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RESEARCH PAPER

Seasonality, worker caste, and the interaction between island area and habitat type influence the thermal tolerance of ants on fragmented habitat islands

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Abstract

Habitat fragmentation is a major cause of biodiversity loss. Fragmentation can alter thermal conditions on the remaining patches, especially at habitat edges, but few studies have examined variations in thermal tolerance of species in fragmented habitats. Ants are sensitive to both habitat fragmentation and temperature changes, and are an ideal taxon for studying these impacts. Here, we focused on the dimorphic ant species *Pheidole nodus* in a fragmented habitat island system (Thousand island lake) in China. We assessed critical thermal maximum (CTmax), minimum (CTmin), and range (CTrange) temperatures for both minor (workers) and major workers (soldiers) of 2307 individuals from 117 edge and interior colonies across 9 islands during relatively hot and cold seasons. Using mixed-effect linear models, we explored the effects of island area, habitat type (edge vs. interior), season, and caste (worker vs. soldier) on CTmax, CTmin, and CTrange. We found temperatures were 1–3 °C higher in edge than interior sites in relatively hot season. Yet, only CTmax and CTrange in edge populations were higher than those of interior sites on smaller islands. CTmax was higher in relatively hot season and CTmin was lower in relatively cold season, indicating seasonal plasticity in thermal tolerance. Workers consistently had higher CTmax and lower CTmin than soldiers. These findings underscore the importance of seasonality, worker caste, and interactive effect between island area and habitat type in shaping thermal tolerance of a dominant dimorphic ant species on fragmented habitat islands. Our study provides a roadmap for integrating thermal biology into studies of how fragmentation impacts biodiversity.

Keywords Cold tolerance · Habitat fragmentation · Heat tolerance · Intraspecific variation · *Pheidole nodus* · Thousand island lake

Introduction

Human activities have profoundly reduced and reshaped continuous habitats across the world, resulting in numerous fragmented habitat patches (Chase et al. 2020; Fahrig 2003; Wilson et al. 2016). Over 70% of global forest habitat occurs within 1 km of its habitat edges (Haddad et al. 2015), implying that many species inhabit edges of forest patches. These

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fragmented forest edges, distinguished by increased solar radiation, exhibit hotter, drier, and more variable microclimatic conditions compared to forest interiors (Laurance 2004; Murcia 1995). One consequence of fragmentation is that species must adapt to these novel conditions or face local extinction (i.e., the edge effect) (Nunes et al. 2023). Despite a few studies on how species persist in edges of fragmented patches through intraspecific trait variation (Silva da Costa et al. 2020; Zheng et al. 2022), they often ignore the traits that are directly associated with temperature (Tuff et al. 2016).

For ectotherms, critical thermal tolerance directly links to their survival, performance and reproduction (Bennett et al. 2021). In fragmented landscapes, daytime mean air temperatures can be 2–5 °C higher at edges relative to the temperatures in the center of the fragment, while maximum air temperatures at edges can be up to 10 °C higher than temperatures at the center of the fragment (Tuff et al. 2016) (Fig. 1A). This challenge is particularly pronounced in fragmented habitat islands surrounded by water, where dispersal to suitable patches is difficult for most species (Palmeirim et al. 2022). Thus, for species to persist in island edge habitats, they would likely need to be able to tolerate higher temperatures (i.e., having a higher critical thermal maximum temperature, hereafter CTmax). On smaller islands, the proximity to water across the entire island amplifies the buffering effect by water (i.e., water has a high specific heat capacity, allowing it to absorb a large amounts of heat), likely minimizing temperature differences between the edges and interiors (Didham and Lawton 1999; Leong et al. 2022b). In this case, CTmax values may be similar between edge and interior populations. Conversely, larger islands may provide thermal refuges, through more complex vegetation structure or a thicker leaf litter layer for interior populations (Frey et al. 2016), potentially amplifying differences in expected CTmax between populations in edge and interior habitats. In contrast, critical thermal minimum temperatures (hereafter CTmin) may remain stable in fragmented islands, as minimum temperatures rarely differ among edge, interior, and patch areas (Ewers and Banks-Leite 2013). Together, critical thermal range (i.e., CTrange = CTmax − CTmin) would exhibit a similar pattern as CTmax. Thus an interactive effect of island area and habitat type is expected on CTmax and CTrange, but not on CTmin (Fig. 1B).

In temperate climates, with seasonal variation in temperature, species may already possess the ability to track temperature changes (Sgrò et al. 2016), exhibiting higher CTmax during relatively hot season and lower CTmin during relatively cold season (Hopkin et al. 2006; Roeder et al. 2021; Sharma et al. 2015) (Fig. 1C). However, habitat fragmentation may lead to seasonal variation in thermal tolerance (Barley et al. 2021). For example, during warmer times of year, edge populations may have higher CTmax values that allow them to cope with extreme temperatures

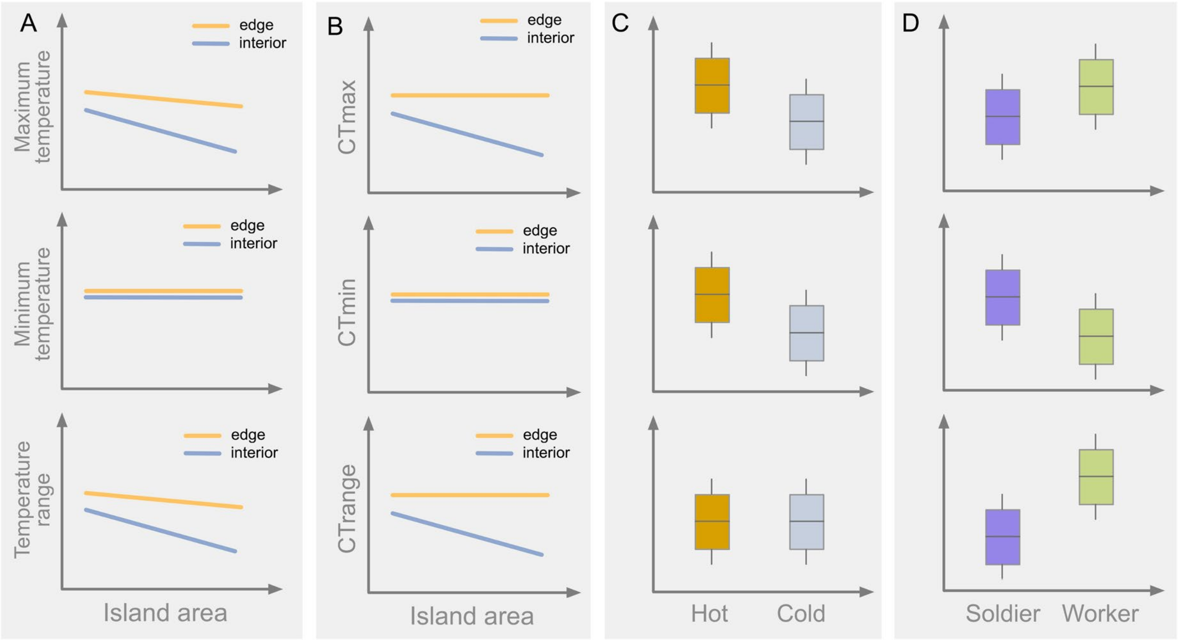

Fig. 1 Hypothesized maximum temperature, minimum temperature, and temperature range on fragmented islands (**A**), as well as critical thermal maximum temperature (CTmax), critical thermal minimum temperature (CTmin), and critical thermal range temperature (CTrange) of ants on fragmented islands (**B**), between season (**C**) and between worker caste (**D**)

through compromising their cold tolerance capacity. The extent to which temperature differs between island edges and interiors during colder times of the year remains largely unknown, as most studies have focused on hot season or non-seasonal regions (Diamond et al. 2017; Tuff et al. 2016). Thus, whether there is a trade-off between CTmax and CTmin in cold season, across habitat edges and interiors, and along a gradient of island area are open questions. Addressing these questions has become increasingly crucial as global climate change intensifies, not only due to rising temperatures but also because of the increasing frequency of extreme climatic events, such as severe cold spells and heat waves (UNISDR 2015). Consequently, species that can cope with both warmer and cooler conditions in seasonal, fragmented habitats may have a significant fitness advantage in a world experiencing escalating fragmentation.

Ants, as one of the most abundant groups in nearly all terrestrial ecosystems (Schultheiss et al. 2022), are sensitive to habitat fragmentation (Leal et al. 2012), exhibit seasonal plasticity in CTmax (Bujan et al. 2020) and serve as a model taxon to study the thermal tolerance in seasonal fragmented habitats (Diamond et al. 2016; Pelini et al. 2012). Notably, ants are social insects with distinct castes, and previous studies have examined differences in CTmax and CTmin between worker and reproductive castes (Coulin et al. 2019; Kay and Whitford 1978) or within polymorphic worker castes (Baudier and O'Donnell 2018; Cerdá and Retana 1997; Yilmaz et al. 2019). However, to the best of our knowledge, no studies have considered the differences in critical thermal tolerance between workers in dimorphic species on fragmented habitat islands. Many species in the genus *Pheidole* are dimorphic: minor workers (hereafter referred to as workers) typically forage outside the colony, while major workers (with disproportionately large heads, hereafter referred to as soldiers) are specialized for colony defense, securing large food resources (Wilson 2003), are primarily active within or surrounding the nest site. Given their task differences, workers may be expected to possess stronger thermal tolerance than soldiers, as they are directly exposed to temperatures outside the nest (Fig. 1D). For similar reasons, the critical thermal tolerance of workers should be affected by the interaction of island area and habitat type. This is a potentially important factor, as ecosystem functions, such as seed dispersal, have been found to be determined by the CTmax of ant species at high temperatures (Nascimento et al. 2022; Stuble et al. 2014). Consequently, the expected elevated CTmax in workers at island edges may accelerate the rate of certain ecosystem functions, buffering the negative effect of habitat fragmentation (Ren et al. 2023).

In this study, we examined variation in thermal tolerance by focusing on *Pheidole nodus* in a fragmented habitat island system (Thousand Island Lake, eastern China; Fig. 2). Previous surveys found that *P. nodus* nests in both edge (i.e., buffer zone) and interior sites of the fragmented islands and is the most abundant ant species (the relative abundance is more than 25% of all ants in this system) (Zhang et al. 2023; Zhao et al. 2020, 2021). By measuring ambient temperature and performing thermal tolerance experiments with live ants across nine islands, we aim to determine (1) whether temperature varies between island edge and interior habitat types and varies with island area? (2) if CTmax, CTmin, and CTrange of *P. nodus* depends on the interactive effects of island area and habitat type (i.e., edges vs interiors), season (i.e., hot vs cold), and worker caste (i.e., workers vs soldiers)? We predicted that (1) Habitat edges on small islands would have the highest maximum temperature in both seasons; (2) the worker caste in warmer season at habitat edges would have the highest CTmax.

Materials and methods

Study site

This study was carried out in the Thousand Island Lake (TIL, 29°22′–29°50′ N, 118°34′–119°15′ E), eastern China (Fig. 2). TIL is a subtropical artificial land-bridge island system created by dam construction in 1959. All fragmented islands in the lake were mountaintops prior to flooding. The region has a subtropical monsoon climate, with hot, humid summers (June to August) and cool, dry winters (December to February) (Si et al. 2014, 2024). The forests on these islands were clear-cut in 1959, and thus succession was initiated from similar starting conditions on each island (Liu et al. 2019). Currently, the dominant vegetation on the islands is Masson pine (*Pinus massoniana*) with some broad-leaved plants, such as *Loropetalum chinensei*, *Vaccinium carlesii* and *Rhododendron simsii* (Hu et al. 2011; Liu et al. 2020) also being abundant. The edges of the islands are dominated by herbaceous plants (e.g., *Rubus hirsutus*, *Rosa laevigata* and *Leonurus japonicus*) (Ren et al. 2023).

TIL provides a unique system to study the thermal tolerance of ants at edges for the following reasons: (1) All fragmented islands in the region have relatively 'fixed' edges because the matrix (i.e. water) is the same around all of the islands, and the highest water level is constant among years (Zheng et al. 2022). (2) The water matrix makes it challenging for most ant species to disperse among islands, and, as a result, ants occurring at the edge likely possess thermal tolerances that have allowed them to persist in these microclimatic conditions. (3) A previous study verified that *P. nodus* forages both in edge and interior habitats of islands and is abundant on all islands (Zhao et al. 2020).

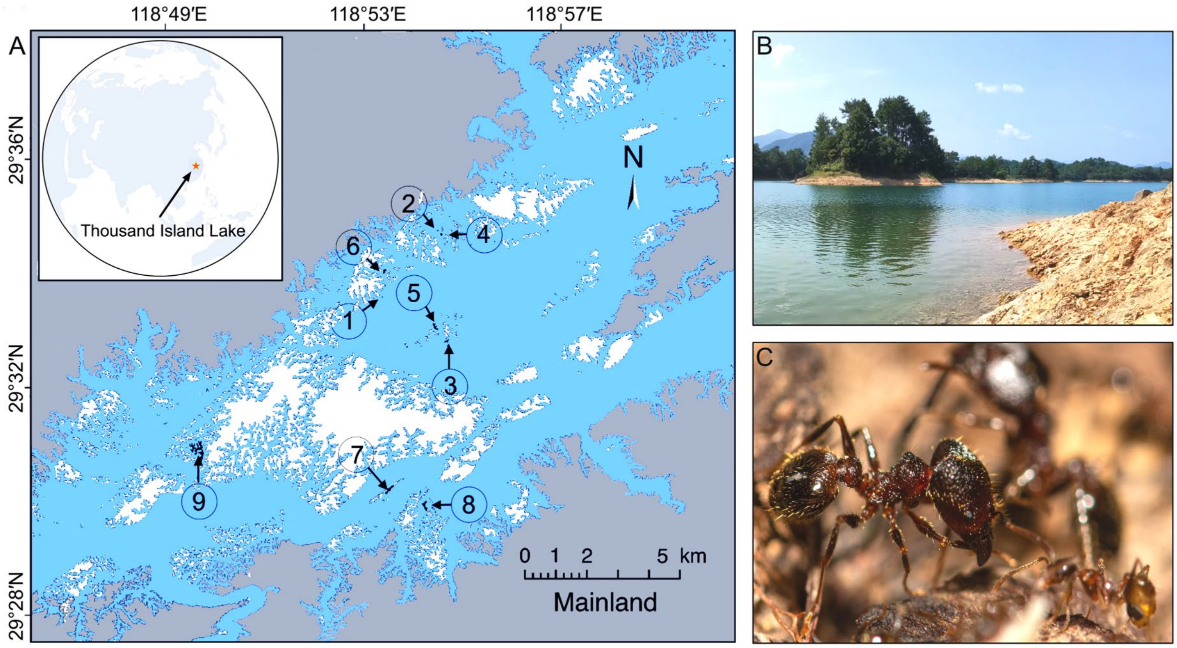

Fig. 2 Study islands and target taxon. **A** The distribution of nine study islands (shaded black). Islands that are coloured white are other islands in the system but were not surveyed as a part of this study. The water matrix is coloured blue. Islands are labelled by increasing area (i.e., #9 is the largest island). **B** the landscape of island #2. **C** The focal ant species *Pheidole nodus;* a major worker [soldier] is pictured on the left, and a minor worker [worker] on the right

Island choice and microclimate data

Based on a previous study, nine islands that ranged in area from 0.13 to 12.02 ha (Zhao et al. 2020) were selected. Both edge and interior sampling sites on the study islands were then set. Specifically, edge sites were set in a buffer zone a few meters outside the forested area where nests of *P. nodus* occur. Interior sites were set in the middle of the forest area on each island, or 150 m away from the edge site directed towards the island centre. Note that for the largest island (island #9 in Fig. 2A), two edge and interior sites were set.

To collect ambient temperature data, thermal iButtons (type DS1922L; Shanghai Wodisen, China) were deployed at each sampling site from July 2022 to December 2023, covering the whole period of the study. The iButtons were placed 0.5 m above the ground and recorded temperature at 30-min intervals (Leahy et al. 2022). All iButtons were enclosed in white plastic tubes to protect them from direct sunlight and precipitation.

Ant sampling

To sample live ants at each site, baits consisting of tuna were randomly placed around the iButtons. Baits containing sugar were avoided because carbohydrate intake would lead to short-term thermal plasticity in the ants (Bujan and Kaspari 2017). Each bait was frequently checked and a brush and aspirator were used to collect ants alive. The ants were identified with a pocket microscope to ensure only *Pheidole nodus* was collected. Before collecting individual ants, foraging routes were checked to ensure that ants foraging on any one bait were from the same colony. The nest was tracked and marked using a plastic plant label in order to resample particular nests. At each site, an attempt was made to collect from three colonies, and ten major workers (soldier) and ten minor workers (worker) for each colony. Ants from the same colony were stored in the same tubes and transported to the lab immediately. When transporting live ants to the lab, a piece of wet tissue and a handful leaflitter from the collection sites were placed in the tube to maintain humidity (Johnson and Stahlschmidt 2020). All tubes were then placed in an incubator with a small bag of ice inside to prevent overheating during transport to the laboratory, following Warren et al. (2020). An insulator was also placed between the tubes and the bag of ice to reduce the impacts of low temperatures (Warren et al. 2018, 2020). The ants were sampled in the summer (i.e., relatively hot season) from July to August 2022 and late autumn (i.e., relatively cold season) from October to November 2023 (Sampling year did not affect our results, see Appendix S1 and Table S1). Sampling in late autumn occurred because by late November, mean daily minimum temperature was lower than 10 °C, and *P.*

nodus was no longer active. The average temperature during relatively hot sampling season (July to August 2022) was 29.17 °C and relatively cold sampling season (October to November 2023) was 16.08 °C according to iButtons. All ants were collected during daytime from 7:00 to 11:00 a.m.

Thermal tolerance experiments

Critical thermal tolerances were measured with a digital dry bath (HX-20LS, HUXI, Shanghai). To avoid potential experimental acclimation, the trials started as soon as possible after transporting the ants to the lab and were all conducted on the same day as collection (Leahy et al. 2022). For each colony, five workers and five soldiers were used to measure CTmax, and the other five workers and five soldiers to measure CTmin. Before the trial, ants were separately allocated into 1.5 mL microcentrifuge vials. The vials were capped with foam plastic to prevent the ants from hiding in the space above the thermal block (Oberg et al. 2012). During the trial, other ants were still stored in tubes.

The CTmax assays were started at 36 °C, following the common starting temperature of other studies (Bujan et al. 2020; Diamond et al. 2012). When the dry bath reached the starting temperature, ten vials were placed in the dry bath. In addition, one empty vial with a thermocouple wire inserted and a foam capped was placed in a random well position. The reading from this thermometer connected with the thermocouple wire measured the actual temperature the ants were exposed to (Leong et al. 2022a). After the ants were put in the dry bath, the temperature was raised by 1 °C every minute, because at this ramping rate the most reliable CTmax values for comparing upper thermal limits could be obtained; see also Leong et al. (2022a). At each increase of 1 °C, the ants were checked by slightly flicking the vial. If an ant lost muscle control (i.e., the onset of spasms), it was removed from the dry bath and the temperature was recorded as its CTmax (Lutterschmidt and Hutchison 1997). The temperature at which ants lost muscle control was regarded as the critical thermal limit rather than lethal temperature, because the former is more relevant to biological survival (Lutterschmidt and Hutchison 1997). Temperature was continuously ramped up until all ants were removed from the dry bath. The CTmin assay was started at 16 °C, and followed a ramping-down rate of 1 °C min^{-1} (Yilmaz et al. 2019). At the conclusion of the thermal experiments, the ants were placed in 90% ethanol for further morphological measurements. CTrange (for both worker and soldier caste) of each colony was the difference between averaged CTmax and CTmin of all tested individuals.

In total, data from 2307 individuals across 117 colonies on 9 study islands were successfully obtained, with 1155 individuals assessed for CTmax, and 1152 for CTmin. Average time between collection in the field and beginning testing was 4 h 1 min (± SD 2 h 14 min) and the maximum time was 6 h and 50 min.

Statistical analyses

To test if ambient temperatures (mean daily maximum, minimum, average, and range of temperature) differed across islands, habitat types (edge or interior), and seasons (relatively hot or cold), these temperature metrics were measured for the duration of the study (relatively hot season: 8th August to 30th August 2022; relatively cold season: 29th October to 22nd November 2023). A set of linear models was constructed to assess the effect of island area, habitat type, season, and their two- and three-way interactions on each temperature metric. These models were ranked according to the corrected Akaike Information Criterion (AICc) using the *dredge* function in the 'MuMIn' package (Barton 2023). The model with the lowest AICc was selected as the 'best' model. Although model averaging was also applied to models with ΔAICc < 2, the results were qualitatively similar. Therefore, the results from the 'best' model were reported in the main text (see Appendix S2; Tables S2–S4). For each 'best' model, estimated marginal means (EMMs) were used to explore pairwise differences across habitat and season combinations (i.e., 'hot edge', 'hot interior', 'cold edge', and 'cold interior') when both factors were included in the model via the *emmeans* function in the 'emmeans' package (Lenth et al. 2023). EMMs provide adjusted group means by accounting for the influence of covariates, such as island area, in the model.

To test if thermal tolerance was affected by the interaction between island area and edge effects and if this effect varied among seasons and between worker castes, mixed-effect linear models were first applied to assess the effects of island area, habitat type, season, caste (worker or soldier) and their two-, three- and four-way interactions among these variables on critical thermal maximum temperature (CTmax), critical thermal minimum temperature (CTmin), and critical thermal range temperature (CTrange) using *lmer* function in the "lme4" package (Bates et al. 2015). For models of CTmax and CTmin, island and colony identity were set as nested random effects (i.e., island/colony as random intercept) to account for autocorrelation of individuals from the same colony and same island. For models of CTrange, only island identity was included as the random effect. The models were then sorted according to AICc fitted with Maximum Likelihood using the *dredge* function in the 'MuMIn' package (Barton 2023). Given the presence of many competing models with similar weights for all thermal tolerance metrics (see Table S6), a single 'best' model with the lowest AICc was not selected. Instead, model averaging was applied to models with ΔAICc < 2 using the *model.avg* function in the 'MuMIn' package (Barton 2023).

Notably, it was observed that season and caste consistently had significant effects on CTmax, CTmin, and CTrange (Tables S6 and S7), indicating strong data separation between seasons and castes. In this case, to simplify the model and better capture the interactive effects between island area and habitat type, the data were separated into four groups, based on season (hot or cold season) and caste (worker or soldier), namely, 'hot worker', 'hot soldier', 'cold worker', and 'cold soldier'. For each group, mixed-effect linear models were applied (with same random effects as described above) to regress CTmax, CTmin, and CTrange against island area, habitat type, and their interactions in each group using *lmer* function in the "lme4" package (Bates et al. 2015). The significance of island area, habitat type, and their interactions was assessed using *Anova()* function with Type III Wald χ^2 tests in the 'car' package (Fox and Weisberg 2019) following Yilmaz et al. (2019). To further evaluate whether significant thermal tolerance–area relationships existed in edge and interior populations for each group, separate regression models were built for CTmax, CTmin and CTrange for edge and interior populations, with island area as the sole predictor. These additional analyses were necessary because the significant interactive effects between island area and habitat type captured in the initial models (see Table S8) did not indicate whether the slope of the tolerance–area relationship was significant within edge or interior sites. In addition, EMMs were applied to all models (fitted with Restricted Maximum Likelihood [REML] algorithm) with ΔAICc < 2 for each thermal tolerance metric to explore pairwise differences across habitat types, seasons, and castes. The EMM results were then averaged across all candidate models for each thermal tolerance metric.

As body size might also influence thermal tolerance within species (Cerdá and Retana 1997; O'Donnell et al. 2020), we further measured the Weber's length (the maximum length measured from the anterior edge of pronotum to posterior edge of propodeum through lateral view) as an indicator of body size. Mixed-effect linear models were used to examine how CTmax and CTmin depended on body size in separate models (i.e., habitat type [edge or interior] combined with caste [worker or soldier]), with island and colony identity as nested random effect. Moreover, as ants may respond to temperature differences via phenotypic plasticity, individuals of the same species might be bigger or have longer legs under warmer temperatures (Sommer and Wehner 2012; Kaspari et al. 2015). Therefore, relative leg length (the sum of hind femur and hind tibia length, then divided by Weber's length to correct for body size) of each individual was measured (Fichaux et al. 2019). Mixed-effects linear models were then used to assess whether Weber's length and relative leg length depended on island area, habitat type, and their interaction, with island and colony as nested random effects. Model averaging was applied and EMMs used to test pairwise differences in Weber's length and relative leg length between habitat types as detailed above. Morphological analyses were conducted separately for workers and soldiers. Note: the morphological traits of only those individuals captured in a relatively hot season were measured.

All models were fitted a with Gaussian distribution and model assumption of normality and homoscedasticity were checked and confirmed through plotting model residuals. Variance inflation was checked, and there was no evidence of collinearity among fixed variables in any model. In all models, island area was $\log_{10}$-transformed to normalize model residuals.

Results

No interactive effect was found among island area, habitat type (edge or interior), and season (relatively hot and cold) on any of the temperature metric, and island area only had a significant effect on mean daily average of temperature (Fig. S1; Table S4). However, island area did not affect any temperature metrices when analyses based on groups among habitat types and seasons were conducted (Table S5). Mean daily maximum, minimum, and average temperature were consistently higher in the relatively hot season than in the relatively cold season (Fig. 3A–C). In the relatively hot season (i.e., summer), edge habitats had the highest mean daily maximum and average temperature (maximum: 39.28 ± 1.76 °C, average: 32.41 ± 0.32 °C; mean ± SD), and both mean daily maximum and average temperatures were significantly (around 3 °C for maximum and 1 °C for average temperature) higher than temperatures in interior habitats (Fig. 3A, C). In the relatively cold season (i.e., late autumn), the mean daily maximum, mean daily minimum and average temperature were similar between edge and interior sites (maximum: around 21.0 °C, minimum: around 12.8 °C, and average: around 16.1 °C; Fig. 3A–C). Edge habitats in the relatively hot season possessed the highest mean daily average of temperature (11.19 ± 1.80 °C), whereas interior sites in the relatively cold season had the lowest (7.45 ± 0.75 °C; Fig. 3D).

Overall, it was found that populations of *P. nodus* had higher CTmax, lower CTmin, and narrower CTrange in the relatively hot season relative to the measurements taken in the relatively cold season (Tables S6 and S7). In addition, the worker caste typically had higher CTmax, lower CTmin, and broader CTrange than did the soldier caste (Tables S6 and S7). Although overall differences in CTmax and CTmin between edge and interior habitats were not found (Tables S6 and S7), the CTrange was slightly broader in interior than in edge habitat (Tables S6 and S7).

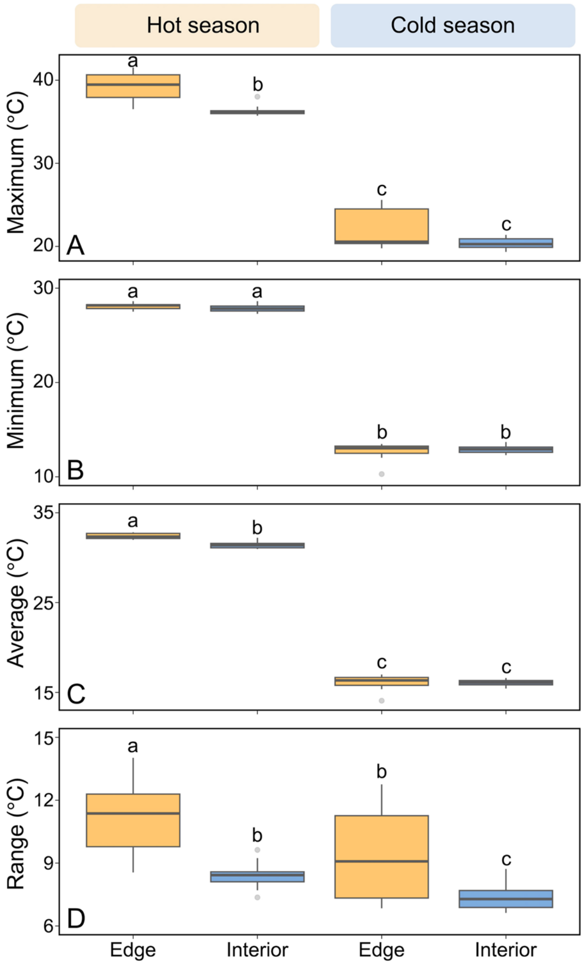

Fig. 3 The ambient temperature among habitat type (edge or interior) and season (relatively hot or cold). Maximum: Mean daily maximum temperature; Minimum: Mean daily minimum temperature; Average: Mean daily average temperature; Range: Mean daily temperature range. Significance among groups were obtained using estimated marginal means on 'best' models with lowest corrected Akaike Information Criterion (AICc) using model selection method (see Method section for more details)

The interaction between island area and habitat type had a significant effect on CTmax and CTrange of both workers and soldiers of *P. nodus* in the relatively hot season (worker CTmax: $\chi^2 = 11.96$, $P < 0.001$; soldier CTmax: $\chi^2 = 9.53$, $P < 0.001$; worker CTrange: $\chi^2 = 6.08$, $P = 0.014$; soldier CTrange: $\chi^2 = 11.08$, $P < 0.001$; Fig. 4A, E, Table S8). It was found that CTmax and CTrange of interior populations increased with island area (worker CTmax: $t = 3.54$, $P = 0.001$; soldier CTmax: $t = 3.00$, $P = 0.047$; worker CTrange: $t = 3.43$, $P = 0.009$; soldier CTrange: $t = 3.87$, $P = 0.004$; Fig. 4A, E, Table S8). However, all three thermal tolerance metrices, for either edge or interior populations, did not vary systematically with island area in the relatively cold season (Fig. 4B, D, F).

After accounting for the effect of island area (i.e., the estimated marginal means, see more details in Methods section), it was found that there were significant differences among season, caste, and habitat type in thermal tolerance (Fig. 5; Table S9). Specifically, the worker caste of *P. nodus* in edge habitats in the relatively hot season had the highest CTmax (43.83 ± 0.55 °C; mean ± SD; Fig. 5A), whereas worker caste in both edge and interior habitats in the relatively cold season had the lowest CTmin (edge worker: 9.23 ± 1.08 °C; mean ± SD; interior worker: 9.05 ± 0.93 °C; mean ± SD; Fig. 5B). Ants in the worker caste in the interior habitat in the relatively cold season had the broadest CTrange (33.81 ± 0.57 °C; mean ± SD; Fig. 5C).

Body size (measured as Weber's length) was not related to the thermal tolerance within *P. nodus* on these study islands (Table S10). Additional analyses that tested whether morphological shifts with island area and between habitat types indicated that the 'best' models include only habitat type for models of worker body size and relative leg length (Table S11). Models examining the drivers of body size for soldiers indicated that the best models were the 'null' model (Table S11). However, contrary to the hypothesis given here, interior workers had larger body sizes and longer relative leg lengths than the edge workers (Fig. 6A, C; Table S12).

Discussion

Here, the critical thermal maximum temperature (CTmax), critical thermal minimum temperature (CTmin), and critical thermal range temperature (CTrange) of a dimorphic ant species, *Pheidole nodus,* at both the edge and interior habitats of fragmented islands in the Thousand Island Lake, China between castes and seasons were examined. It was found that although temperature was higher in edge than interior sites during the relatively hot season, there was no pervasive evidence of elevated CTmax in the ants of the edge populations, except for the population on the smallest island (Fig. 4A). Instead, it was found that (1) there is an interactive effect of island area and habitat type on CTmax and CTrange, where they both higher in the interiors of larger islands than the interiors of smaller islands. (2) CTmax was higher in the relatively hot season, whereas CTmin was lower in relatively cold season. (3) Workers had higher CTmax, lower CTmin, and broader CTrange than soldier caste. These results indicate that seasonality, worker caste, and the interactive effect of island area and habitat type influence the thermal ecology of *P. nodus* on island fragments.

In this study, the maximum and average temperatures in island edge habitats were significantly higher than interior

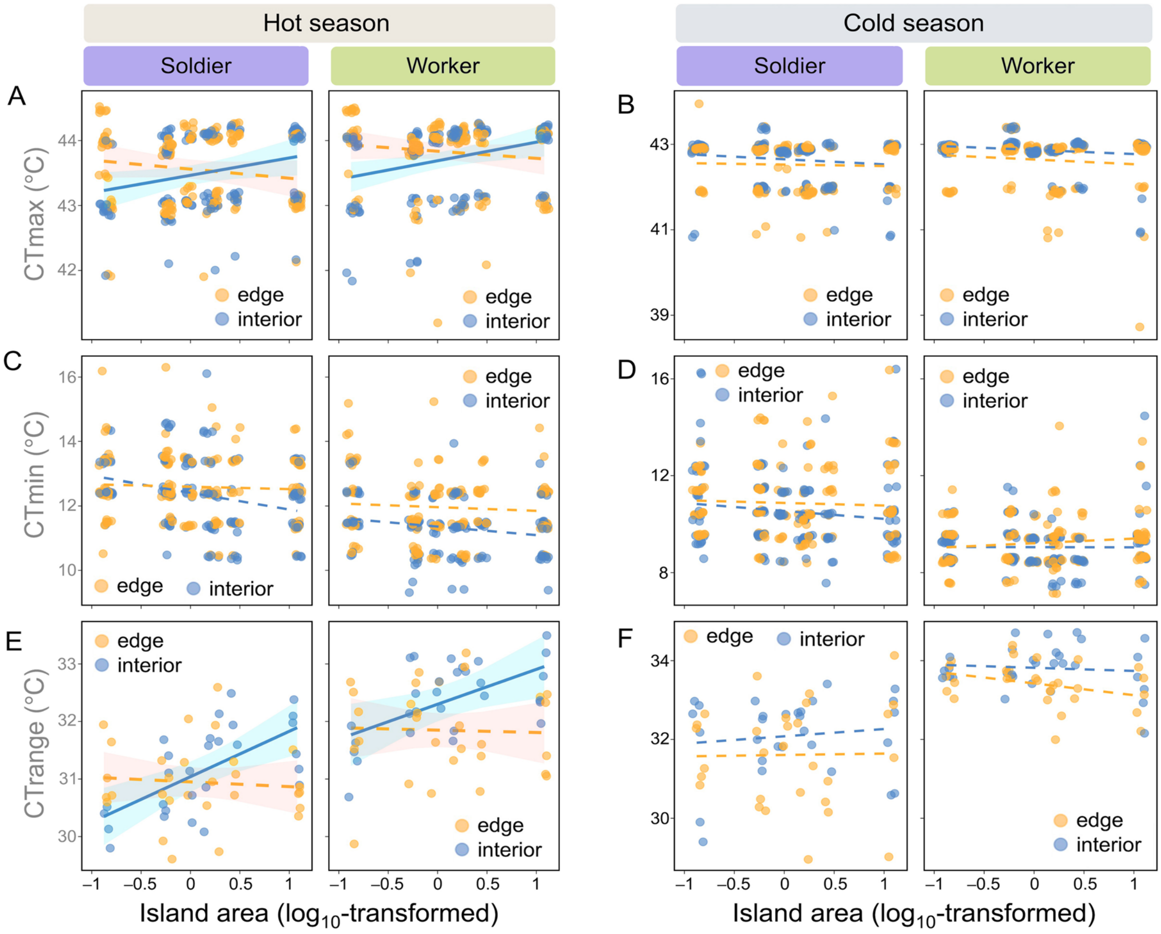

Fig. 4 The effects of island area, habitat type, and their interaction on critical thermal maximum temperature (CTmax, **A** and **B**), critical thermal minimum temperature (CTmin, **C** and **D**), and critical thermal range temperature (CTrange, **E** and **F**) of *Pheidole nodus* on nine fragmented islands in the Thousand Island Lake, China. Models were constructed separately for four groups (seasons [relatively hot or cold] combined with castes [worker or soldier]). The interactive effect between island area and habitat type was significant in models for CTmax (**A**) and CTrange (**E**) for both worker and soldier in hot season. The coloured lines and riboons in **A** and **E** represent the predicted and standard errors estimated by CTmax and CTrange for each habitat type (edge or interior) for island area, respectively. However, for the remaining models, the interactive term was not significant. The coloured lines were added according to the separated model that only contained island area for CTmax, CTmin and CTrange (see Methods for more details). A ribbon for separate models in **B**, **C**, **D**, and **F** was not added for clarity. The solid lines indicate significant relationships at the significance of α = 0.05, whereas the dotted lines indicate non-significant relationships. The position of points were adjusted using *position_jitter()* function in ggplot2 to avoid highly overlapping

habitats during the relatively hot season (i.e., summer), similar to previous findings (Barahona-Segovia et al. 2022). Under such a scenario, it should be expected that most edge populations would have higher CTmax, yet such a pattern for *P. nodus* was not found. One possible explanation is that although the daily mean maximum temperature (~ 39.29 °C) in edge habitats during the summer was relatively high, it was not high enough to influence the CTmax of *P. nodus*, with a CTmax of ~ 43.5 °C. However, it is noted that the iButton used here was located 0.5 m above the ground and the soil surface temperature may have been much higher (Prather et al. 2018). Additionally, the lack of overall differences in CTmax between habitat types could be attributed to the modifying effect of island area on habitat type, where the slopes for edge and interior habitats trend in opposite directions (Fig. 4A).

Despite the above, ants can respond to temperature differences in other ways, such as short-term behavioral shifts or long-term phenotypic shifts (Parr and Bishop 2022; Youngsteadt et al. 2023). For example, larger workers reach equilibrium with ambient temperatures more slowly than do smaller workers, which provides more time for larger individuals to seek thermal refuges (Kaspari et al. 2015). Individuals with relatively longer legs are able to run faster (Feener et al. 1988), which

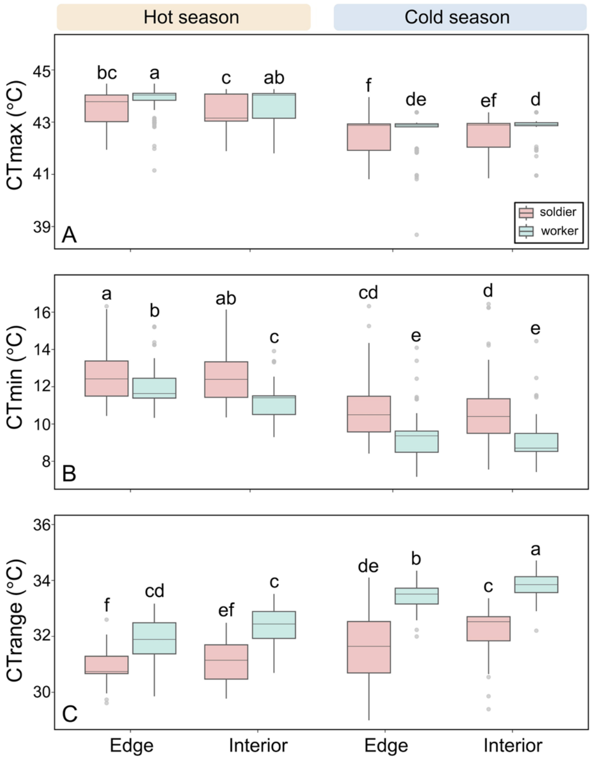

Fig. 5 The differences of critical thermal maximum temperature (CTmax, **A**), critical thermal minimum temperature (CTmin, **B**), and critical thermal range temperature (CTrange, **C**) of *Pheidole nodus* among habitat type (edge or interior), season (relatively hot or cold), and caste (worker or soldier) on nine fragmented islands in the Thousand Island Lake, China. Significance among groups were obtained using estimated marginal means on models with corrected Akaike Information Criterion (ΔAICc) < 2 using model selection method (see Method section for more details)

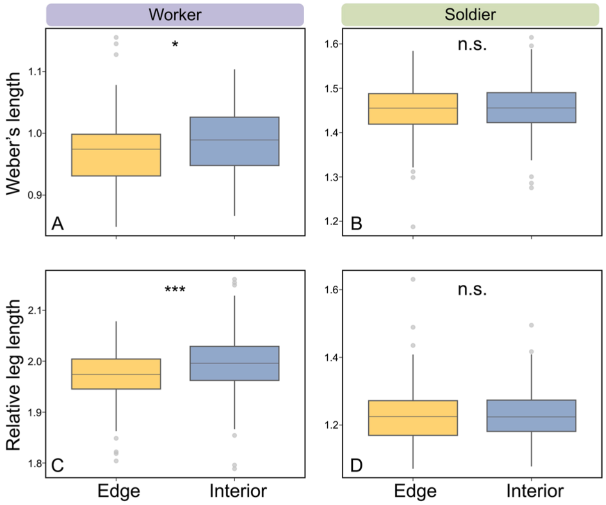

Fig. 6 The differences of Weber's length and relative leg length of worker (**A**, **C**) and soldier (**B**, **D**) caste of *P. nodus* among between edge and interior habitats on nine fragmented islands in the Thousand island lake, China. Significance levels: n.s. non-significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

could facilitate getting through thermally dangerous microclimates more quickly than individuals with shorter legs. In addition, longer legs elevate the body from the ground, resulting in cooler body temperatures (Sommer and Wehner 2012). Thus, based on the thermal perspective, we would anticipate that individuals in edge populations should be bigger and have longer legs, relative to individual workers in interior populations. However, our additional analyses did not find that body size or leg length varied between edge and interior populations as predicted (Fig. 6). Instead, we found interior workers have larger body size and longer relative leg length than edge workers (Fig. 6A, C). This implies that the morphological adaptions of *P. nodus* inhibiting inside and interior of study islands may not be driven by temperature.

Taken together, it seems most likely that individuals in edge populations simply alter their foraging times to avoid high temperatures: based on field observations, workers from edge colonies barely foraged at noon when the air temperatures were closest to, yet the soil surface temperature probably exceed their CTmax during summer. Indeed, a previous study on *P. nodus* also found that workers typically forage between 5 to 8 a.m., and 8 p.m. to 1 a.m. during summer in the *Pinus massoniana* forest (Ma et al. 1997), indicating the ability to flexibly adjust their foraging schedules to avoid lethal temperatures (Bernstein 1979; Spicer et al. 2017). In addition, *P. nodus* likely has a very limited foraging range (i.e., less than 1 m) (sensu Eguchi et al. 2004; Nooten et al. 2022; field observations), restricting edge populations from foraging into interior habitats. Thus, *P. nodus* is able to inhabit edge habitats probably due to their behavioral changes in response to temperature, and not the physiological or morphological shifts.

Interestingly, we found that island area and habitat type had an interactive effect on both CTmax and CTrange during the summer such that CTmax and CTrange were higher for colonies in interior habitats on larger islands than that on smaller islands (Fig. 4A, E). Considering that temperature did not vary systematically with island area (Fig. 3), one possible explanation for the higher CTmax in interior habitats on larger islands comparing to smaller islands could be that the resource intake of colonies varies systematically with island area: larger islands typically possess more, and a more diverse, pool of resources, especially in interior habitats (Wardle et al. 2003). Thus, carbohydrate intake may increase in interior populations on large islands. Increased carbohydrate intake has been positively correlated with CTmax (Freires et al. 2023). While the resources in edge habitats are perhaps limited on either large or small islands, reducing the potential impact of carbohydrate intake on CTmax of edge populations. However, we also note that CTmax was lower in interior populations than edge populations on the smallest island during summer (worker: $t = -3.49$, $P = 0.002$; soldier: $t = -3.76$, $P = 0.001$), which in line with our hypothesis. Although smaller islands have less total edge habitat, the proportion of edge habitat relative to the total area is often higher compared to larger islands. This higher proportion of edge habitat may amplify edge effects (Ewers and Didham 2006), potentially resulting in elevated CTmax values in edge populations on the smallest island.

Seasonal thermal plasticity is common in ants (Bujan et al. 2020; Coulin et al. 2019). Here by examining populations in both the relatively hot and cold seasons, we verified that *P. nodus* also exhibits apparent seasonal plasticity of thermal tolerance, with higher CTmax in summer and lower CTmin in late autumn in our study region. In addition, CTmax is less plastic than CTmin in other terrestrial ectotherms (Hoffmann et al. 2013), including ants (Bishop et al. 2017; Diamond et al. 2018). Indeed, we note that differences within CTmin (i.e., ΔCTmin ≈ 2 °C) is larger than CTmax (i.e., ΔCTmax ≈ 1 °C) between seasons (Fig. 5A, B). The higher CTmax in the summer could also be because of the availability of food resources (Bujan et al. 2020). *P. nodus* is omnivore and was disproportionally found to be feeding on honeydew provided by sap-sucking trophobionts (e.g., aphid) in our study region during the summer (Zhang et al. 2023). Thus, the plentiful carbohydrates in honeydew may lead to a higher CTmax of *P. nodus* (Freires et al. 2023). Despite the effects of seasonal variation in temperature and potentially resource use on CTmax, plasticity in CTmax was lower than plasticity for CTmin, indicating *P. nodus* may be more affected by warming events than cold events.

Worker ants typically had a higher CTmax and CTrange, but lower CTmin, than soldiers irrespective of the habitat type within island or season (Fig. 4). This finding contrasts with a previous study on ten ant species in the genus *Pheidole* in which soldiers were more tolerant to high temperatures than were workers (Tschá and Pie 2019). The difference between this study and the previous study may be due to differences in methodologies to assess thermal tolerance; the previous study used the time to death at a constant temperature of 40 °C as an estimate of thermal tolerance (Tschá and Pie 2019). In their case, soldiers that had larger body size might have had an advantage in constantly resisting high temperatures (Clémencet et al. 2010). However, the ramping method was used here, which may better reflect the realized heat tolerance of each individual (Leong et al. 2022a). It is argued that workers mainly forage outside the nest so they would need to be better able to cope with the ambient temperatures, resulting a higher ability to cope with critical thermal temperatures.

Colonies of dimorphic ant species might be able to persist in changing environments by adjusting their subcaste ratio (Wilson 1968). Previous research has shown that removing soldiers from colonies of *Colobopsis nipponic* may have led to a decrease in the success rate of the colony defence and foraging efficiency (Hasegawa 1997). Although the ratio of soldiers to workers in colonies of *P. nodus* on the study islands was not studied here, results presented here suggest that temperature change will have greater impact on soldier caste (especially for soldiers in edge colonies that have the relatively lowest CTrange; see Fig. 5C) in terms of the thermal tolerance, which may result in the inability to perform their functions in the colony. When the soldier caste is affected, the diet breadth of the colony may be reduced, the ability to defend colonies will be affected, and the food storage capacity of colony might also be reduced (Wilson 2003). Studies have shown that by artificially adjusting the subcaste ratio in colonies of dimorphic species, the remaining worker ants can take on the work of the missing colony members, but only to a certain extent (Sempo and Detrain 2010). However, no studies have quantified how this might ultimately affect colony performance or fitness. Thus, with ongoing global climate change, how colonies of dimorphic ant species respond to the situation where soldier ants are unable to perform their tasks requires further exploration.

Conclusion

In conclusion, we found that the critical thermal tolerance of a dominant dimorphic ant species (*Pheidole nodus*) in a fragmented habitat island system was modulated by seasonality, caste, and the interaction between area and edge effect. Despite the elevated temperature at the edge of these fragmented habitats, edge populations did not exhibit higher CTmax (except for the smallest island), suggesting behavioral adaptations rather than physiological changes to mitigate thermal stress. This study provides empirical evidence on how critical thermal tolerance varies among fragmented habitat islands and underscores the importance of considering multiple factors, including seasonality, worker caste, and habitat characteristics, in understanding the thermal biology of species in fragmented habitats. Our results provide insights for the integration of thermal tolerance research into broader ecological and conservation frameworks, particularly in the context of habitat fragmentation and climate change.

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Author contributions Yuhao Zhao and Xingfeng Si conceived the ideas; Yuhao Zhao, Chenxiao Wu, Nathan J. Sanders, and Chi Man Leong designed the methodology; Yuhao Zhao, Chenxiao Wu, and Jiaxin Li collected the data; Yuhao Zhao and Chenxiao Wu analysed the data; Yuhao Zhao led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Data availability Data available on request from the authors.

Declarations

Conflict of interest The authors declare that they have no conflict of interests for the work reported in this paper.

Animal and human rights statement This article does not contain any studies with human participants or animals performed by the authors.

References

Barahona-Segovia RM, Grez AA, Veloso C (2022) Forestry clear-cuts increase environmental temperatures, affecting the ecophysiological responses of specialized beetles in fragmented landscapes. J Appl Entomol 146:557–569

Barley JM, Cheng BS, Sasaki M, Gignoux-Wolfsohn S, Hays CG, Putnam AB, Sheth S, Villeneuve AR, Kelly M (2021) Limited plasticity in thermally tolerant ectotherm populations: evidence for a trade-off. Proc R Soc B Biol Sci 288:20210765

Barton K (2023) MuMIn: multi-model inference. R package version 1. 47. 5 https://github.com/cran/MuMIn

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Baudier K, O'Donnell S (2018) Complex body size differences in thermal tolerance among army ant workers (*Eciton burchellii* parvispinum). J Therm Biol 78:277–280

Bennett JM, Sunday J, Calosi P, Villalobos F, Martínez B, Molina-Venegas R, Araújo MB, Algar AC, Clusella-Trullas S, Hawkins BA, Keith SA, Kühn I, Rahbek C, Rodríguez L, Singer A, Morales-Castilla I, Olalla-Tárraga MÁ (2021) The evolution of critical thermal limits of life on Earth. Nat Commun 12:1198

Bernstein RA (1979) Schedules of foraging activity in species of ants. J Anim Ecol 48:921–930

Bishop TR, Robertson MP, Van Rensburg BJ, Parr CL (2017) Coping with the cold: minimum temperatures and thermal tolerances dominate the ecology of mountain ants. Ecol Entomol 42:105–114

Bujan J, Kaspari M (2017) Nutrition modifies critical thermal maximum of a dominant canopy ant. J Insect Physiol 102:1–6

Bujan J, Roeder KA, Yanoviak SP, Kaspari M (2020) Seasonal plasticity of thermal tolerance in ants. Ecology 101:e03051

Cerdá X, Retana J (1997) Links between worker polymorphism and thermal biology in a thermophilic ant species. Oikos 78:467–474

Chase JM, Blowes SA, Knight TM, Gerstner K, May F (2020) Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584:238–243

Clémencet J, Cournault L, Odent A, Doums C (2010) Worker thermal tolerance in the thermophilic ant Cataglyphis cursor (Hymenoptera, Formicidae). Insectes Soc 57:11–21

Coulin C, de la Vega GJ, Chifflet L, Calcaterra LA, Schilman PE (2019) Linking thermo-tolerances of the highly invasive ant, *Wasmannia auropunctata*, to its current and potential distribution. Biol Invasions 21:3491–3504

Diamond SE, Sorger DM, Hulcr J, Pelini SL, Toro ID, Hirsch C, Oberg E, Dunn RR (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Global Change Biol 18:448–456

Diamond SE, Nichols LM, Pelini SL, Penick CA, Barber GW, Cahan SH, Dunn RR, Ellison AM, Sanders NJ, Gotelli NJ (2016) Climatic warming destabilizes forest ant communities. Sci Adv 2:e1600842

Diamond SE, Chick L, Perez A, Strickler SA, Martin RA (2017) Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. Biol J Linn Soc 121:248–257

Diamond SE, Chick LD, Perez A, Strickler SA, Martin RA (2018) Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities. Proc R Soc B Biol Sci 285:20180036

Didham RK, Lawton JH (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17–30

Eguchi K, Bui TV, Yamane S (2004) A preliminary study on foraging distance and nesting sites of ants in Indo-Chinese lowland vegetation. Sociobiology 43:445–457

Ewers RM, Banks-Leite C (2013) Fragmentation impairs the microclimate buffering effect of tropical forests. PLoS ONE 8:e58093

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol S 34:487–515

Feener DH, Lighton JRB, Bartholomew GA (1988) Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. Funct Ecol 2:509–520

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, London

Freires ASA, Ferreira CAS, Nascimento G, Arnan X (2023) Carbohydrate-rich diet increases critical thermal maximum in ants. Entomol Exp Appl 171:240–247

Fichaux M, Béchade B, Donald J, Weyna A, Delabie JHC, Murienne J, Baraloto C, Orivel J (2019) Habitats shape taxonomic and functional composition of Neotropical ant assemblages. Oecologia 189:501–513

Frey SJK, Hadley AS, Johnson SL, Schulze M, Jones JA, Betts MG (2016) Spatial models reveal the microclimatic buffering capacity of old-growth forests. Sci Adv 2:e1501392

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hasegawa E (1997) The optimal caste ratio in polymorphic ants: estimation and empirical evidence. Am Nat 149:706–722

Hoffmann AA, Chown SL, Clusella-Trullas S (2013) Upper thermal limits in terrestrial ectotherms: How constrained are they? Funct Ecol 27:934–949

Hopkin RS, Qari S, Bowler K, Hyde D, Cuculescu M (2006) Seasonal thermal tolerance in marine Crustacea. J Exp Mar Biol Ecol 331:74–81

Hu G, Feeley KJ, Wu J, Xu G, Yu M (2011) Determinants of plant species richness and patterns of nestedness in fragmented landscapes: evidence from land-bridge islands. Landsc Ecol 26:1405–1417

Johnson DJ, Stahlschmidt ZR (2020) City limits: heat tolerance is influenced by body size and hydration state in an urban ant community. Ecol Evol 10:4944–4955

Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A (2015) Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Global Change Biol 21:1092–1102

Kay CAR, Whitford WG (1978) Critical thermal limits of desert honey ants: possible ecological implications. Physiol Zool 51:206–213

Laurance WF (2004) Forest-climate interactions in fragmented tropical landscapes. Philos T R Soc B 359:345–352

Leahy L, Scheffers BR, Williams SE, Andersen AN (2022) Arboreality drives heat tolerance while elevation drives cold tolerance in tropical rainforest ants. Ecology 103:e03549

Leal IR, Filgueiras BKC, Gomes JP, Iannuzzi L, Andersen AN (2012) Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodivers Conserv 21:1687–1701

Lenth R, Singmann H, Love J, Buerkner P, Herve M (2023) Emmeans: estimated marginal means, aka least-squares means. R package version 1.8.9. https://github.com/rvlenth/emmeans

Leong CM, Tsang TPN, Guénard B (2022a) Testing the reliability and ecological implications of ramping rates in the measurement of critical thermal maximum. PLoS ONE 17:e0265361

Leong CM, Wang R, Cheung SC, Jaitrong W, Guénard B (2022b) Are thermal constraints shaping foraging ant assemblages in tropical regions? Integrating thermal and morphological traits to understand consequences of land-use transformation. Insect Conserv Diver 16:254–265

Liu J, Coomes DA, Hu G, Liu J, Yu J, Luo Y, Yu M (2019) Larger fragments have more late-successional species of woody plants than smaller fragments after 50 years of secondary succession. J Ecol 107:582–594

Liu J, Matthews TJ, Zhong L, Liu J, Wu D, Yu M (2020) Environmental filtering underpins the island species-area relationship in a subtropical anthropogenic archipelago. J Ecol 108:424–432

Lutterschmidt WI, Hutchison VH (1997) The critical thermal maximum: history and critique. Can J Zool 75:1561–1574

Ma W, Li Z, Wang X, Feng X (1997) Bionomics of *Pheidole nodus* Smith and its preying upon Dendrolimus punctatus (in Chinese). Forest Pest Dis 1:3–6

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62

Nascimento G, Câmara T, Arnan X (2022) Critical thermal limits in ants and their implications under climate change. Biol Rev 97:1287–1305

Nooten SS, Chan KH, Schultheiss P, Bogar TA, Guénard B (2022) Ant body size mediates functional performance and species interactions in carrion decomposer communities. Funct Ecol 36:1279–1291

Nunes MH, Vaz MC, Camargo JLC, Laurance WF, de Andrade A, Vicentini A, Laurance S, Raumonen P, Jackson T, Zuquim G, Wu J, Peñuelas J, Chave J, Maeda EE (2023) Edge effects on tree architecture exacerbate biomass loss of fragmented Amazonian forests. Nat Commun 14:8129

O'Donnell S, Bulova S, Caponera V, Oxman K, Giladi I (2020) Species differ in worker body size effects on critical thermal limits in seed-harvesting desert ants (*Messor ebeninus* and *M. arenarius*). Insectes Soc 67:473–479

Oberg EW, Del Toro I, Pelini SL (2012) Characterization of the thermal tolerances of forest ants of New England. Insectes Soc 59:167–174

Palmeirim AF, Emer C, Benchimol M, Storck-Tonon D, Bueno AS, Peres CA (2022) Emergent properties of species-habitat networks in an insular forest landscape. Sci Adv 8:eabm0397

Parr CL, Bishop TR (2022) The response of ants to climate change. Global Change Biol 28:3188–3205

Pelini SL, Diamond SE, MacLean H, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2012) Common garden experiments reveal uncommon responses across temperatures, locations, and species of ants. Ecol Evol 2:3009–3015

Prather RM, Roeder KA, Sanders NJ, Kaspari M (2018) Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants. Ecology 99:2113–2121

Ren P, Didham RK, Murphy MV, Zeng D, Si X, Ding P (2023) Forest edges increase pollinator network robustness to extinction with declining area. Nat Ecol Evol 7:393–404

Roeder KA, Roeder DV, Bujan J (2021) Ant thermal tolerance: a review of methods, hypotheses, and sources of variation. Ann Entomol Soc Am 114:459–469

Schultheiss P, Nooten SS, Wang R, Wong MKL, Brassard F, Guénard B (2022) The abundance, biomass, and distribution of ants on Earth. Proc Natl Acad Sci USA 119:e2201550119

Sempo G, Detrain C (2010) Social task regulation in the dimorphic ant, Pheidole pallidula: the influence of caste ratio. J Insect Sci 10:3

Sgrò CM, Terblanche JS, Hoffmann AA (2016) What can plasticity contribute to insect responses to climate change? Annu Rev Entomol 61:433–451

Sharma NK, Akhtar MS, Pandey N, Singh R, Singh AK (2015) Seasonal variation in thermal tolerance, oxygen consumption, antioxidative enzymes and non-specific immune indices of Indian hill trout, Barilius bendelisis (Hamilton, 1807) from central Himalaya, India. J Therm Biol 52:166–176

Si X, Pimm SL, Russell GJ, Ding P (2014) Turnover of breeding bird communities on islands in an inundated lake. J Biogeogr 41:2283–2292

Si X, Jin T, Li W, Ren P, Wu Q, Zeng D, Zhang X, Zhao Y, Zhu C, Ding P (2024) TIL20: a review of island biogeography and habitat fragmentation studies on subtropical reservoir islands of Thousand Island Lake, China. Zool Res Diver Conserv 1:89–105

Silva da Costa W, Da Cunha M, Pena JF, Rodrigues P, de Andrade IM, Valladares F, Franca Barros C (2020) Intraspecific variation in functional wood anatomy of tropical trees caused by effects of forest edge. Forest Ecol Manag 473:118305

Sommer S, Wehner R (2012) Leg allometry in ants: extreme long-leggedness in thermophilic species. Arthropod Struct Dev 41:71–77

Spicer ME, Stark AY, Adams BJ, Kneale R, Kaspari M, Yanoviak SP (2017) Thermal constraints on foraging of tropical canopy ants. Oecologia 183:1007–1017

Stuble KL, Patterson CM, Rodriguez-Cabal MA, Ribbons RR, Dunn RR, Sanders NJ (2014) Ant-mediated seed dispersal in a warmed world. PeerJ 2:e286

The United Nations Office for Disaster Risk Reduction (UNISDR) (2015) The human cost of weather related disasters 1995–2015. https://www.unisdr.org/2015/docs/climatechange/COP21_WeatherDisastersReport_2015_FINAL.pdf. Accessed 21 May 2017

Tschá MK, Pie MR (2019) Correlates of ecological dominance within Pheidole ants (Hymenoptera: Formicidae). Ecol Entomol 44:163–171

Tuff KT, Tuff T, Davies KF (2016) A framework for integrating thermal biology into fragmentation research. Ecol Lett 19:361–374

Wardle DA, Hörnberg G, Zackrisson O, Kalela-Brundin M, Coomes DA (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. Science 300:972–975

Warren RJ, Bayba S, Krupp KT (2018) Interacting effects of urbanization and coastal gradients on ant thermal responses. J Urban Ecol 4:juy026

Warren RJ, Candeias M, Lafferty A, Chick LD (2020) Regional-scale environmental resistance to non-native ant invasion. Biol Invasions 22:813–825

Wilson EO (1968) The ergonomics of caste in the social insects. Am Nat 102:41–66

Wilson EO (2003) Pheidole in the new world: a dominant, hyperdiverse ant genus. Harvard University Press, Harvard

Wilson MC, Chen XY, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landsc Ecol 31:219–227

Yilmaz AR, Chick LD, Perez A, Strickler SA, Vaughn S, Martin RA, Diamond SE (2019) Remarkable insensitivity of acorn ant morphology to temperature decouples the evolution of physiological tolerance from body size under urban heat islands. J Therm Biol 85:102426

Youngsteadt E, Prado SG, Keleher KJ, Kirchner M (2023) Can behaviour and physiology mitigate effects of warming on ectotherms? A test in urban ants. J Anim Ecol 92:568–579

Zhang X, Dalsgaard B, Staab M, Zhu C, Zhao Y, Gonçalves F, Ren P, Cai C, Qiao G, Ding P, Si X (2023) Habitat fragmentation increases specialization of multi-trophic interactions by high species turnover. Proc R Soc B Biol Sci 290:20231372

Zhao Y, Dunn RR, Zhou H, Si X, Ding P (2020) Island area, not isolation, drives taxonomic, phylogenetic and functional diversity of ants on land-bridge islands. J Biogeogr 47:1627–1637

Zhao Y, Sanders NJ, Liu J, Jin T, Zhou H, Lu R, Ding P, Si X (2021) β diversity among ant communities on fragmented habitat islands: the roles of species trait, phylogeny and abundance. Ecography 44:1568–1578

Zheng S, Didham RK, Yu M, Webber BL (2022) Species-level CWM values mask contrasting intra- versus interspecific trait shifts at subtropical forest edges. Ecography 2022:e05837