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LETTER

Heat tolerance variation reveals vulnerability of tropical herbivore–parasitoid interactions to climate change

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Abstract

Assessing the heat tolerance (CTmax) of organisms is central to understand the impact of climate change on biodiversity. While both environment and evolutionary history affect CTmax, it remains unclear how these factors and their interplay influence ecological interactions, communities and ecosystems under climate change. We collected and reared caterpillars and parasitoids from canopy and ground layers in different seasons in a tropical rainforest. We tested the CTmax and Thermal Safety Margins (TSM) of these food webs with implications for how species interactions could shift under climate change. We identified strong influence of phylogeny in herbivore–parasitoid community heat tolerance. The TSM of all insects were narrower in the canopy and parasitoids had lower heat tolerance compared to their hosts. Our CTmax-based simulation showed higher herbivore–parasitoid food web instability under climate change than previously assumed, highlighting the vulnerability of parasitoids and related herbivore control in tropical rainforests, particularly in the forest canopy.

KEYWORDS

body size, climate change, CTmax, Lepidoptera, microclimate, phylogeny, trophic interaction

INTRODUCTION

Temperature is an important environmental driver affecting organisms' fitness and distributions, especially for ectotherms (Andersen et al., 2015; Huey & Berrigan, 2001). As climate change continues to drive global temperatures upwards, assessing the impact from high temperatures is crucial in understanding how the environment shapes ectotherm assemblages (McNamara et al., 2021; Wiescher et al., 2012) and predicting how climate change will impact ecosystem functions (Sinclair et al., 2016). Temperature rise could affect the performance and fitness of ectotherms in multiple ways including behaviour (Logan et al., 2015), fecundity (Zeh et al., 2012) and physiology (Angilletta Jr et al., 2002). One of the most widely used proxies to standardise and evaluate physiological heat tolerance is critical thermal maximum temperature (CTmax), usually defined as the temperature at which ectotherms become unresponsive under heat (Rezende et al., 2011). Identifying factors influencing CTmax is important in understanding the mechanisms behind heat tolerance and evaluating the vulnerability of ectotherms under warming.

CTmax is a physiological trait that can be shaped by intrinsic evolutionary processes, resulting in closely related species sharing similar critical thermal attributes (i.e. high phylogenetic conservation and signal) (Boyle et al., 2021; Diamond et al., 2012). Alternatively, extrinsic factors such as thermal environments can alter the evolutionary influence on CTmax, acting as environmental filters (Leahy et al., 2022). In such cases, sympatric species can show similar CTmax values independent of their evolutionary backgrounds. For example, ectotherms from hotter environments (e.g. forest canopies) which often have higher CTmax compared to ectotherms from cooler environments, showing low phylogenetic conservation (i.e. phylogenetic signal) (Baudier et al., 2015; Duarte et al., 2012; García-Robledo et al., 2016; Leahy et al., 2022; Oliveira et al., 2021). CTmax, can also be influenced by intrinsic organismal characteristics such as body size (Gillooly et al., 2001). In this case, larger ectotherms are typically found to be more vulnerable to acute heat stress due to their higher oxygen demands during brief heat exposure (Rubalcaba & Olalla-Tárraga, 2020), and smaller ectotherms are more vulnerable under longer heat exposure (Klockmann et al., 2017; Leiva et al., 2019; Peralta-Maraver & Rezende, 2021). Ultimately, the interplay of intrinsic and extrinsic factors is expected to determine inter-specific variation of CTmax among ectothermic organisms (Boyle et al., 2021; Kaspari et al., 2015). It remains unclear, however, whether the individual and interactive effects of these factors can modulate species interactions and community heat tolerances (Kaspari et al., 2015).

Species interactions are important for ecosystem processes (e.g. pollination, herbivory) (Mouillot et al., 2011). Hence, examining and evaluating how species interactions will be affected by high temperature is crucial in predicting climate change impacts (Boukal et al., 2019; Boulangeat et al., 2018). Although some studies have looked at simulated extinctions in species interaction networks under climate change (Schleuning et al., 2016; Sonne et al., 2022), thermal tolerance has not been included in these simulations. In temperate regions, heat tolerance studies from few species have found that CTmax was generally lower at higher trophic levels (Agosta et al., 2018; Machekano et al., 2018; Voigt et al., 2003). However, species interaction under climate change has rarely been studied in species-rich ecosystems such as tropical rainforests (Bartley et al., 2019; Boyle et al., 2021).

Seasonal tropical rainforests provide an ideal natural laboratory for addressing the above gaps. Seasonality and vertical stratification create diverse microclimates characterised by hotter conditions in forest canopies (less shading and higher solar radiation) and dry seasons (change in solar zenith angles) compared to ground layers and wet seasons (De Frenne et al., 2021; Leahy et al., 2022). In these ecosystems, species interactions, especially herbivore–parasitoid, play an important role in regulating herbivory (Vidal & Murphy, 2018), which is crucial in maintaining biodiversity and energy flow (Hairston Jr & Hairston Sr, 1993; Cannon et al., 2021). Considering the higher vulnerability of tropical ectotherms to climate change (Deutsch et al., 2008; Sunday et al., 2014), understanding how extrinsic and intrinsic factors (e.g. microclimates, phylogeny, body size) influence heat tolerance (CTmax) among herbivores and their parasitoids may help to better understand and predict ecological dynamics in tropical forest communities in the future.

We sampled lepidopteran herbivores and associated parasitoids in a species-rich seasonal evergreen tropical rainforest with marked vertical and seasonal stratification of microclimates (Nakamura et al., 2017; Figure 1). Being mostly herbivorous, Lepidoptera is one of the two most diverse herbivore groups in the tropics and important herbivores globally (Basset et al., 2012; Dyer et al., 2007). We hypothesised that (1) species experiencing hotter microclimates (generated from vertical stratification and seasonality) have higher CTmax; (2) species with larger body sizes have lower CTmax; (3) given different CTmax across trophic levels, herbivore–parasitoid food webs become more vulnerable to extinction under climate warming. This work improved our understanding of mechanisms behind thermal adaptation and predicted potential responses of trophic interactions under climate change.

MATERIALS AND METHODS

Study site and field sampling

Our study site is in Xishuangbanna Nature Reserve, Yunnan, China, (21°54′N, 101°46′E) between 600 and 800 m a.s.l. (Figure 1). The vegetation in our study site is seasonal evergreen tropical rainforest with over 400 tree species dominated by *Parashorea chinensis* (Dipterocarpaceae), reaching to a ~60 m tall emergent layer (referred to canopy in our study hereafter; Cao et al., 2006). We sampled from late April to May and from late Oct to Nov in 2019 and 2020. These two periods are similar in rainfall, but April–May is hotter than Oct–Nov, and thereafter they are referred to as hot season and cool season, respectively, throughout the text (Figure 1). We searched for larval lepidopteran herbivores (leaf miners, leaf rollers, free feeders) from *P. chinensis* both in the canopy and ground saplings.

We used a canopy crane to access different parts of tree canopies within the area the crane can reach (11,304 m^2; Nakamura et al., 2017). We selected eight *P. chinensis* trees and searched for herbivores by visually checking leaves in a standardised method (Supporting information). We repeated the same sampling protocol twice during hot season in 2019 (total 72,295 leaves sampled). We also repeated the canopy sampling in cool season, but no young leaves

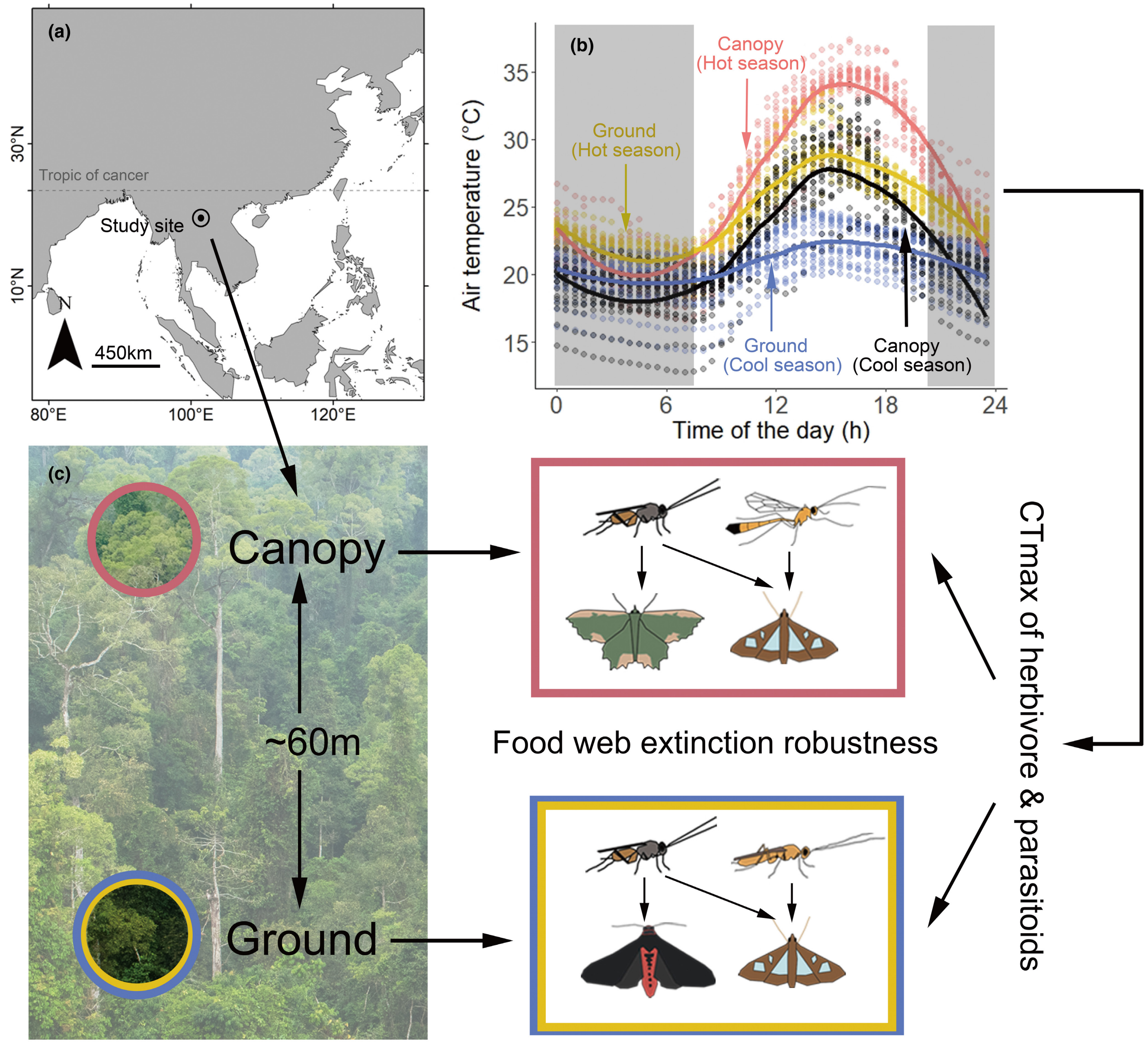

FIGURE 1 Study site (Xishuangbanna nature reserve, Yunnan, China) (a); daily temperature change and variation (lines represent the means, dots are daily raw data lasted for 21 days and grey shadowed areas indicate nights) among forest layers (canopy and ground) and seasons (hot season: Apr–May; cool season: Oct–Nov) (b); and sampling of canopy and ground food webs (lepidoptera herbivores & parasitoids) and CTmax of each organism from different seasons (c). Lines, circles and rectangles in red pink, yellow and blue colour represent canopy hot season, ground hot season and ground cool season respectively. Black line in (b) indicate temperature data from canopy cool season where we found no herbivores and parasitoids.

were present in the canopy, and we found no herbivores during the pilot survey (totalling 3542 leaves from nine branches in three trees), so we excluded canopy samples in cool season. For the ground layer, we visually searched all the saplings in our study site shorter than 2 m both in hot (2020; 130,472 leaves) and cool season (2019; 52,320 leaves). During our sampling we also recorded air temperature at canopy and ground level (hot and cool seasons) every 30 min with four data loggers (HOBO U23-001; Onset, USA) from the sun-shielded microclimate weather station installed at 60 m and 1.5 m above ground near the canopy crane tower.

Lab rearing and heat tolerance experiments

We reared herbivores in plastic containers to adults or parasitoids in a field laboratory. We kept the containers at constant temperature with air conditioning. In the hot seasons, our rearing temperature was 26°C and in the cool seasons it was 23.5°C. We selected these temperatures to represent the average natural temperature they experienced in the field to maximise rearing success. Given that CTmax represents long-term evolutionary acclimatisation, and short-term acclimation ability of CTmax in tropical arthropods is often minimal (Seebacher et al., 2015; Kellermann & Sgrò, 2018; Morley et al., 2019), adult CTmax bias induced by rearing temperature is therefore unlikely. Our rearing success rate is higher than 60% and was similar between seasons and forest layers (Supporting information).

We tested the heat tolerance of herbivores and parasitoids ~12 h after emerging using a Grant-TX200 water bath (accuracy 0.01°C). We tested the adult stage because CTmax could be influenced by other confounding factors that are difficult to control during larvae stages (Box 1). We placed individual herbivore and parasitoid into airtight 40 ml transparent containers. We began the experiments at 30°C with a ramping rate of 0.2°C min^{-1} (Box 1; Boyle et al., 2021). We recorded the temperature at which each herbivore or parasitoid individual lost muscle movement as its critical maximum temperature (CTmax). This temperature did not represent physical death but ecological death as they could recover afterwards.

We generated two sets of CTmax values: first set used observed CTmax values from individual insects, and the second set we assigned the maximum CTmax recorded for a given species to all individual insects that belong to that same species. The second set of data represents the highest heat tolerance that any individuals of a species could achieve, and test results from this maximum CTmax metric could be interpreted as the potential plasticity of a given species (of the populations we collected) in response to increasing temperature. To better compare vulnerability of the species under warming, we also calculated 'Thermal Safety Margins (TSM)', as the difference between CTmax of individual insects and the mean air temperatures (Clusella-Trullas et al., 2021). We averaged air temperatures for each forest stratum in each season during our sampling periods. We calculated maximum TSM using the maximum CTmax values of individual species to account for the potential plasticity in a similar way as maximum CTmax. It should be noted that although TSM is useful in comparing relative vulnerability, the absolute TSM values have limited biological inference (Clusella-Trullas et al., 2021).

Species identification and body size measurements

We separated herbivores and parasitoids into morphospecies based on adult and larval morphological features and verified with taxonomic literatures (Table S1) and DNA barcoding. (Supporting information). We assessed the body size of herbivores and parasitoids, by measuring thorax width with a 0.01 mm calliper. We used thorax width as body size proxy as it is more stable (body length often shrinks due to water loss) and biologically relevant (e.g. wings cannot perform thermoregulation in our experimental conditions).

BOX 1 Standard measurements of critical thermal maximum (CTmax)

CTmax provides valuable ecological information only when measuring methodology are standardised and comparable. Apart from the extrinsic and intrinsic factors we tested here, other factors such as ontogeny (Kingsolver & Buckley, 2020), body condition (Rezende et al., 2011), parasitism (Mutamiswa et al., 2018) could also affect CTmax measurements in our study. Using newly emerged adults instead of wild-caught caterpillars accounted for these potential biases.

In addition, ramping speed (the rate of temperate rising) is also important in CTmax measurements. Faster ramping speed will produce higher CTmax, and large-bodied insects heat up more slowly than small ones, resulting higher heat tolerance readings for larger bodied insects, while slow ramping speed may prolong the experiment duration and cause insects to collapse by suffocation (Rezende et al., 2011).

We tested our 0.2 °C min^{-1} ramping rate with pilot runs on a large-bodied sphingid moth (Thorax dimension 9 × 15 × 8 mm) and found that this slow ramping rate maintained the same temperatures across the container, the insect and the water, minimising the potential bias of thermal inertia caused by different body sizes. We also ensured the ramping speed was not so slow (<1.5 h) that insects were killed by suffocation (moths with same setting in room temperatures survived for at least 6 h). We also monitored the relative humidity inside each container during heat tolerance experiments with iButton data loggers (DS1923, USA) and found 95% relative humidity during our experiments, allowing us to rule out desiccation as a confounding factor.

Microclimate and intrinsic factors on CTmax

To test whether species experiencing hotter microclimates (generated from vertical stratification and seasonality) have higher CTmax, we assessed the phylogenetic signal in heat tolerance metrics among herbivores and parasitoids. We used Phylogenetic Generalised Least Squares (PGLS) models with forest layer, season, body size and the interaction between layer and season as fixed explanatory variables and species identity as a random factor. Since the herbivores were reared under similar conditions to buffer the potential influence of local environments, we did not use geographical locations (e.g. tree identity) that could potentially produce short-term microclimate differences as random factors. Since we did not find herbivores in the canopy layers during cool season, we did not force an interaction term between season and forest layer, as the missing data (absence of data in the canopy cool season) cannot validate the direction of the identified interactions.

We built phylogenetic trees of our herbivores and parasitoids with measured CTmax for PGLS analysis. For herbivores, we obtained phylogenetic relations and divergence times using the phylotranscriptomic reconstruction from Kawahara et al. (2019), which included all major lepidopteran lineages. We trimmed the phylogenetic tree to remove species not presented in this study and species with no CTmax data. For species not available in the tree, we used the closest related species following recent family level phylogeny works (Murillo-Ramos et al., 2019; Wang et al., 2015; Zahiri et al., 2012; Figure S1). For parasitoids, we followed the only coarse backbone phylogeny available (Branstetter et al., 2017) and calibrated with family level phylogeny (Bennett et al., 2019; Li et al., 2016; Stireman III et al., 2019; Zhang et al., 2020; Figure S2).

In the PGLS analysis, we used CTmax, maximum CTmax, TSM and maximum TSM as response variables separately. For each of these four response variables, we separately tested herbivores and parasitoids, as their evolutionary history are very distant from each other (different Orders) and not informative. Since the resolution of phylogenetic trees for parasitoids and herbivores are different, we also performed the PGLS analysis for herbivores separately with family-level phylogenetic tree to examine the effect of tree resolution. The influence of phylogenetic relationships was estimated by calculating Pagel's λ optimised using maximum-likelihood transformation. Pagel's λ is a measure of the phylogenetic signal of the residuals of the PGLS models. For this, our models considered cases of Brownian model of evolution ($\lambda = 1$; expected phenotypic divergence is proportional to divergence time) and star phylogeny ($\lambda = 0$; no correlation between species) (Freckleton et al., 2002; Pagel, 1999). We compared candidate models with Akaike's information criterion (AIC; the lower the AIC estimate, the higher the fit of the model). We used R packages APE (Paradis et al., 2004) and caper (Orme et al., 2013) for phylogenetic analyses.

Heat tolerance comparison between trophic levels

To assess the potential influence of climate change at different trophic levels, we used the same dataset as previous analysis and compared CTmax, maximum CTmax, TSM and maximum TSM separately. We fitted Generalised Linear Mixed Models (GLMM) with the R package lme4, including trophic level (herbivore and parasitoid) as explanatory variables and forest layer and season as random factors. Since our herbivores (Lepidoptera) and parasitoids (Diptera and Hymenoptera) are from different orders and distantly related, phylogenetic signals are unlikely to be strong enough to shape heat tolerance traits so we did not include a phylogeny component to preserve model simplicity (de Bello et al., 2015).

Vulnerability of herbivore–parasitoid interactions under warming

To estimate the vulnerability of herbivore–parasitoid interactions, we built quantitative food webs using parasitism incidences for each forest layer and season. Since our DNA barcoding results found the morpho-species approach effective in identifying caterpillar species, we used the abundance of caterpillar morpho species with multiple individuals and the number of caterpillars from which adult parastioids emerged, to assemble quantitative herbivore–parasitoid food webs (Supporting information).

We used two approaches to examine the vulnerability of herbivore–parasitoid interactions under future warming. First, because greater species overlap between seasons and forest layers would indicate higher chances of species survival if they could shift their phenology or forest stratum, we used species overlap across seasons and forest layers as an indirect qualitative way to infer the possibilities of network 'rewiring' (Bartley et al., 2019). To quantify the sampling completeness of herbivores and parasitoids, we calculated sampling coverages with R package 'iNext' for different forest layers and seasons (Hsieh et al., 2016). Since we obtained a high coverage of herbivores and only three networks (i.e. canopy hot, ground cool and ground hot seasons), we directly used Venn's graph with R package 'VennDiagram' to illustrate the species overlap between seasons and forest layers (Chen & Boutros, 2011).

If potential food web rewiring is unlikely to occur, we then tested whether variation in TSM among herbivore species would change the stability of food webs under warming, which results in network loss and subsequent species extinction. Since decreases in herbivore populations will lead to a decreased parasitoid population more than the other way around, we simulated extinction of herbivores to see how this would affect the existence of parasitoids and network stability (secondary extinction: Memmott et al., 2004). We built three weighted (with abundance) bipartite networks (i.e. canopy hot, ground cool and ground hot seasons) with known TSM. We calculated a metric called 'robustness' in R package 'bipartite' (Dormann et al., 2008). Robustness with the lowest value (0) indicates an unstable food web where loss of one herbivore host species will lead to the loss of all network nodes and, subsequently, all parasitoid species, whereas the highest value (1) indicates a robust, stable food web where parasitoid species do not become extinct until all of the herbivore species become extinct (Burgos et al., 2007). We simulated the herbivore extinction based on: (1) realistic extinction sequence of the species with the lowest to highest TSM (we used mean and maximum TSM of each species), (2) random selection of species from the least abundant to the most common using null model approach (Burgos et al., 2007). Null models that randomly generate networks with specific ways (in our case, from the least to most common species) have been widely used in network analysis to control the uncertainties by limited sample sizes (Dormann et al., 2009). We ran the null model 10,000 times and compared the distribution of the null model robustness values against those obtained from more realistic extinction scenarios. We chose the function 'vaznull' to generate our null model (Vázquez et al., 2007). We compared robustness values between realistic extinctions and randomly selected extinctions for each of the three networks separately.

RESULTS

Field data summary

The microclimates between different seasons and forest layers were distinct with higher and more variable temperatures recorded in the forest canopy than ground. Daily air temperature (Mean ± SE) in the canopy layer during our sampling was 26.34 ± 5.54°C, the ground layer was 24.57 ± 3.08°C in hot season and 20.75 ± 1.90°C in cool season. Corresponding mean daily maximum air temperatures were 34.82 ± 1.42, 30.07 ± 1.87 and 22.82 ± 1.47°C (Figure 1).

In total, we collected 204 species of herbivores ($N = 875$; canopy hot 233, ground hot 285, ground cool 357) and 53 species of parasitoids ($N = 165$; canopy hot 70, ground hot 18, ground cool 77). These represent over 90% of the herbivore assemblages found on *Parashorea chinensis*, and over 50% for parasitoids according to rarefaction curves (Figure S3). Our rearing success rates (proportion of caterpillars developed into adults and parasitoids) were similar between forest layers and seasons. (61.03% in canopy hot season, 62.25% in ground cool season, 65.96% in ground hot season). CTmax was finally assessed for 124 species of herbivores ($N = 455$) and 32 species of parasitoids ($N = 139$).

Microclimate and intrinsic factors on CTmax

Our four heat tolerance metrics (CTmax, maximum CTmax, Thermal Safety Margin-TSM and maximum TSM) showed very strong phylogenetic signals ($\lambda > 0.87$) for both herbivores and parasitoids, except for CTmax and TSM in parasitiods (Table S2).

For all the PGLS candidate models, all the best models included phylogenetic component (herbivore: Tables S3–S6; parasitoid: Tables S7–S10). Results from the best models showed that for herbivores, season and forest layer significantly affected all of our four metrics. For herbivores, both CTmax and TSM were lower in the canopy than ground in hot season. Seasonal differences of the ground herbivores showed lower CTmax but higher TSM in the cool season. Body size (i.e. thorax width) also showed strong phylogenetic signal and was positively correlated with all the metrics except maximum TSM (Table 1; Figure 2a,b; Figure S4a,b). Parasitoids showed similar results to those found in herbivores. However, season and forest layer were not significant for maximum CTmax and body size showed no significant influence on mean CTmax, mean TSM and maximum TSM (Table 2; Figure 2c,d; Figure S4c,d). PGLS analysis with a family-level phylogenetic tree of the herbivores produced similar results except for the relationship with body size in maximum CTmax and maximum TSM (Tables S11–S15).

Heat tolerance comparison between trophic levels

Within the same season and forest layers, herbivores had 2.03–2.57°C higher CTmax (95% CI; $F_{(1,590)} = 282.92$, $p < 0.0001$, Figure 2c), 2.03–2.56°C higher maximum CTmax (95% CI; $F_{(1,590)} = 281.46$, $p < 0.0001$, Figure S4c) compared with parasitoids. Herbivores also had 1.34–1.85°C wider Thermal Safety Margin (95% CI; $F_{(1,590)} = 153.23$, $p < 0.0001$, Figure 2d), and 1.33–1.84°C wider maximum Thermal Safety Margin (95% CI; $F_{(1,590)} = 152.32$, $p < 0.0001$, Figure S4d) compared with parasitoids.

Vulnerability of herbivore–parasitoid interactions under warming

Species overlaps between different forest layers and seasons were low for both herbivores and parasitoids (Figure 3a), and the shared connections between our three networks were very low with only one incidence where one parasitoid species was found in both hot and cool seasons (Figure 3b).

Null models from extinction simulations found removing species randomly produced similarly moderate robustness values across three food webs (Figure 3c). Food webs in the canopy hot season and ground cool season have lower robustness value when species are removed based on decreasing TSM values than when they were removed randomly. However, this was not the case for the food web in the ground layer during the hot season. In addition, simulation using maximum TSM increased robustness of the food webs in the canopy hot season. However, robustness value was even higher for ground hot season using mean instead of maximum TSM, and no differences between the mean and maximum TSM in ground cool season. (Figure 3c).

TABLE 1 Significance of the variables included in the best GLS models (df = 1447) for herbivores and their coefficients

Response variables	Explanatory variables	Coefficients	SE	*F*-value	*p*-value
Herbivore CTmax	Body size	0.32	0.07	33.91	<0.0001***
	Season (cool, hot)	−1.47	0.17	39.17	<0.0001***
	Forest layer (canopy, ground)	−1.11	0.16	48.02	<0.0001***
Herbivore Maximum CTmax	Body size	0.13	0.05	11.14	0.0009***
	Season (cool, hot)	−0.417	0.16	6.64	0.0103**
	Forest layer (canopy, ground)	−0.45	0.17	23.60	<0.0001***
Herbivore Thermal Safety Margin	Body size	0.32	0.07	18.33	<0.0001***
	Season (cool, hot)	2.35	0.17	680.58	<0.0001***
	Forest layer (canopy, ground)	−2.89	0.16	321.04	<0.0001***
Herbivore Maximum Thermal Safety Margin	Body size	0.13	0.05	1.78	0.1822
	Season (cool, hot)	3.40	0.16	1553.17	<0.0001***
	Forest layer (canopy, ground)	−2.22	0.16	365.64	<0.0001***

Note: All the best models included phylogenetic component (lambda = 1). Significant codes: $***p<0.0001$, $**p<0.01$.

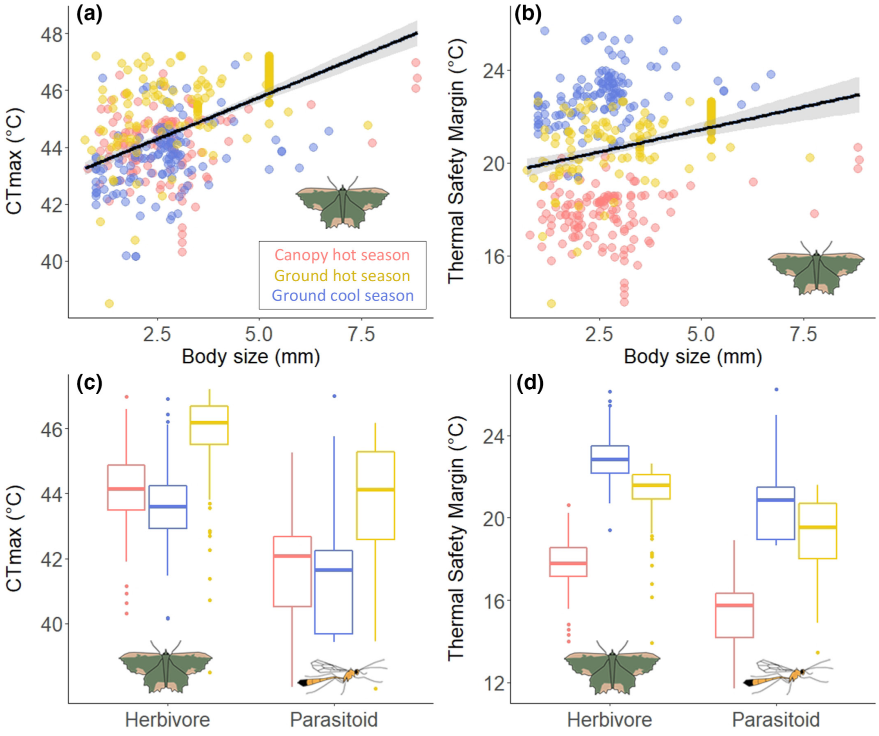

FIGURE 2 CTmax (a, c) and thermal safety margins (b, d) of herbivores and parasitoids from different forest layers and seasons. Shapes in red pink indicate data from canopy hot season, in yellow indicate ground hot season, in blue indicate ground cool season. Lines in a, b are fitted linear models with shadow areas representing 95% CI. Detailed results are in Tables 1 and 2. Maximum CTmax and maximum thermal safety margin results are similar and shown in Figure S4.

DISCUSSION

Microclimates affecting heat tolerance

Our findings partially support our first hypothesis, indicating that microclimate differences are important in shaping heat tolerances in tropical forest ectotherms. Species sampled in the hot season had a higher heat tolerance than those in the cool season. Microclimate differences have been found to affect thermal tolerance in other ectothermic groups (butterflies: Montejo-Kovacevich et al., 2020; ants: Bujan et al., 2020; amphibians: Pintanel et al., 2019; lizards: Herrando-Pérez et al., 2019). Specifically, rainforest ants inhabiting the canopy (hotter microclimates) were characterised by higher heat tolerances compared to ants in cooler understories (Kaspari et al., 2015). However, our findings showed a counter gradient signal (lizards: Hodgson & Schwanz, 2019; insects: Oliveira et al., 2021)

TABLE 2 Significance of the variables included in the best GLS models (df = 1135) for parasitoids and their coefficients

Response variables	Explanatory variables	Coefficients	SE	*F*-value	*p*-value
Parasitoid CTmax	Body size	0.48	0.28	3.24	0.07
	Season (cool, hot)	−1.61	0.55	4.05	0.046*
	Forest layer (canopy, ground)	−1.66	0.71	5.52	0.02*
Parasitoid Maximum CTmax	Body size	0.56	0.05	8.38	0.004**
	Season (cool, hot)	−1.02	0.16	2.23	0.14
	Forest layer (canopy, ground)	−0.94	0.16	2.30	0.13
Parasitoid Thermal Safety Margin	Body size	0.48	0.28	3.12	0.08
	Season (cool, hot)	2.20	0.54	60.09	<0.0001***
	Forest layer (canopy, ground)	−3.44	0.71	23.44	<0.0001***
Parasitoid Maximum Thermal Safety Margin	Body size	0.56	0.20	1.28	0.26
	Season (cool, hot)	2.79	0.48	127.12	<0.0001***
	Forest layer (canopy, ground)	−2.71	0.62	19.14	<0.0001***

Note: All the best models included phylogenetic component (lambda = 1). Significant codes: ***$p<0.0001$, **$p<0.01$, *$p<0.05$.

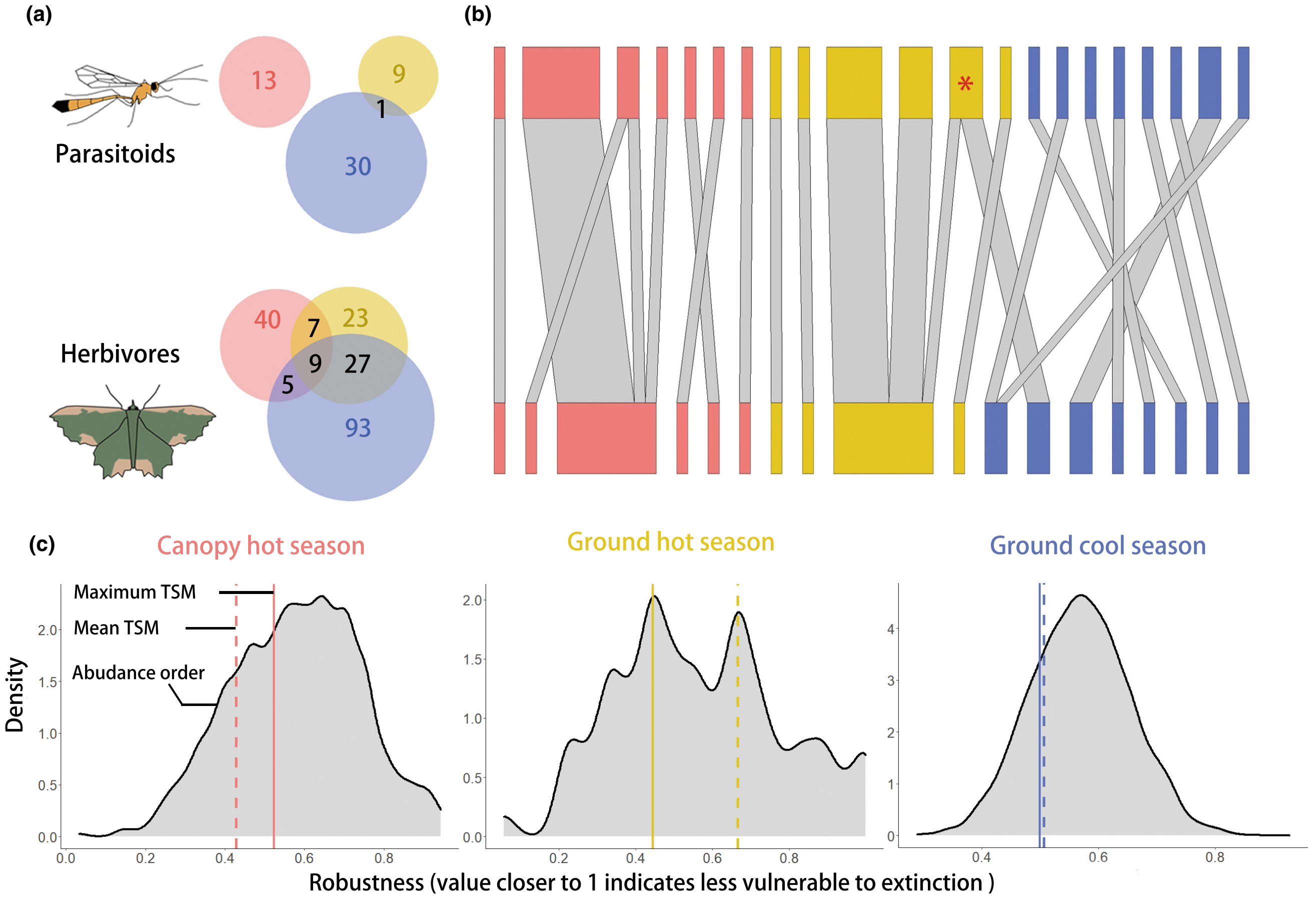

FIGURE 3 Species overlap (a) and the quantitative bipartite food webs (b) of parasitoids (upper) and herbivores (lower) from the canopy hot season (pink), ground hot season (yellow) and ground cool season (blue). Extinction robustness based on mean thermal safety margins (TSM) (dashed lines) and maximum thermal safety margins (TSM) (solid lines) in comparison to robustness values generated from abundance order-based extinctions (null models) (c). Numbers in (a) represent number of species. Colour code in (a–c) represent same seasons and forest layers. Red aster in (b) indicates the only shared species between ground layer hot season and cool season. The food webs in (b) show interactions used for the robustness analysis (c). Density curves in (c) are from null models ran 10,000 times. Because we were unable to measure CTmax for singleton herbivores with parasitoids, we were unable to carry out food web extinction analysis with all the species collected. (canopy hot season food webs included eight parasitoid species reared from six herbivore species, ground hot season included six parasitoid species reared from four herbivore species and ground cool season included nine parasitoid species reared from eight herbivore species.

where hotter canopy ectotherms have lower heat tolerances. This trend may be due to the phylogenetically conserved CTmax and the limited species overlap identified between forest layers. However, the observed counter gradient patterns could also reflect organismal constraints for species from hotter microclimates (e.g. limited physiological plasticity; Kellermann & Sgrò, 2018; Morley et al., 2019; Seebacher et al., 2015). Here, maximum CTmax and maximum TSM did not change the overall heat tolerance patterns (within the populations we sampled). This suggests that even if individual insects can increase their CTmax to the maximum value of the same species we recorded, the overall heat tolerance patterns across microclimate gradients would not change. On the other hand, behavioural thermoregulation (e.g. microclimate selection) might be the main strategy to cope with the heat, and to buffer selection pressure for physiological tolerance (Huey et al., 2003; Wenda et al., 2021). The lower CTmax in canopy species we found may represent more dependence on behavioural thermoregulation, which could not be accounted for in laboratory-based CTmax experiments (Hodgson & Schwanz, 2019; Oliveira et al., 2021).

Intrinsic traits affect thermal tolerance

Intrinsic traits are also crucial in driving heat tolerance and CTmax of ectotherms. After controlling for strong phylogenetic signal, we identified body size as important predictor of CTmax for herbivores but not parasitoids, with larger herbivores more tolerant to heat (Second hypothesis). Limited body size variation might contribute to the insignificance influence of this trait on CTmax in parastioids. Studies have shown organisms with different body sizes have different metabolic rates, and smaller ectotherms during short periods of heat exposures (a few hours) survive better (Boyle et al., 2021; Klockmann et al., 2017; Leiva et al., 2019; Peralta-Maraver & Rezende, 2021), contradicting with our findings. The positive relationship between CTmax and herbivore body size is unlikely due to methodological biases and overestimation of CTmax in large-bodied insects, as our experimental settings allowed simultaneous change in temperatures between the water and the insect bodies cores regardless of insect sizes (see text Box 1; Rezende et al., 2011). The mechanisms behind our size-CTmax relationship need further investigation.

Climate change effects on food webs

Our results show parasitoids have lower heat tolerance and narrower TSMs than their herbivore hosts. Lower heat tolerance in higher trophic levels has also been identified in other ectothermic groups (Boyle et al., 2021; Furlong & Zalucki, 2017; Montserrat et al., 2013; Voigt et al., 2003; but no difference in Franken et al., 2018). The mechanism behind is largely unknown (Voigt et al., 2003). It is possible that heat tolerance differences between trophic levels were driven by body size differences, since parasitoids are usually smaller than their herbivore hosts. Dietary and metabolic rate differences may be alternative explanations (Bujan & Kaspari, 2017). Higher vulnerability of parasitoids under heat was also supported by studies of parasitoid larvae development and behaviours (Moore et al., 2021; Quenta Herrera et al., 2018).

Top-down control is important in regulating herbivore populations, especially in the tropics (Rodríguez-Castañeda, 2013; Roslin et al., 2017; but see Wenda et al., 2022). Considering the high vulnerability under heat identified for higher trophic levels, we predict that predation pressure from parasitoids could be released under warming, causing heat-resilient herbivores to increase their abundance. This can potentially cause a cascading effect on host plants and tropical ecosystem functions (Coley, 1998; Marino et al., 2018). It is important to highlight that parasitoids interact with herbivores during caterpillar stage, when herbivore CTmax are generally found to be higher than adults (Bawa et al., 2021; Mutamiswa et al., 2018). This cascading effect might be more serious given the wider heat tolerance mismatch between the trophic levels.

Apart from the trophic level differences in heat tolerances, we found heat tolerance variation within trophic level could also affect the stability of the networks. Although comparing the vulnerabilities to warming among our three food webs is not our goal here, two out of the three networks showed that removing species randomly by their relative abundance overestimated food web robustness to extinction. Herbivore–parasitoid networks in the canopy (hot season) and ground (cool season only) are highly vulnerable if extinction occurs according to the TSM of individual species. In addition, studies have shown extinctions produced by randomly generated null models tend to underestimate robustness compared to realistic extinction events with additional ecological information (Dormann et al., 2009; e.g. temperate lake predator–prey food webs: Srinivasan et al., 2007). Although we do not have enough food web level replicates to test statistically how our null-model generated extinction potentially underestimates robustness values, we suspected the differences between realistic extinction and our heat tolerance-based robustness values would be wider than we identified.

Higher vulnerability of canopy species under climate change

Apart from the three hypotheses tested, our results also suggest higher risks under climate change for species inhabiting the canopy (hot season) in tropical rainforests, in line with other single trophic level studies (Kaspari et al., 2015; Leahy et al., 2022; Mau et al., 2018). Canopy herbivores and parasitoids in the cool season were entirely absent or occurred in very low densities due to the phenology of our host tree. The low overlap of herbivore and parasitoid assemblages between canopy hot season and ground cool season suggests that these species did not shift vertically to the ground layer during seasonal changes. Examination of our canopy herbivores in the hot season showed that at least 61% (the rest without enough data to classify) are polyphagous and feed on diverse tree species (unpublished data). We suspect these canopy herbivores and associated parasitoids occurring during the hot season may diapause or move horizontally to feed on other canopy tree species with young leaves (Janzen, 1993). This lack of vertical movement together with the different morphological and physiological traits between canopy and understory leaves may have facilitated the stratification of insects and food webs into separate canopy and ground species, as we previously found at this location in adult moths (Ashton et al., 2016), challenging their abilities to use the cooler microclimates provided by forest understories under climate change (Basham & Scheffers, 2020).

More importantly, we found strong phylogenetic signal in CTmax, especially for herbivores, suggests the importance of species evolutionary background in shaping the community heat tolerance (Diamond et al., 2012; Kaspari et al., 2015). Lineages of herbivores and parasitoids that share the same evolutionary history may be entirely wiped out by temperature related extinction and cause high risk of ecosystem services due to climate change in the forest canopy (Díaz et al., 2013).

Limitations

Our study was facilitated by the use of a canopy crane and in a well-studied forest. Detection of species interactions is in general more difficult than detecting species (Goldwasser & Roughgarden, 1997), especially for tropical forests with high diversity. This was reflected by our high coverage of herbivores but only half coverage of parasitoids from rearing. Food web structure may have changed if we reared more parasitoid species. However, the null model approach we used controls for the uncertainty from low sample size (Dormann et al., 2009), and studies found weighted quantitative metrics (e.g. robustness we calculated here) were less sensitive to insufficient sampling of species interactions than qualitative metrics from both simulation (Banašek-Richter et al., 2004) and empirical study (Tylianakis et al., 2007).

Our herbivores were from a single plant species (*P. chinensis*) from one site, lacking the generality of our implications across different tree species and locations. However, as both generalist and specialist herbivores interact with common plants (Bascompte & Jordano, 2007), the dominant role this tree species plays in the local plant community suggests our pattern may well represent the herbivore–parasitoid interactions in this forest system. Despite seasonal evergreen rainforest dominated by Dipterocarpaceae similar to our site is one of the major vegetation types in mainland southeast Asia (Brearley et al., 2016), further sampling across forest types and biogeographical regions is required to better understand herbivore–parasitoid responses to climate change.

CONCLUSIONS

Increased overheating stress is one of the major mechanisms organisms suffered from climate change and communities of interacting species are responding in different ways to climate change, however our understanding is limited often to temperate systems or only a few interacting species. Our study provides new understandings of the heat tolerance of interacting herbivores and parasitoids in a species-rich tropical ecosystem. We showed extrinsic thermal environments (microclimates) and intrinsic traits all affected species heat tolerance in tropical rainforests. Including heat tolerances variations among species and trophic levels have produced a higher vulnerability of canopy species and herbivore–parasitoid food web stability under climate change than previously assumed. This can potentially cause releases in top-down control of herbivores and cascading effect on the whole tropical forest ecosystem. We highlight the vulnerability of herbivory, an important ecological process in tropical rainforests, especially in the forest canopies. Prioritising climate change impact studies on the most sensitive tropical canopy organisms will enable us to read the early warnings of temperature rise on complex ecosystems, enabling us to better understand climate change impact on the ecosystem as a whole and take proper mitigation approaches.

AUTHOR CONTRIBUTIONS

Cheng Wenda and Louise A. Ashton conceived the idea. Cheng Wenda did the field and laboratory work. Akihiro Nakamura and Bartosz M. Majcher helped the field work and laboratory work. Juan Diego Gaitán-Espitia and Jaiber J. Solano-Iguaran performed phylogenetic analysis. Cheng Wenda did the rest of the analysis and wrote the first draft of the manuscript. All authors contributed substantially to the revisions.

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SUPPORTING INFORMATION

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

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