heat tolerance because eusocial species can regulate nest temperatures through colony-level thermoregulatory behaviours (Jarimi et al., 2020; Gonzalez et al., 2022c), whereas solitary species must rely primarily on individual physiological and behavioural responses to cope with thermal stress (deHaan et al., 2025; Gonzalez et al., 2020). This broad ecological and evolutionary diversity

of bees makes them particularly well suited for investigating which ecological and evolutionary factors drive variation in thermal limits.

Despite growing interest in quantifying the sensitivity of bees to heat stress, the factors driving variation in heat tolerance across species remain poorly understood (Baena-Díaz et al., 2026). Comparisons among studies are often complicated by substantial methodological variation (Baena-Díaz et al., 2026). For instance, experimental factors such as ramping rate and acclimation temperature can strongly influence critical thermal maxima (CT_{max}) estimates, which measure the upper thermal limits of a species (Terblanche et al. 2007; and Kovacevic et al. 2019; Gonzalez et al., 2022b; Weaving et al., 2022), and methodological differences across studies can thus obscure underlying biological patterns (Noble et al., 2022). In addition, CT_{max} is highly phylogenetically conserved (Kellermann et al., 2012; Araújo et al., 2013; Hoffmann et al., 2013), and ignoring phylogenetic relatedness among species can lead to biased inferences about the drivers of variation in heat tolerance because ecological traits can covary with shared evolutionary history (Pottier et al., 2024). Consequently, identifying ecological drivers of heat tolerance evolution requires a quantitative synthesis that accounts for methodological differences among studies and phylogenetic relatedness among species.

In this study, we conducted a systematic review and meta-analysis of experimental studies measuring the CT_{max} of bees to identify the drivers of variation in heat tolerance across species. We focused on CT_{max} because it is a widely used proxy for upper physiological limits and one of the most commonly studied traits in thermal biology (Kovacevic et al. 2019; Baena-Díaz et al., 2026). Specifically, we examined (1) how CT_{max} varies among bee species; (2) how variation in CT_{max} is broadly associated with climate zone, nesting ecology, sociality, body size, sex, and experimental methodology; and (3) how these factors interact to shape heat tolerance across the bee tree of life. We hypothesized that tropical and above-ground nesting bees would exhibit higher CT_{max} than temperate and below-ground nesting bees. However, we did not have *a priori* directional predictions for sociality, body size, or sex, given conflicting reports in the literature.

MATERIALS AND METHODS

We used the PRISMA-EcoEvo Checklist to report this systematic review and meta-analysis (Table S1; O'Dea et al., 2021).

Literature search

We conducted a systematic review using the Scopus (accessed through Mahidol University, Thailand) and Web of Science (accessed through the University of Gothenburg, Sweden) databases, covering all dates available at the time of the search (1997 to 16 January 2026). We used the following search string: TITLE-ABS-KEY(("CTmax" OR "Critical Thermal Maximum" OR "thermal tolerance" OR "heat tolerance" OR “upper thermal limits” OR “thermal critical range” OR “upper critical temperature”) AND ("bee" OR "bees")).

We identified 196 records across both databases, with 72 duplicates (see PRISMA flow diagram in Fig. S1). We manually assessed titles and abstracts for relevance, and no records were excluded from this initial screening phase. Therefore, the full text of each study was retrieved and evaluated in detail. Studies were eligible for inclusion if they reported experimentally determined critical thermal maximum (CT_{max}) in adult bees (Hymenoptera: Apoidea) using a thermally controlled apparatus such as a water bath, dry bath (aluminium block), or programmable environmental chamber. CT_{max} is defined as the upper thermal limit for an organism, or the temperature at which it loses motor function and is unable to escape from conditions leading to death (Cowles & Bogert, 1944). Therefore, studies needed to clearly define the CT_{max} endpoint, such as loss of motor function, muscle spasms, or failure to flip right-side up. Additionally, studies had to specify the initial temperature and increase temperature gradually with a constant ramping rate, rather than subjecting individuals to sudden heat exposure. We therefore excluded studies that measured time to heat stupor at constant temperatures. Finally, the studies needed to report sufficient data for extraction (e.g., sample sizes, means and standard deviations, or the raw data from which we could extract such values). We also included an additional study of the authors (da Silva et al., 2026) that was under review at the time of the search.

In total, we found 35 studies that met the criteria for our systematic review (Atmowidjojo et al., 1997; Kovac et al., 2014; Oyen et al., 2016; Hamblin et al., 2017; Oyen & Dillon, 2018; Burdine & McCluney, 2019; Sánchez-Echeverría et al., 2019; Gonzalez et al., 2020, 2022a, 2022b, 2022c, 2023, 2024a, 2024b, 2025; Pimsler et al., 2020; da Silva et al., 2021; Maebe et al., 2021; Christman et al., 2022; Barrett et al., 2023; Bretzlaff et al., 2023; Johnson et al., 2023; Nacko et al., 2023; Naumchik & Youngsteadt, 2023; Sepúlveda & Goulson, 2023; Barreiro et al., 2024; Gudowska & Moroń, 2024; Jones et al., 2024; Léger et

al., 2024; Robinson & Baudier, 2024; deHaan et al., 2025; Elmer et al., 2025; Poore et al., 2025; Ratoni et al., 2025a; da Silva et al., 2026).

Moderator variables

Prior to analysis, we identified potential moderator variables that we hypothesized might explain variation in heat tolerance across bee species, such as climate zone (Kovac et al., 2014), nesting behaviour (deHaan et al., 2025; da Silva et al., 2026), sociality (Hamblin et al., 2017; Ostwald et al., 2024), sex (Feuerborn et al., 2023), body size (Gonzalez et al., 2022c; Gonzalez et al., 2024a), ramping rate (Oyen & Dillon, 2018), and acclimation temperature (Terblanche et al., 2007). We also extracted information about other experimental sources of variation directly from the publications: initial temperature of the ramping assay, experimental apparatus (water bath, dry bath, or experimental chamber), number of trials (whether each study bee was used in a single CT_{max} trial, or tested in a CT_{min} trial before the CT_{max} trial), and bee source (wild versus commercial). Given the small number of studies that used experimental chambers (n = 7 effect sizes from 4 studies), we included them in the dry bath category. For articles that reported data for multiple levels of a moderator (e.g., multiple acclimation temperatures, ramping rates, etc.), we extracted a separate effect size for each level. Ten studies (206 effect sizes) either did not acclimate bees in the laboratory or did not report acclimation temperature.

Data on climate zone was obtained from the Global Biodiversity Information Facility (www.gbif.org; GBIF Secretariat, 2026) and we classified bees as tropical (distribution was restricted within the Tropics of Cancer (23.4°N) and Capricorn (23.4°S)), temperate (distribution fell outside this tropical region), or tropical and temperate (distribution crossed either tropical line). For nesting behaviour, we classified bees as below-ground or above-ground nesting, which was sometimes reported in the source article, but often had to be retrieved from other published literature (Table S2). When nesting ecology could not be found for specific species, we used data from congeners (Table S2). We recognize that the microclimatic conditions experienced by bees during foraging and nesting are likely to be more biologically relevant predictors of thermal tolerance than our coarse classifications of climate zone and nesting behaviour. However, precise locality information and detailed life history data were unavailable or inconsistently reported across studies, precluding finer-scale analyses. Body size was approximated from intertegular distance (ITD) since ITD is the

most widely used proxy for bee body size in CT_{max} studies (Gonzalez et al., 2024b). Moreover, ITD directly reflects the size of the thorax, which houses the flight muscles, and is closely correlated with other measures of overall body size, such as dry mass (Greenleaf et al., 2007). For species in which ITD values were not directly reported, we obtained data from museum databases or other published sources or measured photographed specimens (Table S3), but could not find data for 48 bee species (59 effect sizes).

For sociality, we originally attempted to classify bees into three groups: eusocial (species that live in complex, cooperative colonies with reproductive division of labour and cooperative brood care), social (species that obligately or facultatively form small social groups of fewer than 20 bees, including species that are sometimes solitary and sometimes social), or solitary (species in which all females are fertile and construct their own nests independently). Subsocial species (females provide extended care to offspring but adult females do not nest together) and communal species (females nest together but all females are fertile and provision their own offspring independently) were also categorized as solitary given that all females construct and provision their own nests. However, given the small sample size for social bees (7 effect sizes, 7 species), and the fact that sociality is variable or unknown for many non-eusocial bees (136 effect sizes from 85 bee species), we decided to pool social bees with solitary bees since the effects of climate change on social bees are expected to be more similar to those of solitary bees (e.g., thermoregulation at the individual level) than those of eusocial bees (e.g., thermoregulation collectively achieved by hundreds to thousands of individuals within a hive). We therefore retained two categories for sociality: eusocial (113 effect sizes across 44 species) and non-eusocial (226 effect sizes across 154 species) (Table S2).

Data extraction and effect size calculation

We conducted all analyses in R v.4.4.2 (R Core Team, 2024). We used an arm-based meta-analytic approach to analyse CT_{max} as our response variable (Pottier et al., 2024). We calculated effect sizes and sampling variances from means, standard deviations, and samples sizes using the “escalc” function (“metafor” package version 4.8-0; Viechtbauer, 2010). When means and SD were not reported, we calculated them from the raw data. We extracted multiple effect sizes from each publication that reported data for multiple bee species, or reported data separately for more than one sex, acclimation temperature, or

ramping rate, in order to explain heterogeneity in effects among studies (Noble et al., 2022). When studies reported data separately for levels of factors that we did not analyse (e.g., year or elevation), we pooled the data. From the 35 studies that met our criteria, we extracted 339 effect sizes from 198 bee species. S. Karnchananiyom screened the literature and extracted the data, and all extracted data were checked for accuracy by multiple co-authors (A. Stewart, N. Warrit, and K. Wayo).

Statistical analyses

We conducted multilevel meta-analytic models using the "rma.mv" function ("metafor" package, version 4.8-0; Viechtbauer 2010). We included the following factors as random effects to account for non-independence: phylogenetic relatedness among species, species ID (similarity among species not explained by phylogenetic relatedness, such as shared ecological niches; Cinar et al., 2022), study ID (effect sizes from the same study may be more similar due to shared experimental conditions and location), and effect size ID (within study effects). We created a phylogeny of our study species from a recent bee phylogeny with over 4,500 species (Henríquez-Piskulich et al., 2024). Of our 198 study species, 124 matched directly with the original tree, 69 were grafted onto the branches of represented sister species, and 5 were grafted onto the branches of sister genera (see Fig. S2, Table S4 for details). We assigned branch lengths using Grafen's method ("compute.brlen" function, "ape" package, version 5.8-1; Paradis & Schliep, 2019) and we calculated the phylogenetic correlation matrix using the "vcv" function ("ape" package, version 5.8-1; Paradis & Schliep, 2019).

To examine variation in CT_{max} across bee species, we first fitted uni-moderator models with each of the 11 moderators of interest: climate zone, nesting behaviour, sociality, sex, body size (ITD), ramping rate, acclimation temperature, initial temperature, experiment type (water bath, dry bath, or experimental chamber), number of trials (CT_{max} only, or CT_{min} and CT_{max}), and bee source (wild versus commercial). We used exploratory graphs to check for potential interactions between climate zone, nesting, and sociality. We found that the interaction between nesting and sociality may explain significant variation in CT_{max}, so we also fitted a model with nesting, sociality, and their interaction. For each model, we calculated marginal means using the "emmeans" function ("emmeans" package, version 1.10.6; Lenth 2024) to test for significant differences between moderator levels. We

then fitted two full models for model selection, one with all moderators of interest, including ITD (which excluded 59 effect sizes for the 48 bee species with unknown ITD), and one without ITD (which retained all 339 effect sizes across 198 bee species). We excluded acclimation temperature from these models for 3 reasons: we lacked data for 206 effect sizes, acclimation temperature explained less than 1% of variation in CT_{max}, and acclimation temperature was highly correlated with initial temperature (Pearson's correlation: $r = 0.71$, $p < 0.001$). Thus, we fitted the full models with the remaining moderators and the nesting-by-sociality interaction, and used the "dredge" function ("MuMIn" package, version 1.48.11; Bartoń, 2025) for model selection. To assess the relative contribution of each moderator among the top models ($\Delta AICc < 2$), we calculated the relative variable importance (RVI) by summing the Akaike weights across all models in which the moderator appeared. We then fitted our final model based on the model selection results and calculated marginal means to examine differences between moderator levels. We visualized all results using the "ggplot2" (version 3.5.2; Wickham, 2016), "ggtreeExtra" (version 1.16.0; Xu et al., 2021), and "orchaRd" (version 2.1.3; Nakagawa et al., 2023) packages.

Sensitivity analyses and publication bias

We conducted sensitivity analysis at the study and species levels to assess the robustness of our meta-analytic results. To examine whether any one single study or species affected the validity of our findings (Viechtbauer & Cheung, 2010), we applied a leave-one-out approach by iteratively re-fitting the model 35 times (removing a single study ID in each iteration) and 198 times (removing a single species in each iteration) and tested whether individual studies or species disproportionately influenced model estimates (Notes S1).

We also tested for publication bias, which can arise when certain findings, such as non-significant results, are less likely to be published, potentially skewing the available evidence (Egger et al., 1997; Lagisz et al., 2021). To test for publication bias we fitted models that included either sampling variance or the square root of the sampling variance as moderators (Notes S2; cf. Nakagawa et al., 2022).

RESULTS

Overview of the dataset

We extracted a total of 339 effect sizes from 35 studies (Fig. 1A) and 198 bee species (Fig. 1B-E). The studied taxa spanned 5 families: Apidae (n = 152 effect sizes, 77 species), Colletidae (n = 92 effect sizes, 57 species), Halictidae (n = 78 effect sizes, 51 species), Megachilidae (n = 16 effect sizes, 12 species), and Andrenidae (n = 1 effect size, 1 species). The most studied genera were *Lasioglossum* (n = 50 effect sizes, 32 species), *Hylaeus* (n = 47 effect sizes, 25 species), *Bombus* (n = 47 effect sizes, 13 species), and *Apis* (n = 20 effect sizes, all of which came from a single species, *A. mellifera*). More data came from temperate species (n = 154 effect sizes, 79 species) than from tropical species (n = 73 effect sizes, 62 bee species) or species found in both temperate and tropical regions (n = 112 effect sizes, 57 bee species) (Fig. 1E). Above-ground nesting bees (n = 179 effect sizes, 109 species) were slightly better represented than below-ground nesting bees (n = 160 effect sizes, 89 species) (Fig. 1E). Consistent with the greater diversity of non-eusocial bees, our dataset contained more effect sizes for non-eusocial species (i.e., solitary and social; n = 226 effect sizes, 154 species) than for eusocial species (n = 113 effect sizes, 44 species) (Fig. 1E). We obtained more effect sizes for female bees (n = 192) than male bees (n = 98), and sex was not reported for 49 effect sizes.

Uni-moderator models

Of the uni-moderator models tested, only ramping rate (β = 3.67; 95% CI = 2.04, 5.29; $p < 0.001$), nesting ($\Delta\beta_{above\text{-}below}$ = 1.17; 95% CI = 0.32, 2.01; p = 0.007), and climate ($\beta_{tropical}$ = 46.2, 95% CI = 42.3, 50.1; $\beta_{temperate}$ = 46.3, 95% CI = 42.5, 50.1; $\beta_{tropical/temperate}$ = 47.2, 95% CI = 43.3, 51.0; p = 0.007) were significantly correlated with CT_{max} (Table 1). For every 1°C per minute increase in ramping rate, we estimated that CT_{max} increases by 3.67 ± 0.83°C (mean ± SE). Species that nest above ground had significantly higher CT_{max} than those that nest below ground, with an estimated difference of 1.17 ± 0.43°C (mean ± SE). However, we found a significant interaction between nesting and sociality (Fig. 2, Fig. 3C). While the heat tolerance of above and below ground nesters did not differ significantly among eusocial bee species ($\Delta\beta_{above\text{-}below}$ = 0.95; 95% CI = -0.86, 2.76; p = 0.29), they did among non-eusocial bees ($\Delta\beta_{above\text{-}below}$ = 1.24; 95% CI = 0.27, 2.20; p = 0.01). The CT_{max} of above-ground non-eusocial species was 1.24 ± 0.47°C (mean ± SE) higher than those of

below-ground non-eusocial species (Fig. 3C). Broadly distributed species spanning both tropical and temperate regions had the highest CT_{max}, which were significantly higher than that of temperate species ($\Delta\beta_{tropical/temperate\text{-}temperate}$ = 0.85; 95% CI = 0.10, 1.60; p = 0.02) and marginally significantly higher than tropical species ($\Delta\beta_{tropical/temperate\text{-}tropical}$ = 0.95; 95% CI = -0.10, 2.00; p = 0.08). In contrast, the CT_{max} of tropical and temperate species did not differ significantly ($\Delta\beta_{temperate\text{-}tropical}$ = 0.10; 95% CI = -1.02, 1.23; p = 0.97).

Multi-moderator models

Model selection performed on both full multi-moderator models (with and without ITD) yielded comparable results. Both analyses retained eight top models (ΔAICc < 2), all of which included nesting behaviour, climate zone, and ramping rate (Table 2), which aligned with the significant moderators identified from uni-moderator analyses. The final model therefore contained these three moderators. Above-ground nesting species exhibited significantly higher thermal tolerance than did below-ground nesting species ($\Delta\beta_{above\text{-}below}$ = 1.33; 95% CI = 0.47, 2.19; p = 0.003; Fig. 3A). Moreover, broadly distributed species spanning tropical and temperate regions had significantly higher CT_{max} values than did species found in temperate regions ($\Delta\beta_{temperate\text{-}tropical/temperate}$ = -0.94; 95% CI = -1.66, -0.21; p = 0.01) and tropical regions ($\Delta\beta_{tropical\text{-}tropical/temperate}$ = -1.06; 95% CI = -2.09, -0.04; p = 0.04), but CT_{max} values did not differ significantly between tropical versus temperate species ($\Delta\beta_{temperate\text{-}tropical}$ = 0.13; 95% CI = -0.97, 1.22; p = 0.95) (Fig. 3B). Finally, CT_{max} increased significantly with ramping rate, by approximately 1.41°C for every 1°C per minute increase in ramping rate (β = 1.42; 95% CI = 0.79, 2.04; p < 0.001; Fig. 3D). The other 7 moderators (sociality, sex, ITD, initial temperature, experimental apparatus, number of trials, bee source) were not statistically significant (Fig. S3-S9; Notes S3).

The best model explained 96.2% of variation in CT_{max} (conditional R^2), and the moderators (ramping rate, nesting, and climate zone) explained 10.0% (marginal R^2) (Table 2). Of the four random factors included in the model, study ID (49.7%) and phylogenetic relatedness (42.9%; Fig. 4) explained the most heterogeneity, followed by effect size ID (4.2%) and species (3.1%). Leave-one-out sensitivity analyses showed that results were robust to the removal of single studies and bee species (Notes S1). Finally, we found small but significant evidence for publication bias (Notes S2). The average CT_{max} across all bee

species dropped slightly from 46.4°C to 46.3°C when sampling variance was added to the final model, or 45.9°C when the square root of variance was fitted (Notes S2).

DISCUSSION

Understanding the ecological and evolutionary drivers of variation in thermal tolerance is important for predicting risks imposed by climate change on bees. Here, we show that nesting ecology, sociality, and biogeography are important drivers of heat tolerance evolution. We also show that variation in heat tolerance is highly clustered phylogenetically, likely reflecting adaptation to past environmental conditions. Below, we discuss the implications of these results to our ability to predict heat tolerance and climate vulnerability in bees.

Nesting ecology and sociality jointly drive heat tolerance evolution

We found that nesting ecology was the strongest predictor of variation in heat tolerance among bee species. Consistent with our original hypothesis, below-ground nesting bees had lower thermal tolerance than above-ground nesting bees. Nests constructed below ground are thermally buffered, experiencing less intense heat than above-ground nests (da Silva et al., 2026; Mullan et al., 2026). Conversely, bees that nest above ground are subjected to direct insolation (if the nest receives direct sunlight), diffuse solar radiation, and relatively high temperature fluctuations characteristic of exposed habitats (deHaan et al., 2025; Mullan et al., 2026). Consequently, above-ground nesting bees likely experience greater selection pressure to evolve high heat tolerance compared to below-ground bees (Bračić et al., 2026; da Silva et al., 2026; Mullan et al., 2026). Other studies have also reported higher thermal tolerance in above-ground than below-ground nesting bees in Fiji, Australia and Japan (da Silva et al., 2021, 2026; Hearn et al., 2026), and our meta-analysis confirms the generality of this pattern across species.

While sociality alone was not a statistically significant predictor of heat tolerance variation, we found a significant interaction between nesting ecology and sociality. Notably, below-ground nesting bees had significantly lower heat tolerance than above-ground bees in solitary and social species, but not among eusocial species (Fig. 3C). One possible explanation for this pattern is that eusocial species may rely on collective behavioural thermoregulation, resulting in weaker selection for physiological heat tolerance, even in above-ground nesting

species. In contrast, solitary species (and social species that form small groups but independently provision their own nests) do not benefit from such collective behaviour. Thus, weaker opportunities for behavioural thermoregulation could have contributed to the evolution of higher thermal tolerance in above-ground solitary and other non-eusocial species. Indeed, collective thermoregulation among eusocial bees is well documented, and includes behaviours such as fanning (convective cooling), spreading water droplets across the comb (evaporative cooling), nest evacuation or bearding (large numbers of workers remain on the outside of the hive to reduce metabolic heat inside the hive), and heat shielding (workers place their ventral surfaces against the hive to absorb heat, then move elsewhere to dissipate heat away from the hive) (Bonoan et al., 2014; Ostwald et al., 2016; Stabentheiner et al., 2021; Zhao et al., 2021; Jhawar et al., 2023). Other studies examining the effects of sociality on bee thermal tolerance are limited. Burdine and McCluney (2019) found that highly eusocial honey bees had lower CT_{max} than primitively eusocial bumble bees, and they also suggested that low heat tolerance in honey bees may be due to greater hive thermoregulation and therefore less selection for heat tolerance, consistent with our findings. Hamblin et al. (2017) reported higher heat tolerance among social species than solitary species, but they used a different classification system for sociality (as they classified subsocial species with eusocial), and their results at the species level are generally consistent with ours (e.g., eusocial species had among the lowest CT_{max} and subsocial species among the highest). Therefore, mixed findings about how sociality drives the evolution of heat tolerance could be dependent, in part, on nesting ecology.

Heat tolerance in bees is shaped not only by species ecology, but also reflects their evolutionary history. Phylogenetic relatedness explained 43% of the variation in our meta-analysis. Other studies have also demonstrated that heat tolerance is phylogenetically conserved in bees (da Silva et al., 2026) and other ectotherms (Araújo et al., 2013; Hoffmann et al., 2013; Holzmann et al., 2026). These strong patterns may reflect constraints on the evolution of heat tolerance or may result from local adaptation to similar habitats and selective pressures among closely related species, although the relative contributions of these processes are difficult to disentangle because nesting ecology is also phylogenetically conserved (Kellermann et al., 2012; Araújo et al., 2013; da Silva et al., 2026). Mapping nesting ecology and sociality onto the phylogeny shows that heat tolerance appears to be highly conserved in some bee lineages, regardless of life history (Fig. 4). For example, most

non-eusocial Apidae nest above ground and have high heat tolerance, but below-ground nesting species within the clade (e.g., *Peponapis*, *Melissodes*, *Ptilothrix*, *Exomalopsis*) have retained high heat tolerance despite their cooler nesting sites (Fig. 4). Among the eusocial Apidae, which includes below-ground nesting bumble bees (*Bombus* spp.) and above-ground nesting honey bees (*Apis* spp.) and stingless bees (Meliponini), heat tolerance is generally low across the clade (Fig. 4), which may reflect phylogenetic inertia or reduced selection for heat tolerance in eusocial species, as discussed in the previous paragraph. On the other hand, heat tolerance appears to be more labile among the Colletidae, where transitions to below-ground nesting across different genera are often associated with lower heat tolerance compared to above-ground nesting colletids (Fig. 4). Overall, the strong phylogenetic patterns found by our meta-analysis suggest that it may be possible to infer the heat tolerance of unstudied bee species from sister taxa, particularly if nesting ecology and sociality are known.

Contrary to our original hypothesis, we found no evidence that heat tolerance differs between temperate and tropical species. However, geographic breadth appears to be important. Our study shows that the species whose distributions span both temperate and tropical areas had, on average, the highest heat tolerance. Other studies have demonstrated that wide-ranging species exhibit higher heat tolerance and acclimation capacity than those with narrow ranges, supporting the hypothesis that higher thermal limits can enable greater geographic expansion (Lancaster 2016; Diamond & Chick, 2018; Markle and Kozak, 2018). Thus, bee species with broad distributions could have expanded their niche, in part, because of their high heat tolerance. In contrast, species with narrower distributions might be especially vulnerable to global warming due to their lower heat tolerance, particularly species that are already living close to their thermal limits and thus have small thermal safety margins (Deutsch et al., 2008; Kingsolver et al., 2013). While our meta-analysis provides evidence for trends at broad scales, other studies have demonstrated that inferences based on regional or global patterns likely obscure important microclimate variation in thermal exposure (Pintanel et al., 2025; da Silva et al., 2026). Given that life history data for most bee species is limited or entirely absent, more detailed information about the microclimate conditions experienced by different bee species (e.g., nesting depth for below-ground species; nesting height, substrate, and solar exposure for above-ground species; and preferred foraging habitats and times) is necessary to help refine our coarse-scale results.

We found that neither sex nor body size (as measured by ITD) was associated with variation in heat tolerance, which is congruent with mixed findings in the literature (Feuerborn et al., 2023; Medina et al., 2023; Boustani et al., 2024). For example, previous studies have reported that queens have lower heat tolerance than males (Feuerborn et al., 2023), that males have lower heat tolerance than queens (Medina et al., 2023), that sexes do not differ in heat tolerance (Jones et al., 2024; Gonzalez et al., 2020, 2025), and that results vary largely between species (Boustani et al., 2024). Findings are similarly mixed for body size. While some studies report a positive correlation between body size and heat tolerance (Oyen et al., 2016; Barrett et al., 2023; Gonzalez et al., 2024b; Jones et al., 2024), others found a negative (Feuerborn et al., 2023; Ratoni et al., 2025b), or no correlation (Maebe et al., 2021; Gonzalez et al., 2023; Gudowska & Moroń, 2024; da Silva et al., 2026). Such heterogeneity in findings indicates that sex and body size are unlikely to be universal drivers of heat tolerance across bee species.

Heat tolerance is influenced by ramping rate but not by other methodological factors

Among the methodological factors considered, we found that variation in heat tolerance was most strongly associated with ramping rate. The positive correlation between ramping rate and CT_{max} is well documented (Terblanche et al., 2007; Oyen & Dillon, 2018; Kovacevic et al., 2019; Gonzalez et al., 2022b; Gudowska & Moroń, 2024; Baena-Díaz et al., 2026). This pattern occurs because slower ramping rates prolong exposure to sublethal high temperatures, allowing heat injury to accumulate and lead to physiological failure at lower measured heat tolerance limits (Oyen & Dillon, 2018). In contrast, with faster ramping rates, organisms have less time to accumulate physiological stress and cellular damage, allowing them to reach higher limits (Sørensen et al., 2013). In our meta-analysis, most studies used a ramping rate of 0.5°C/min (14 studies) or 0.25°C/min (9 studies), although some studies used rates as low as 0.1°C/min or as high as 1.5°C/min. There has been considerable debate about which ramping rate is most appropriate, with some contending that faster ramping rates reduce the confounding effects of dehydration and starvation (e.g., Santos et al., 2011), and others arguing that slower ramping rates are more reflective of warming rates in nature (e.g., Terblanche et al., 2011). It is therefore important to consider the relevance of a given ramping rate when assessing the heat tolerance of bees and other ectotherms.

Another methodological factor commonly reported to influence heat tolerance is acclimation or initial ramping temperature (Gunderson & Stillman, 2015; Kingsolver & Umbanhowar, 2018; Semsar-Kazerouni & Verberk, 2018; Weaving et al., 2022; Turriago et al., 2023; Ruthsatz et al., 2024). Like ramping rate, initial temperature affects the length of exposure to sublethal high temperatures (Kingsolver & Umbanhowar, 2018), while warmer acclimation temperatures can induce physiological responses that increase heat tolerance, such as the upregulation of heat-shock proteins (Dalvi et al., 2012; Colinet et al., 2013; Wang et al., 2013; Metz et al., 2025). However, our meta-analysis found little evidence that acclimation affected bee heat tolerance. The apparent lack of an acclimation effect may reflect substantial biological and methodological variation among studies, although numerous experiments have also reported limited acclimation capacity (Oyen & Dillon, 2018; Sepúlveda & Goulson, 2023; Gonzalez et al., 2024b; Gudowska & Moroń, 2024; Elmer et al., 2025; Poore et al., 2025). One possible explanation is that acclimation treatments may have been generally too mild or too short to elicit physiological responses. None of the studies included in our review used acclimation temperatures above 38°C, and most acclimated bees for less than one hour, whereas significant induction of heat-shock proteins has typically been observed only after exposure to higher temperatures or much longer acclimation periods (Ma et al., 2019; Li et al., 2023; Kuo et al., 2023; Kim et al., 2024). Nevertheless, some studies acclimating bees for over 3 weeks still did not observe any changes in heat tolerance (Elmer et al., 2025; Poore et al., 2025). An alternative explanation for the limited acclimation capacity of bees is that behavioural thermoregulation may weaken selection for physiological plasticity, as predicted by the Bogert effect (Bogert, 1949; Huey et al., 2003). Given the high variation in microclimates that can occur over relatively small scales in terrestrial habitats, terrestrial ectotherms such as bees may generally rely on behavioural thermoregulation, thus reducing selection for high thermal plasticity (Gunderson & Stillman, 2015; Pottier et al., 2022). Examples of behavioural strategies for avoiding high temperatures include selecting cooler nest sites (e.g., in the shade, or deeper underground) and foraging during cooler times of the day (Frankie et al., 1988; Cane, 1991; Hranitz et al., 2009; Wilson et al., 2020; de Farias-Silva & Freitas, 2021; Robinson & Baudier, 2024). Distinguishing among these explanations will require experiments spanning a broader range of acclimation temperatures and durations across a more representative diversity of bee species.

Interestingly, we found no evidence for variation in measured heat tolerance between experimental apparatuses, bee sources, or number of trials. However, our analyses pooled diverse bee taxa, which may limit our ability to detect species-level differences. While the number of trials was not significant, bees tested for CT_{min} before CT_{max} did have lower CT_{max} values on average than bees tested for CT_{max} alone (Fig. S8). Thus, prolonged exposure to stressful conditions may result in lower measured heat tolerance. However, studies directly comparing the two treatments generally show that testing CT_{min} before CT_{max} does not reduce CT_{max} measurements (Oyen & Dillon, 2018; Gonzalez et al., 2022b). Moreover, using the same bee individual to test both CT_{min} and CT_{max} may be necessary for species that are rare or difficult to catch, or for endangered species, where catching the fewest individuals possible is preferable.

Limitations and future directions

Our meta-analysis revealed important patterns across diverse bee species, but the generality of our inferences is limited by geographic and taxonomic biases. We obtained CT_{max} measurements from North and Central America, Europe, and Australia, with no such published studies conducted in Asia, Africa, and most of South America (Fig. 1A). Moreover, our dataset covers just 1.3% of Apidae (77 of ~6,000 species), 0.3% of Megachilidae (12 of ~4,100 species), 1.5% of Halictidae (51 of ~3,500 species), 0.03% of Andrenidae (1 of ~3,000 species), and 2.3% of Colletidae (57 of ~2,500 species), with no representatives from Mellitidae (~200 species) or Stenotritidae (~21 species). Therefore, large geographic and taxonomic gaps limit the scope of our inferences. Measures of heat tolerance in bees are particularly needed from Asia, Africa, and South America, which are also predicted to be among the areas most affected by climate change (Fan et al., 2021; Yang and Zhao, 2024).

Another limitation is incomplete and imprecise life history data. While the 198 species in this study are some of the most common and best studied bee species out of the approximately 20,000 described species, we still have limited life history data for many taxa. This lack of data precludes finer categorization of our ecological moderators, and likely contributes to their relatively low explanatory power. For example, above-ground nests can be exposed (e.g., *Apis dorsata* and *A. florea*), built in small stems (e.g., *Ceratina* spp.), or constructed in large tree cavities (e.g., *Xylocopa* spp.), while below-ground nests can occur at different depths, all of which are subject to different thermal conditions (Michener, 2007; da

Silva et al., 2026). Nevertheless, such detailed nesting information is not available for most species. Similarly, there is considerable variation in temperature within climate zones (Bonebrake and Deutsch, 2012; Scheffers et al., 2014), meaning that the broad categories of "tropical" and "temperate" do not capture the fine-scale thermal environments experienced by species, which can forage in different habitat types (e.g., open versus forested) and exhibit different daily and seasonal activity patterns. Finally, sociality spans a continuum (e.g., solitary, subsocial, communal, quasisocial, semisocial, primitively eusocial, highly eusocial), but detailed information is lacking for most non-eusocial species. There is considerable nuance within each of the ecological moderators, and additional knowledge on the life history of bees will be a valuable asset for future studies of heat tolerance and beyond.

CONCLUSIONS

Our meta-analysis demonstrates that heat tolerance in bees is shaped by a combination of ecological, evolutionary and methodological drivers. Nesting ecology emerged as the strongest ecological predictor of heat tolerance, while sociality and biogeography were also influential. Strong phylogenetic structuring indicates that evolutionary history contributes to variation in heat tolerance across bee lineages and may reflect adaptations to past environments. Although substantial geographic, taxonomic, and life-history data gaps remain, the broad patterns identified here provide a foundation for improving predictions of heat tolerance in unstudied species based on their ecology and phylogeny. Obtaining measurements of heat tolerance across underrepresented regions and taxa, together with more detailed information on the microclimates experienced by different species, will further improve our understanding of the drivers of heat tolerance evolution. Such knowledge will strengthen predictions of the vulnerability of bees to climate change and help inform conservation strategies to safeguard the pollination services upon which both natural ecosystems and agricultural production depend.

AUTHOR CONTRIBUTIONS

Suntaree Karnchananiyom: Conceptualization (equal); Data Curation (equal); Formal Analysis (equal); Investigation (lead); Methodology (equal); Visualization (equal); Writing – Original Draft Preparation (equal); Writing – Review & Editing (equal). **Natapot Warrit**: Investigation (supporting); Supervision (supporting); Writing – Review & Editing (equal).

Patrice Pottier: Formal Analysis (supporting); Methodology (supporting); Writing – Review & Editing (equal). **Kanuengnit Wayo**: Investigation (supporting); Visualization (equal); Writing – Review & Editing (equal). **Carmen R. B. da Silva**: Investigation (supporting); Writing – Review & Editing (equal). **Vanessa Kellermann**: Investigation (supporting); Writing – Review & Editing (equal). **Alyssa B. Stewart**: Conceptualization (equal); Data Curation (equal); Formal Analysis (equal); Funding Acquisition (lead); Investigation (supporting); Methodology (equal); Project Administration (lead); Supervision (lead); Visualization (equal); Writing – Original Draft Preparation (equal); Writing – Review & Editing (equal).

ACKNOWLEDGMENTS

We thank the authors of the original studies for providing data and answering our questions. This study was partially supported by Scholarships for Ph.D. Student from Mahidol University, awarded to S.K. under the supervision of A.B.S.

DATA AVAILABILITY STATEMENT

All data and code from this study are publicly available in Mendeley Data at https://data.mendeley.com/datasets/t94yn435wp/1 [DOI: 10.17632/t94yn435wp.1].

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SUPPORTING INFORMATION

Table S1. PRISMA-EcoEvo Checklist for systematic reviews and meta-analyses in ecology and evolutionary biology.

Table S2. Bee nesting and sociality data with references.

Table S3. Bee intertegular distance (ITD) data with references.

Table S4. Details of phylogenetic tree construction and grafting.

Figure S1. PRISMA flow diagram of systematic review.

Figure S2. Phylogenetic tree of the 198 bee species included in the meta-analysis.

Figure S3. Orchard plot showing bee heat tolerance by sociality.

Figure S4. Orchard plot showing bee heat tolerance by sex.

Figure S5. Correlation between intertegular distance and bee heat tolerance.

Figure S6. Correlation between initial temperature and bee heat tolerance.

Figure S7. Orchard plot showing bee heat tolerance by bee source.

Figure S8. Orchard plot showing bee heat tolerance by number of experimental trials.

Figure S9. Orchard plot showing bee heat tolerance by experimental apparatus.

Figure S10. Mean heat tolerance for all 198 bee study species included in the meta-analysis.

Notes S1. Results of leave-one-out sensitivity analyses.

Notes S2. Results of publication bias analyses.

Notes S3. Estimated marginal means for all moderators in the full meta-analytic models.

963 **Table 1.** Results of uni-moderator meta-analytic models examining the effects of 6
964 methodological moderators and 5 biological or ecological moderators on the heat tolerance
965 (CT_{max}) of bees. For categorical moderators, category levels are italicized and the reference
966 level is indicated in parentheses. ITD = intertegular distance. P-values are for the omnibus
967 test, and significant moderators are highlighted in bold.

	Moderator	Estimate	t	95% CI	k	P-value
Methodological	**Ramping Rate**	3.67	4.44	2.04, 5.29	339	**<0.001**
	intercept	44.76	23.32	40.86, 48.67		
	Acclimation Temperature	-0.003	-0.09	-0.08, 0.07	133	0.931
	intercept	46.22	28.70	42.89, 49.54		
	Initial Temperature	0.07	0.46	-0.23, 0.36	339	0.648
	intercept	44.72	10.55	36.09, 53.35		
	Experiment (dry bath)	46.58	24.08	42.64, 50.51	339	0.789
	water bath	-0.33	-0.27	-2.78, 2.13		
	Number of Trials (CT_{max})	46.50	24.57	42.65, 50.35	339	0.759
	CT_{min} + CT_{max}	-0.29	-0.31	-2.18, 1.59		
	Bee Source (commercial)	46.20	23.21	42.15, 50.25	339	0.681
	wild	0.32	0.41	-1.22, 1.86		
Biological/Ecological	**Nesting** (above)	47.22	25.37	43.44, 51.01	339	**0.007**
	below	-1.17	-2.73	-2.01, -0.32		
	Sociality (eusocial)	46.32	22.85	42.20, 50.45	339	0.857
	non-eusocial	0.16	0.18	-1.60, 1.92		
	Climate Zone (temperate)	46.31	24.81	42.50, 50.11	339	**0.007**
	tropical	-0.10	-0.22	-1.00, 0.80		
	tropical/temperate	0.85	2.79	0.25, 1.45		
	Sex (female)	46.33	24.11	42.42, 50.25	339	0.150
	male	-0.25	-1.32	-0.63, 0.13		
	unknown	0.56	1.22	-0.34, 1.45		
	ITD	-0.11	-0.56	-0.51, 0.28	280	0.579
	intercept	47.06	27.21	43.53, 50.59		

968

969 **Table 2.** Top meta-analytic models (ΔAICc < 2) obtained from model selection, calculated
970 using the 'dredge' function from the MuMIn package. Note: Results were the same
971 regardless of whether or not ITD (intertegular distance) was included in the full model.

Rank	Model	df	AICc	ΔAICc	Weight
1	Ramping Rate + Nesting + Climate	9	1426.2	0.00	0.220
2	Ramping Rate + Nesting + Climate + Number of Trials	10	1426.9	0.70	0.155
3	Ramping Rate + Nesting + Climate + Sex	11	1427.0	0.85	0.144
4	Ramping Rate + Nesting + Climate + Initial Temperature	10	1427.5	1.34	0.113
5	Ramping Rate + Nesting + Climate + Sociality	10	1427.8	1.57	0.100
6	Ramping Rate + Nesting + Climate + Number of Trials + Sex	12	1427.8	1.64	0.097
7	Ramping Rate + Nesting + Climate + Bee Source	10	1428.0	1.84	0.088
8	Ramping Rate + Nesting + Climate + Initial Temperature + Sex	12	1428.1	1.90	0.085

972

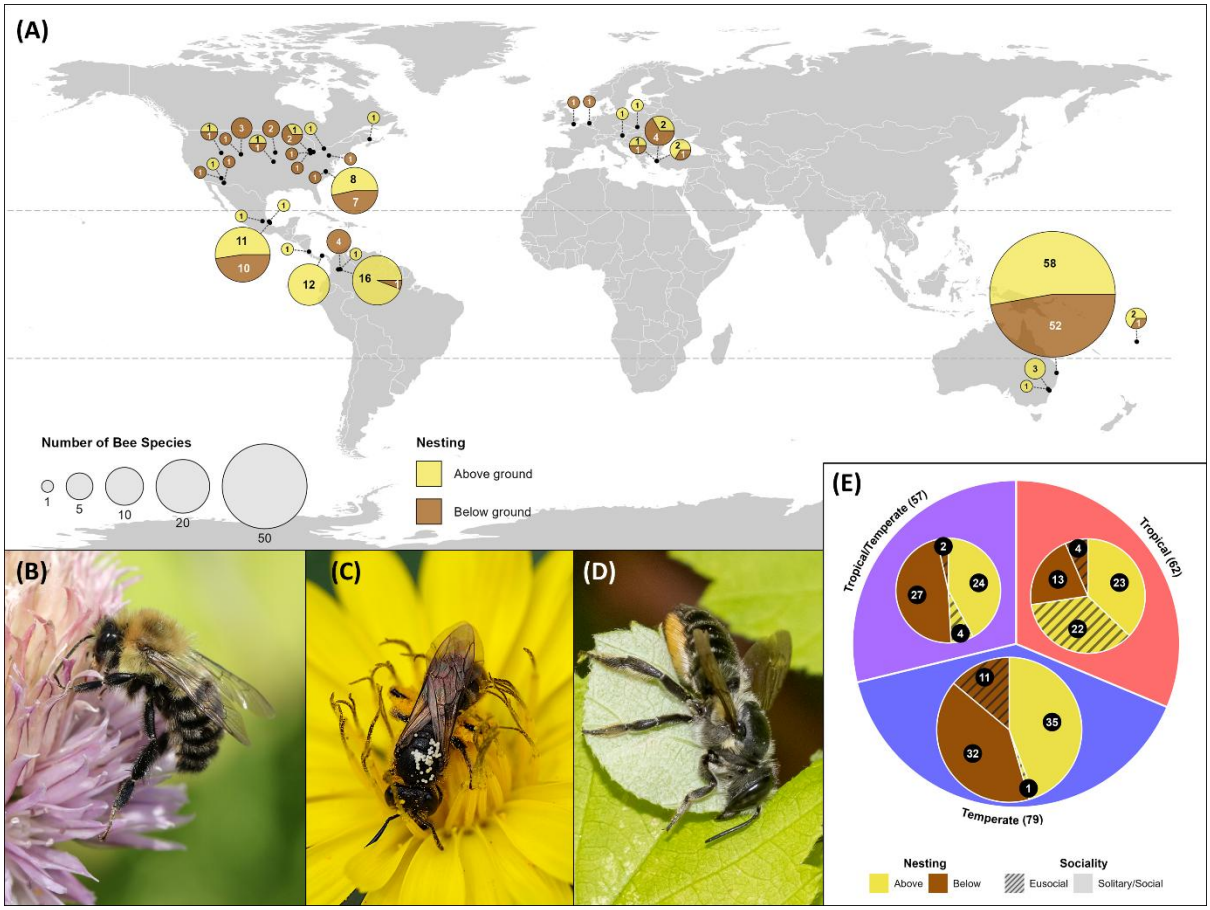
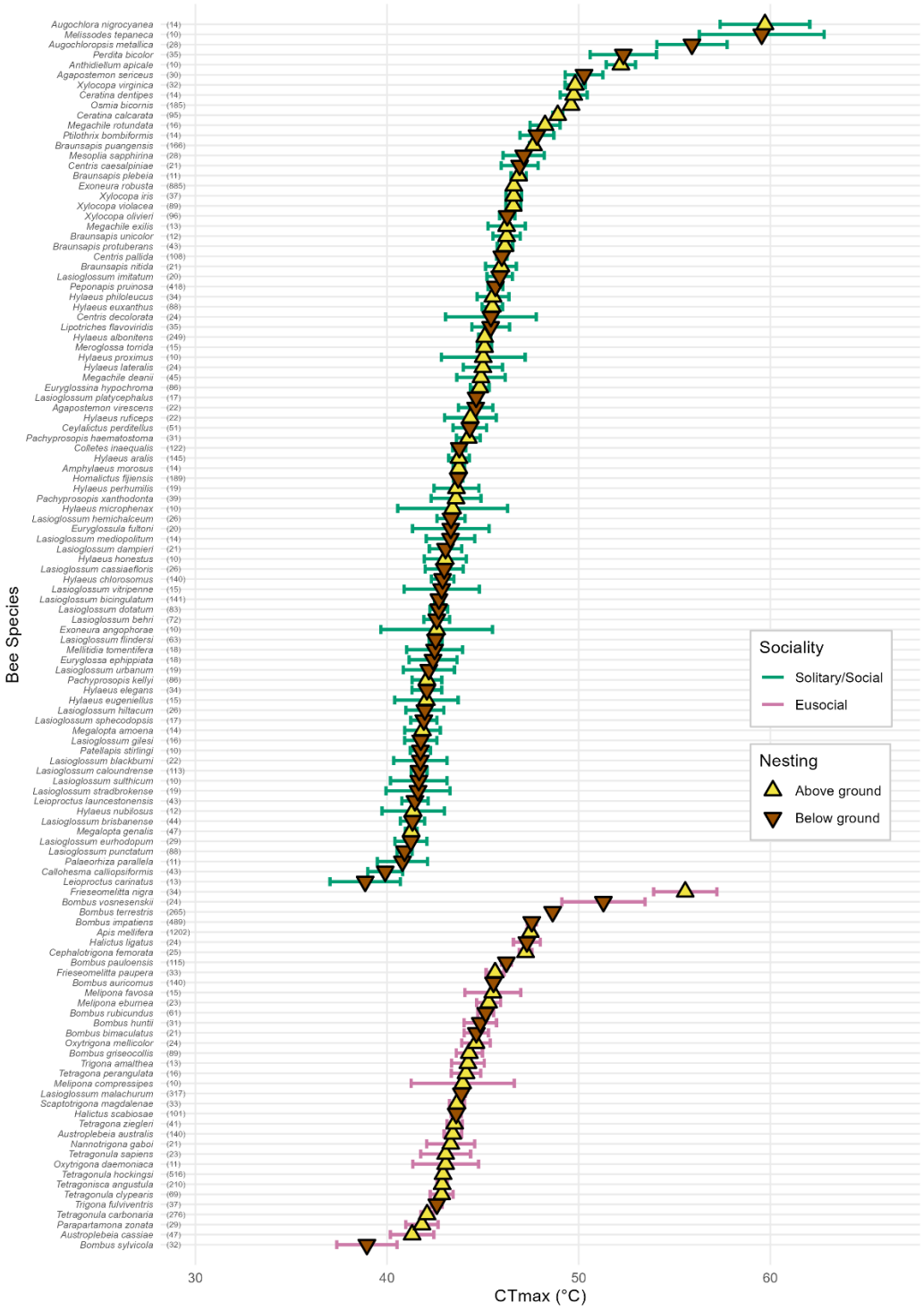


Figure 1. (A) Map showing the locations of the 35 studies included in the meta-analysis. Pie chart size is proportional to the number of bee species tested for heat tolerance, with yellow representing above-ground nesting species and brown representing below-ground nesting species. Dashed lines indicate the Tropics of Cancer and Capricorn. (B-D) Photos of three of the bee species included in the meta-analysis: (B) *Bombus impatiens* (family Apidae; photo by Jeremy Gatten via iNaturalist (CC-BY-NC 4.0)), (C) *Lasioglossum malachurum* (family Halictidae; photo by Aurea&Ramon via iNaturalist (CC-BY-NC 4.0)), (D) *Megachile mendica* (family Megachilidae; photo by Denis Doucet via iNaturalist (CC-BY-NC 4.0)). (E) Pie chart of the 198 bee species included in the meta-analysis, summarizing the number of species representing each climate zone, nesting behaviour, and sociality type.



984

985 **Figure 2.** Mean heat tolerance (CT_{max}) with 95% confidence intervals (coloured horizontal
986 lines) for the 122 bee study species with sample sizes of at least 10 individuals (pooled
987 across all studies, shown in parentheses). Below-ground nesting bee species (brown
988 downward triangles) have significantly lower CT_{max} values on average than do above-ground
989 nesting bee species (yellow upward triangles) among non-eusocial bees (green) but not
990 among eusocial bees (pink). [See Fig. S10 for a graph of all 198 bee study species.]

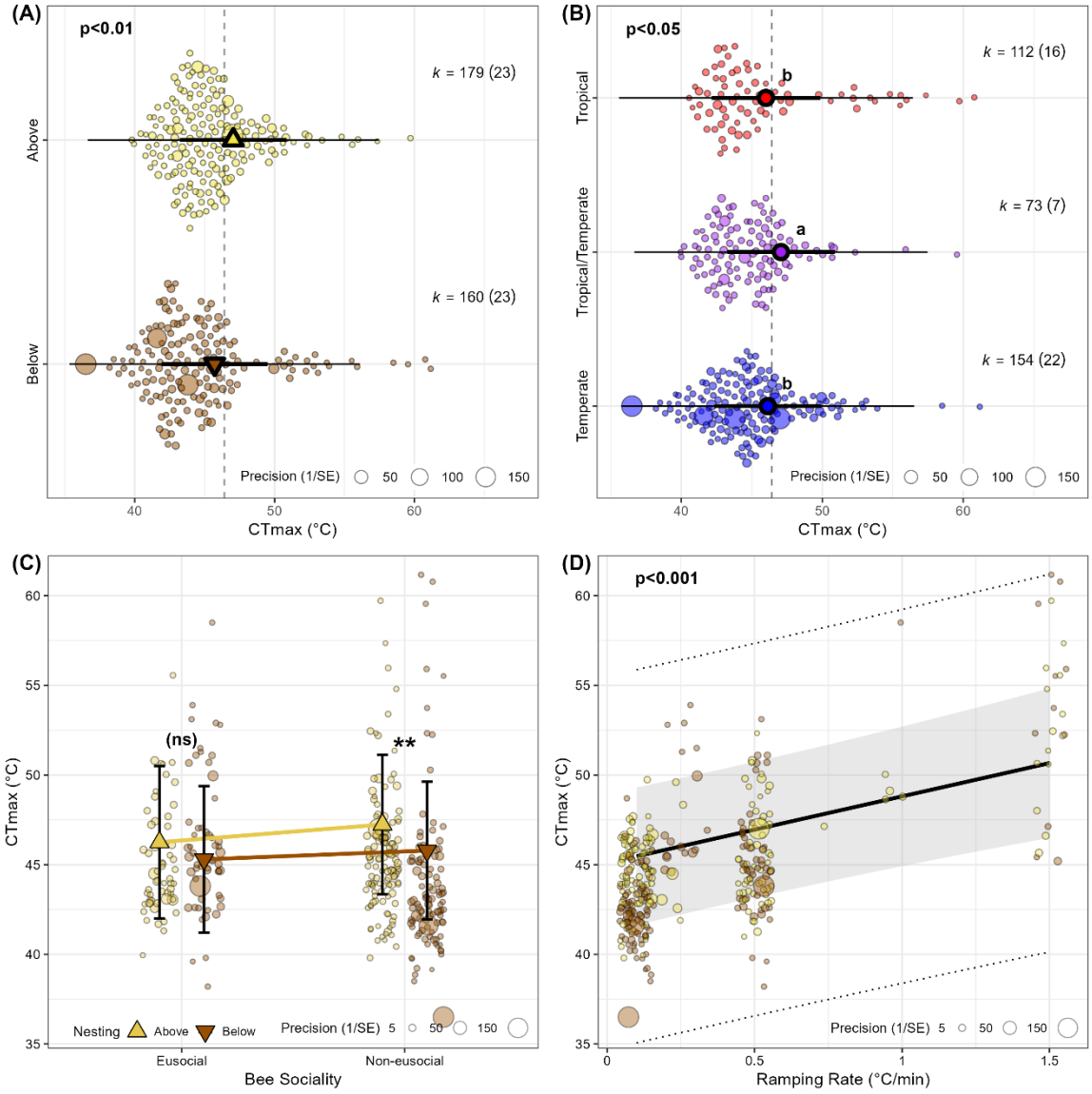


Figure 3. Model estimates based on the final multi-moderator model. Orchard plots showing bee heat tolerance (CT_{max}) by (A) nesting ecology and (B) climate zone (zones with different letters are significantly different). Triangles/circles with thick black outlines represent model-estimated means; thick and thin horizontal lines indicate 95% confidence intervals (CI) and prediction intervals (PI), respectively; dashed vertical lines indicate the model intercept. Sample sizes are given as the number of effect sizes (k), followed by the number of studies in parentheses. (C) Predicted CT_{max} (± 95% CI) predicted from the meta-analytic model testing the nesting × sociality interaction (ns, not significant; **, $p < 0.01$). (D) Correlation between CT_{max} and experimental ramping rate; solid line shows the predicted meta-regression slope, shaded grey region shows the 95% CI, and dotted lines show the 95% PI. In all panels, coloured circles represent individual effect sizes, with circle size proportional to estimate precision (1/SE).

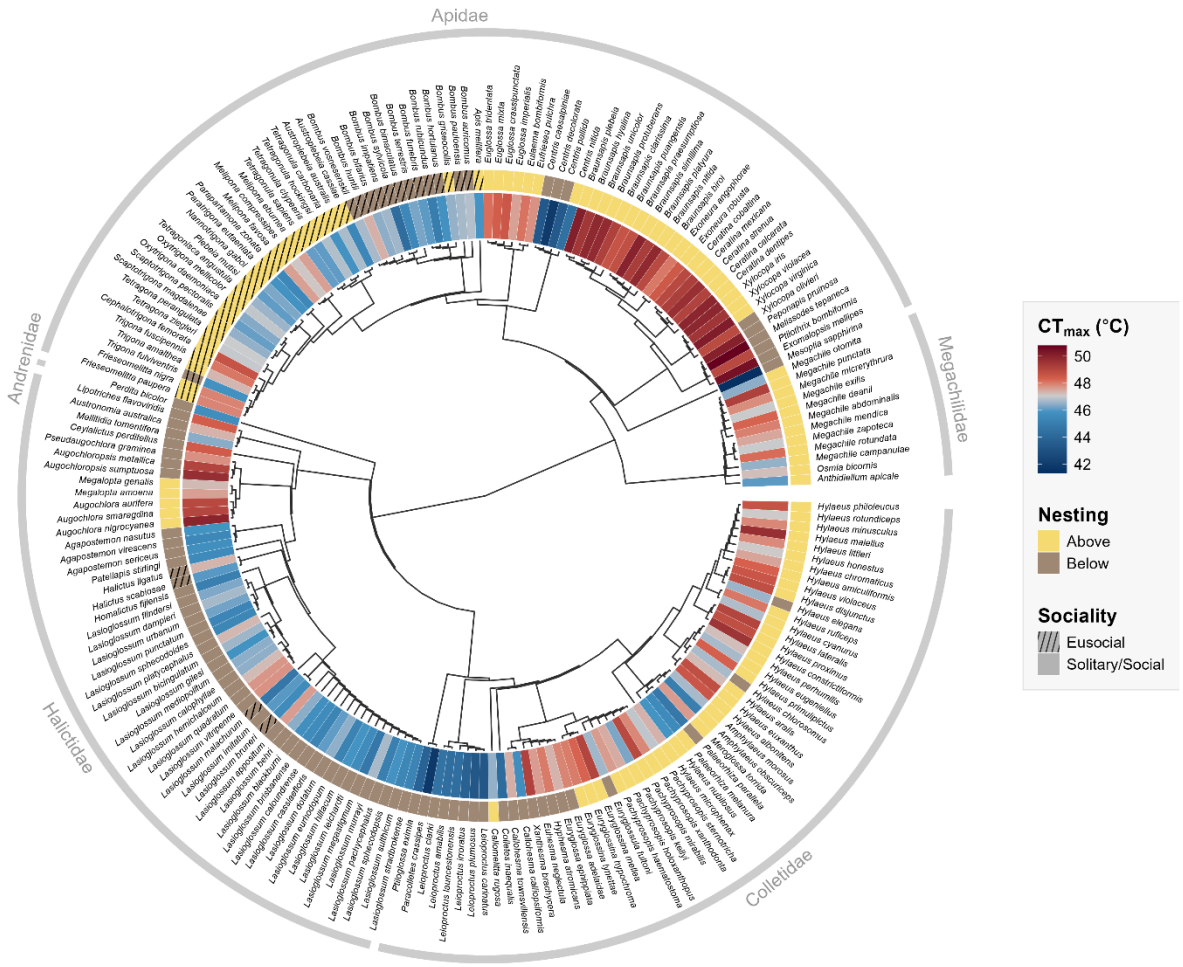


Figure 4. Phylogenetic tree of the 198 bee species included in the meta-analysis, showing heat tolerance (CT_{max}), nesting behaviour, and sociality. Phylogenetic relatedness accounted for 43% of the heterogeneity in CT_{max}, and below-ground nesting species exhibited significantly higher heat tolerance than above-ground nesting species ($\Delta\beta_{above\text{-}below}$ = 1.33; 95% CI = 0.47, 2.19; p = 0.003). CT_{max} values are predicted based on the final model, which accounts for the differences in ramping rate used by different studies. Outer grey arcs delineate the five bee families represented in the meta-analysis.