

RESEARCH ARTICLE

Animal functional traits

Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil palm–forest mosaic

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Abstract

1. Temperature change is an often-assumed, but rarely tested, mechanism by which sensitive species may decline in forest landscapes following habitat degradation, fragmentation and destruction.
2. Traits mediate how species respond to environmental change, with physiological, morphological and behavioural traits key to determining the response of ectotherms to temperature.
3. We collected data on traits linked to thermal sensitivity (critical thermal maxima, body size, cuticle lightness and pilosity) for 46 dung beetle species (*Scarabaeinae*) in a forest–oil palm mosaic in Malaysian Borneo. By combining these data with a large-scale community sampling campaign (>59,000 individuals sampled from >600 traps) and an airborne Light Detection and Ranging-derived thermal map, we investigated how traits mediate species- and community-level responses to temperature.
4. Using hierarchical models, we found that critical thermal maxima predicted how species respond to maximum temperatures. These results were mirrored in community-level analyses alongside similar patterns in other thermal traits. Increased body size and decreased pilosity were associated with higher temperatures, while cuticle lightness showed a complex relationship with temperature across the disturbance gradient.
5. Our findings highlight the potential mechanisms by which forest specialists decline in human-modified landscapes, resulting in changes to community patterns and processes.

KEYWORDS

body size, coloration, ctmax, functional traits, LiDAR, oil palm, pilosity, tropical forest

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1 | INTRODUCTION

Temperatures are rising in the tropics, both from rapid land-use change (Senior et al., 2017) and anthropogenic climate change (Malhi & Wright, 2004). Understanding the scale and magnitude of rising temperature effects on biodiversity is more urgent than ever, as regional and local climate change may synergistically drive the decline of sensitive species (Frishkoff et al., 2016). In particular, understanding temperature-related threats to insects is of importance given the key role they play in driving ecosystem functioning, and their reported global declines (Wagner, 2020).

Many tropical forests are highly degraded (Senior et al., 2017) and fragmented (Haddad et al., 2015), with remnant forests varying in their ability to act as microclimatic refugia in hostile agricultural landscapes (Williamson et al., 2021). As such, microclimate varies considerably across oil palm–forest mosaics due to differences in vegetation (Jucker et al., 2018) and/or proximity to habitat edges (Williamson et al., 2021), resulting in a gradient of increasing disturbance and temperature across such landscapes (Jucker et al., 2020). Forests also exhibit a temperature gradient from the floor to the canopy (Hardwick et al., 2015), making lowland tropical landscapes three-dimensional in their thermal complexity.

Insect body temperature, development and physiology are intrinsically and tightly linked to microclimate at a fine scale (Pincebourde & Woods, 2020). Coupled with the fact that in the tropics, ectotherms may already be operating close to their thermal maxima (Deutsch et al., 2008), and that tropical species tend to be isolated from cool refugia and are adapted to limited temperature variation (Wright et al., 2009), the outlook for tropical invertebrates may be bleak. Although many studies have investigated how tropical invertebrates respond to environmental gradients, few have identified the underlying physiological or morphological traits, such as critical thermal limits, body size or cuticle lightness, that may predict the response of communities to local-scale temperature increases (Bartomeus et al., 2018; Boyle et al., 2020).

Dung beetles are recognised as useful ecological indicators in tropical forests. Not only are their community responses correlated with those of many other taxa, but they can also be sampled with relative ease and at low cost (Nichols & Gardner, 2011), and carry out key ecosystem functions (Nichols et al., 2008). Tropical dung beetle community responses have been linked to temperature gradients associated with land-use, vegetation and topography (Gebert et al., 2019; Larsen, 2012; Williamson et al., 2021). Thermal niche differentiation is an important factor influencing variation in dung beetle diversity (Verdú et al., 2007), and recently studies have linked temporal and spatial differences in dung beetle abundance and activity to physiology (Gotcha et al., 2020; Verdú et al., 2019). Critical thermal maxima (CT_{max}) are being used increasingly to demonstrate how invertebrate physiology is linked to responses to microclimate in tropical forests (Boyle et al., 2020; Kaspari et al., 2015), and to investigate dung beetle ecology across different biomes (e.g. Gotcha et al., 2020; Machekano et al., 2021; Sheldon & Tewksbury, 2014; Verdú et al., 2019). That said, studies to-date on dung beetle CT_{max} have been restricted to investigating one or a handful of species

(with the notable exception of early work by Gaston & Chown, 1999), rather than community-level patterns.

Many morphological traits, from exoskeleton thickness (Amore et al., 2017) to coloration (Stanbrook et al., 2021) and body size (Verdú et al., 2006), are thought to influence invertebrate thermal sensitivity. Cuticular lightness is largely dictated by melanin levels (True, 2003). There are different hypotheses for how such melanism can mediate species responses to temperature. First, as darker species absorb more solar radiation, they will be more prevalent in cooler environments (Clusella-Trullas et al., 2007). In contrast, another hypothesis states that with increased solar radiation in hotter environments, darker species will be more prevalent, as they can mitigate the deleterious effects of UV-B radiation (Bishop et al., 2016). Similarly, and finally, as darker individuals also have less permeable cuticles, they are predicted to be dominant in drier (and thus hotter) areas (Law et al., 2020). Indeed, a recent study of ants in Borneo showed that species are darker in the canopy (Law et al., 2020). Different hypotheses are thought to be of varying importance in different systems, however (Bishop et al., 2016; Law et al., 2020; Stanbrook et al., 2021). Similarly, the relationship between body size and land-use change is complex, with different associations depending on taxa, region and study (e.g. Fritz et al., 2009; Nichols et al., 2013; Pocock, 2011). In dung beetles, some studies have found negative associations with body size and disturbance responses (Braga et al., 2013; Gardner et al., 2008), but a recent meta-analysis by Fuzessy et al. (2021) found that body size increased with disturbance, although this pattern was only detected in agricultural landscapes. Finally, hair retards the loss of heat from the body, meaning that in cooler environments, hair density should be greater (Peters et al., 2016). Indeed, pilosity is a useful trait for predicting bee responses to climate change (Peters et al., 2016).

Given that the response of species to environmental stressors can be complex (Parrett et al., 2019; Raine et al., 2018), and that taxa may exhibit similar thermal sensitivities through different combinations of morphological and/or physiological adaptations, resolving broad patterns of trait-mediated responses to temperature can be challenging. Identifying such response patterns is vital, however, if we are to understand how future temperature change will affect community patterns and processes. Indeed, predicting responses to climate change using traits is of paramount importance to tropical entomologists, as the natural histories of most insects are unknown, while traits can be measured from a few individuals (Brousseau et al., 2018).

To investigate the efficacy of physiology as a means of predicting species and community responses to temperature, we collected critical thermal maxima (CT_{max}) for dung beetles (*Scarabaeinae*) in an oil palm–forest mosaic in Borneo. In addition to physiological measurements, we collected body size, cuticle lightness and pilosity data. By combining our trait measurements with community data and Light Detection and Ranging (LiDAR)-derived microclimatic projections of temperature, we investigated how communities and species respond to temperature gradients across the landscape, and

how this is mediated by their traits. Based on previous studies, we hypothesised that species with more positive associations with temperature would exhibit higher CT_{max} (Boyle et al., 2020) and lower pilosity (Peters et al., 2016). We expected that dung beetle body size and cuticle lightness would mediate species responses to temperature in our study landscape, but were unsure as to the directionality of the relationship due to competing hypotheses in the relevant literature (body size—Gardner et al., 2008; Fuzessy et al., 2021; cuticle lightness—Bishop et al., 2016; Law et al., 2020; Stanbrook et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Study site

All work was carried out across, or in close proximity to, the Stability of Altered Forest Ecosystems (SAFE) project (116.57'E–117.42'E, 4.38'N–4.46'N), a large-scale fragmentation experiment in Sabah, Malaysian Borneo with standardised sampling points across the landscape in both oil palm plantation and forest (Ewers et al., 2011). The natural vegetation of the area is lowland dipterocarp forest that underwent selective logging in the 1970s, and in some areas, a second round of selective logging in the 2000s (Struebig et al., 2013) followed by salvage logging in 2013 and 2015. Much of the landscape is now oil palm plantation, with a large tract of continuous logged forest to the north. The climate of the region is relatively aseasonal, although there is a wetter season from October to March. The mean annual rainfall is ~2700mm and mean annual temperature is 26.7°C (Walsh & Newbery, 1999), although Borneo has become hotter since these measurements were taken (Chapman et al., 2020).

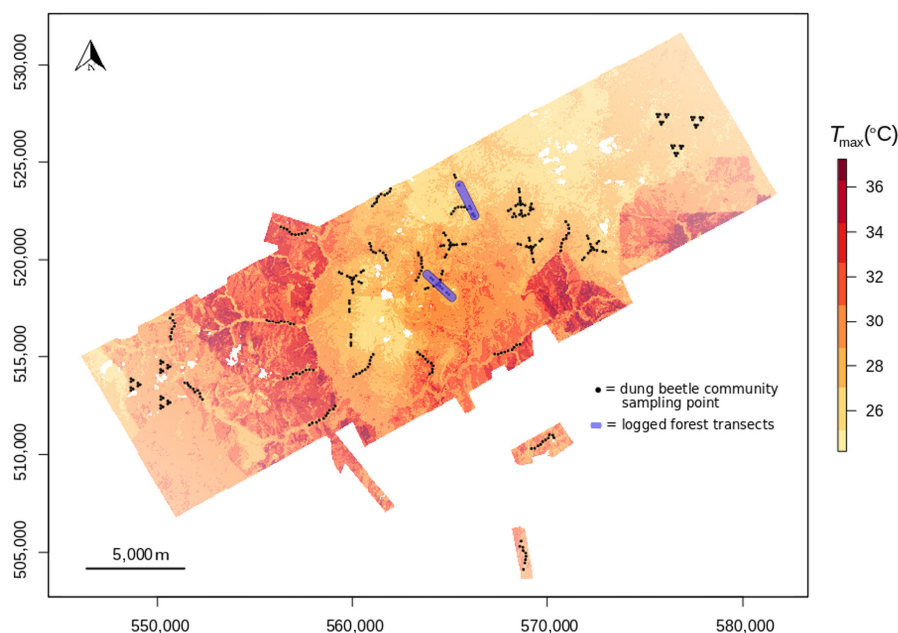
2.2 | Dung beetle community sampling

Standardised 30g human dung-baited pitfall traps (following Slade et al., 2011) were deployed for 48 hr at a time across the study landscape (31 sites in oil palm and forest of varying disturbance levels), in a series of three trapping campaigns in 2011, 2015 and 2017/2018 (hereafter referred to as sampling campaigns, Table S1; Figure 1). All trapping was conducted between September and April to coincide with the marginally wetter part of the year when dung beetles are most active. Traps set in riparian areas were deployed in transects of 10 trapping points spaced approximately 200m apart and on alternating sides of the river (see Williamson et al., 2021). Non-riparian traps were deployed at SAFE second-order sampling points spaced a minimum of 175 m apart (see Ewers et al., 2011). Beetles were stored in 70% ethanol in a freezer and were identified using reference collections at Universiti Malaysia Sabah and Oxford University Museum of Natural History. Samples were collected under permits EPU Ruj. UPE: 40/200/19/2712; MBMC Project No. 129; and SaBC Access Licences JKM/MBS.1000-2/2(381), JKM/MBS.1000-2/2JLD.6(63) and JKM/MBS.1000-2/2JLD.7(83).

2.3 | Dung beetle physiological and morphological traits

To measure dung beetle physiology, we conducted additional sampling targeting both terrestrial and arboreal dung beetles. Terrestrial dung beetles were collected using non-lethal, human dung-baited pitfall traps (following Parrett et al., 2019) along logged forest transects (Figure 1), and two transects in nearby oil palm plantations, between October and December 2017, in September 2018, and in March 2019. Additional aerial traps were

FIGURE 1 LiDAR-derived projections of mean daily maximum temperature (T_{max}) with dung beetle community sampling points. Coordinates are in the universal transverse Mercator system. Critical thermal maximum (CT_{max}) sampling for logged forest was undertaken on individuals from logged forest transects (see below)



set within logged forest to target arboreal species (see Supporting Information, Methods). All traps were baited with 30g of homogenised human dung for 24 hr.

A total of 623 beetles from 46 species ($n = 1\text{--}56$ individuals per species, mean = 13.5, median = 10) were transported to the laboratory and stored in a cool, dark location for a maximum of 4 hr before measuring thermal tolerances. Individuals were placed in 50 ml polyethylene tubes and submerged in a water bath (Grant Instruments TFX200) at 34°C for 5 min. The temperature was then increased by 0.1°C/min up to a maximum of 43.5°C, to minimise delayed responses to temperature increases, but also limit death by desiccation (see Boyle et al., 2020). The critical thermal maximum (CT_{max}) was recorded as the temperature at which muscles started spasming uncontrollably and individuals could no longer right themselves or walk down the tube (see Sheldon & Tewksbury, 2014). A thermocouple ensured temperature lag between tubes and water never exceeded 0.2°C. Ethical approval for the CT_{max} assays was granted by Queen Mary University London's Animal Welfare and Ethical Review Board. All other sampling did not warrant ethical approval.

Three morphological trait measurements expected to be related to the response of beetles to temperature changes were taken. Body length (clypeus to pygidium), lightness and pilosity were measured for 364 beetles of 37 species (all of which had associated CT_{max} data, $n = 1\text{--}40$ individuals per species, mean = 9.8, median = 3) from the 2015 and 2018 riparian trapping campaigns. Measurements were taken in Microsoft Paint using images generated with a Leica M205C stereo microscope with a MC190 HD camera. Lightness was measured as the 8-bit luminance values (0 = black, 255 = white) taken from the front of the pronotum and the back right of the right elytra (Figure S1). Following Roquer-Beni et al. (2020), pronotal and elytral hair density (hairs/mm²) was estimated from a 0.1 × 0.1 mm area on the side of the pronotum and elytra (Figure S1). Pronotal and elytral values were averaged to give a mean lightness and pilosity for each individual.

Functional guilds (daily activity pattern and nesting strategy) were assigned following Gray et al. (2014) and Davis and Sutton (1998) for qualitative comparisons, but were not investigated statistically, due to the strong non-independence of data that arises on account of shared evolutionary history.

2.4 | Statistical analyses

2.4.1 | Interspecific CT_{max}

To assess whether physiological thermal tolerances varied across taxa, we constructed one-way ANOVAs of CT_{max} as predicted by species. Estimated marginal means (EMMs) were used post hoc to compare the CT_{max} of taxa (Tukey-adjusted). Significance was ascertained using likelihood ratio tests (LRTs) through comparison to the respective null model using the *lme4* package (Zeileis & Hothorn, 2002).

2.4.2 | Community trait responses to microclimate

Community-weighted means (CWMs) of CT_{max} , body length, lightness and pilosity were generated for each community sample using the formula:

$$CWM = \sum_i^S p_i x_i,$$

where S is the species richness, p_i is the proportional abundance of a species and x_i is the species mean trait value.

Mean daily maximum temperature (T_{max}) was extracted for each of 629 community samples at 331 unique points from existing data generated by Jucker et al. (2018). Jucker et al. (2018) constructed structural equation models of microclimate using data from ground-based, microclimate sensors as predicted by vegetative (plant area index and maximum canopy height) and topographic (topographic position index, aspect, elevation and slope) airborne LiDAR metrics collected in 2014. Generated models were used to predict microclimate across the SAFE project landscape at a resolution of 50 × 50 m (Jucker et al., 2018). T_{max} was used here over other microclimatic variables as thermal extremes drive species responses to climate change (Vasseur et al., 2014).

We defined separate mixed-effects models of each of the CWM traits (CT_{max} , length, lightness and pilosity) with sampling campaign as a fixed effect, T_{max} or habitat type as a fixed effect and community sampling point as a random effect (to control for repeated sampling and annual differences in climate and forest structure) in *lme4* (Bates et al., 2015). We repeated models without oil palm communities, to ascertain whether landscape-level results were consistent with those of only forest sites. Additive models containing habitat type and T_{max} were not run due to covariance. LRTs were used to compare all models to their respective null model (containing only sampling campaign and sampling point terms). To test the robustness of these models, we also fit a T_{max} and a habitat model for each sampling campaign independently. As sites were not repeatedly sampled within a campaign, these were linear regressions with no random effect of sampling point.

2.4.3 | Linking species' traits to temperature responses

For each species with a total abundance across community samples of >100 individuals, we ran a generalised linear mixed-effects model (Poisson error-family) of species abundance with sampling campaign and T_{max} as fixed effects, and sampling point as a random effect, using the *glmmTMB* package (Brooks et al., 2017). Estimates of the T_{max} coefficient were used as a proxy for species' responses to temperature for subsequent analyses (hereafter referred to as species temperature responses).

To investigate whether species' traits predicted temperature responses, while accounting for phylogenetic relatedness, we

ran generalised linear mixed-effects models using Markov chain Monte Carlo (MCMC) techniques in the *MCMCglmm* package (Hadfield, 2010). We constructed a maximal model of species temperature responses containing CT_{max} , body length, mean lightness and mean pilosity as fixed effects, and a covariance matrix of phylogenetic distance as a random effect (Supporting Information, Methods; Figure S3). Models were iterated 5,000,000 times, with a thinning interval of 500 iterations and a burn-in of 50,000. An inverse-Gamma distribution of the covariate residual variance structure and the random factor were used as uninformative priors ($V = 1, \nu = 0.02$). Each model was run three times with random seeds. Chain mixing was assessed using potential scale reduction factors and the results of the three models were checked for qualitative equivalence. The model with the median deviance information criterion was then selected as representative. Significance was ascertained using p_{MCMC5} (Hadfield, 2010). Non-significant fixed effects were sequentially removed and models were re-fit until a minimum adequate model remained. Posterior distributions, sampling traces and effective sample sizes were examined to assess model fit. To test the robustness of results, we repeated the models using slopes estimated from each sampling campaign independently.

To test whether any of our morphological traits were associated with physiology, we ran a maximal model of CT_{max} as predicted by body length, mean lightness and mean pilosity using the same methods as described for the above temperature response models. All analyses were carried out in R v4.0.5 (R Development Core Team, 2008).

3 | RESULTS

3.1 | Interspecific CT_{max}

We recorded CT_{max} for 623 individuals representing 46 species from 11 genera (Figure 2), making this the most species-rich study of dung beetle CT_{max} to date. CT_{max} varied significantly among species ($X^2_{1,2} = 1,144.9, p < 0.001$, LRT compared to a null model) and genera ($X^2_{1,2} = 598.3, p < 0.001$). Of species and genera where $n \geq 3$, *Oniticellus tessellatus* and *Onthophagus* agg. *pacificus* had the highest and lowest CT_{max} ($42.70^\circ\text{C} \pm 0.31\text{SE}$ and 38.19°C respectively), with *Oniticellus* and *Onthophagus* exhibiting the highest and lowest CT_{max} by genus (42.70 and 39.09°C respectively). *Catharsius dayacus* and *C. renaudpauliani*—sister species that account for the majority of dung beetle biomass across Bornean oil palm–forest mosaics (Gray et al., 2014; Slade et al., 2011)—had different CT_{max} (Tukey-adjusted comparison of EMMs, $p < 0.001$, Figure 3), with the undisturbed-forest specialist *C. dayacus* having a lower CT_{max} than the habitat generalist *C. renaudpauliani* ($CT_{max} = 39.94^\circ\text{C} \pm 0.09$ and $41.56^\circ\text{C} \pm 0.07$ respectively). This difference held true when excluding oil palm plantation samples for *C. renaudpauliani* (logged forest $CT_{max} = 41.23^\circ\text{C} \pm 0.09$, Tukey's HSD test, $p < 0.001$). *Onthophagus trituber* was another noteworthy species, with the second-highest

CT_{max} ($42.57^\circ\text{C} \pm 0.13$) despite belonging to the genus with the lowest mean CT_{max} (Figure 2; see Figure S5).

3.2 | Community trait responses to microclimate

We sampled 59,597 dung beetles in community traps, 59,004 of which belonged to the 46 species with associated CT_{max} data, and 58,658 of which belonged to the 37 species with associated morphological trait data (length, lightness and pilosity).

A T_{max} increase of 1°C was associated with a $0.088^\circ\text{C} (\pm 0.018\text{SE})$ increase in community CT_{max} ($X^2_{1,2} = 23.1, p < 0.001$, LRT compared to a null model, Table S5), resulting in a predicted difference of 0.52°C in community CT_{max} (from 40.27 to 40.79°C , Figure 4) across the T_{max} range of the sampling points (26.29 – 32.28°C). Oil palm communities had a higher CT_{max} than logged forest communities ($X^2_{1,2} = 62.7, p < 0.001$, $40.97^\circ\text{C} \pm 0.07$ and $40.41^\circ\text{C} \pm 0.02$, respectively, Figure 4; Table S5). Community body length also increased with T_{max} ($X^2_{1,2} = 47.2, p < 0.001$, $1.08\text{ mm} \pm 0.15$ per 1°C increase in T_{max} , Table S5, Figure 4) and was predicted by habitat type ($X^2_{1,2} = 88.4, p < 0.001$, $12.31\text{ mm} \pm 0.16$ in logged forest to $18.04\text{ mm} \pm 0.52$ in oil palm plantation, Table S5; Figure 4). Lightness showed a relationship with a second-order polynomial of T_{max} ($X^2_{1,2} = 52.4, p < 0.001$, LRT compared to a model without the polynomial, Table S5), with lightness peaking at intermediate temperatures and with more extreme communities being darker (Figure 4). Lightness did not vary significantly between habitat types (Table S5). Pilosity decreased with T_{max} ($X^2_{1,2} = 18.1, p < 0.001$, $-5.98\text{ hairs/mm}^2 \pm 1.37$ per 1°C decrease in T_{max} , Table S5; Figure 4), and was higher in logged forest than oil palm ($X^2_{1,2} = 54.4, p < 0.001$, $99.65\text{ hairs/mm}^2 \pm 1.53$ and $59.33\text{ hairs/mm}^2 \pm 4.97$, respectively, Table S5, Figure 4). The effect of T_{max} on body length and lightness was comparable when only considering forest sites (Table S6), indicating that these results were not just driven by extreme oil palm communities. Models were robust to being fit on data from single sampling campaigns, with the notable exception of community lightness across habitats, which showed a significantly lighter community in oil palm in 2011, but a significantly darker community in 2015 (Table S7).

3.3 | Linking species traits to temperature responses

Species with more positive associations between abundance and T_{max} had higher CT_{max} when accounting for phylogeny (posterior mean species temperature response = 0.43 , UCI = 0.60 , LCI = 0.24 , $p_{MCMC} < 0.001$, Table S8; Figure 5). CT_{max} was not predicted by any morphological trait when controlling for phylogeny (Table S9). CT_{max} and body length had phylogenetic signal; temperature responses, lightness and pilosity did not (Table S4). Models using data from a single trapping campaign did not show associations between species traits and temperature responses, although this could be due to a loss of statistical power, as the posterior means of CT_{max}

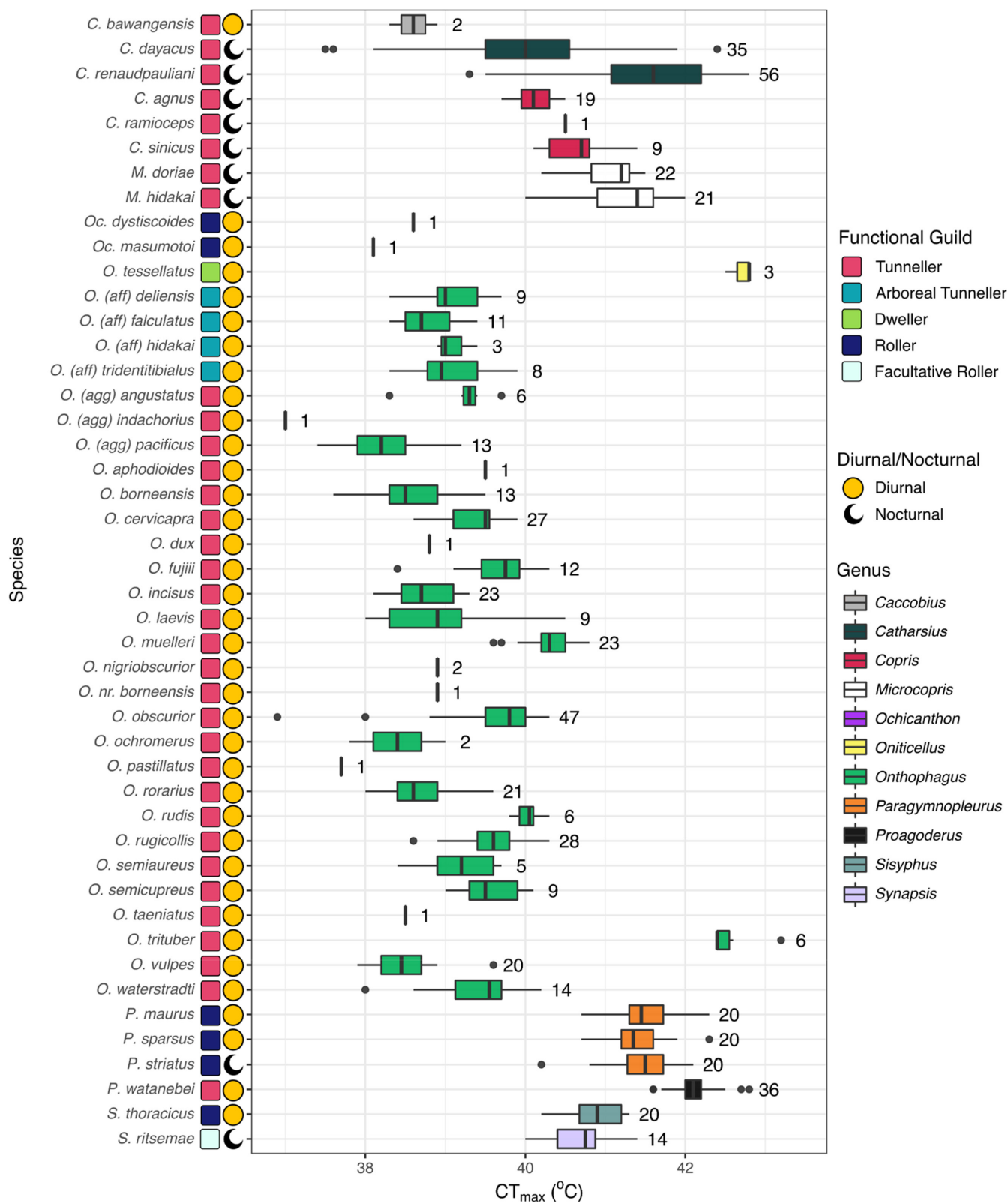


FIGURE 2 Boxplots of mean dung beetle critical thermal maxima (CT_{max}). Boxes are composed of the median and hinge values (25th and 75th percentiles), with whiskers of \pm interquartile range $\times 1.5$. Data outside of this range are denoted by black circles. Numbers beside boxplots denote sample sizes. Species are grouped by genus

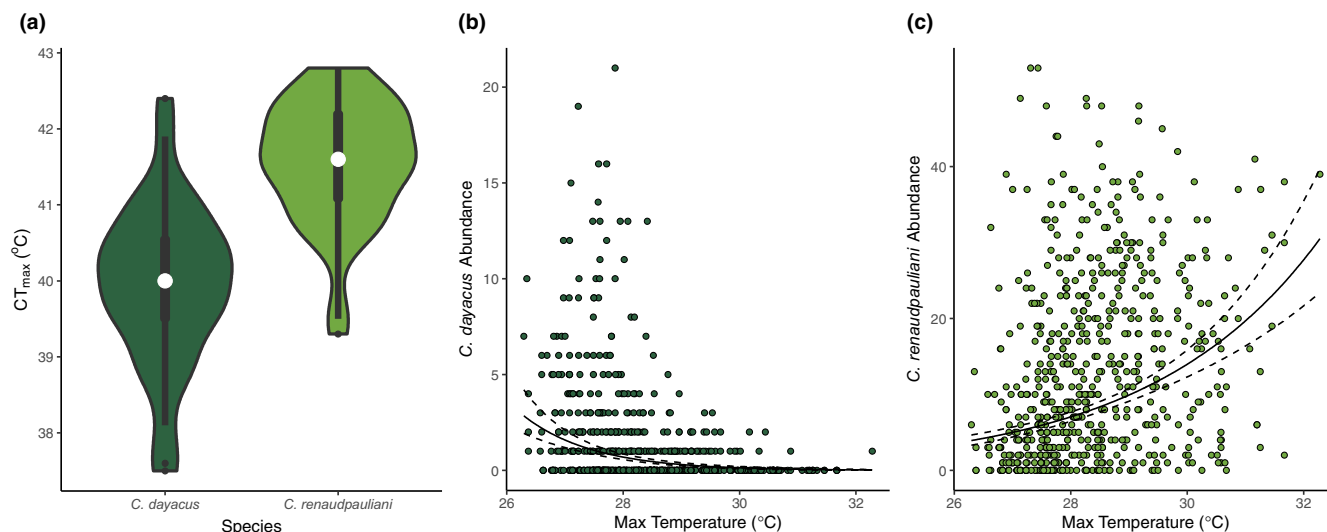


FIGURE 3 (a) Violin plots of critical thermal maxima (CT_{max}) of sister species *Catharsius dayacus* and *C. renaudpauliani*. CT_{max} differed between the two species (Tukey-adjusted comparison of EMMs, $p < 0.001$). White circles are median values. Boxplots are dark lines with boxes between the hinge values (25th and 75th percentiles) and whiskers are the hinge values \pm interquartile range $\times 1.5$. Data outside of this range are denoted by dark circles. (b, c) Scatterplots of *C. dayacus* and *C. renaudpauliani* abundances, respectively, as a function of T_{max} (mean daily maximum temperature). Each point represents abundance for that species from the community sampling campaigns. T_{max} was extracted from microclimate projections generated by Jucker et al. (2018). Solid lines represent the back-transformed abundance estimates from generalised linear mixed-effects models containing sampling campaign and T_{max} as fixed effects, and sampling point as a random effect (Poisson error distribution), with 95% confidence intervals denoted by dashed lines (effect of T_{max} on abundance was significant for both species, $p < 0.001$)

were qualitatively similar to the full model posterior mean, if non-significant (Table S8).

4 | DISCUSSION

By combining data from airborne LiDAR-derived temperature maps, dung beetle community sampling campaigns and thermoregulatory trait measurements, we demonstrate that CT_{max} is a useful trait for understanding dung beetle responses to local-scale temperature change. Community-level CT_{max} increased from logged forest to oil palm plantations, and with daily maximum temperature (T_{max}). In addition, species with high CT_{max} tended to have high abundance in locations with high maximum temperatures. Together, the species- and community-level linking of upper thermal limits to thermal sensitivity represent strong evidence for the importance of physiology in driving responses to anthropogenic disturbance. In addition, we demonstrated that other morphological traits associated with thermoregulation are predicted by temperature across the disturbance gradient. In particular, we uncover a complex relationship between community-level cuticle lightness and temperature, with lighter-coloured communities associated with intermediate temperatures, and darker ones with thermal extremes.

We found that community-level CT_{max} increased with maximum daily temperature, both across the whole landscape, and when only considering forest habitats. Importantly, we also demonstrated that species with higher CT_{max} had relatively high abundances in hotter parts of the landscape, while accounting for

effects of phylogenetic relatedness. Taken in conjunction, these results cement the idea that physiology is a critical determinant of species responses to local temperature and demonstrate the efficacy of using CT_{max} values as proxies for thermal sensitivity (despite prominent criticisms—see Rezende et al., 2014). Boyle et al. (2020) also demonstrated comparable results for ants in the same landscape, with community CT_{max} increasing 0.2°C for every 1°C maximum daily temperature increase (compared to 0.088°C here). Larger effect sizes in ants may be due to the biology of the taxa in question. Ant workers are flightless, exploring their environment in proximity to their nest. Dung beetles, in contrast, are volant and able to travel long distances in oil palm landscapes (Gray et al., 2018). Taxon-specific differences in vagility will alter the scale at which temperature drives their distributions. Furthermore, most species in this study bury in the soil as part of their nesting strategy (tunnellers and rollers), allowing them to thermoregulate behaviourally. We find anecdotal evidence supporting this idea, as *Oniticellus tessellatus* had the highest CT_{max} and is the only non-fossorial species represented here. Ascertaining larval survival rates under controlled temperatures may pinpoint thermal bottlenecks in species' life cycles (Dahlke et al., 2020) and identify temperature as a primary driver of species responses to land-use.

Although CT_{max} exhibited a phylogenetic signal, we identified several closely related dung beetle species with divergent physiologies. Sister species *Catharsius dayacus* and *C. renaudpauliani* are the largest dung beetles in Borneo, together comprising most of the dung beetle biomass across habitats (Slade et al., 2014). From

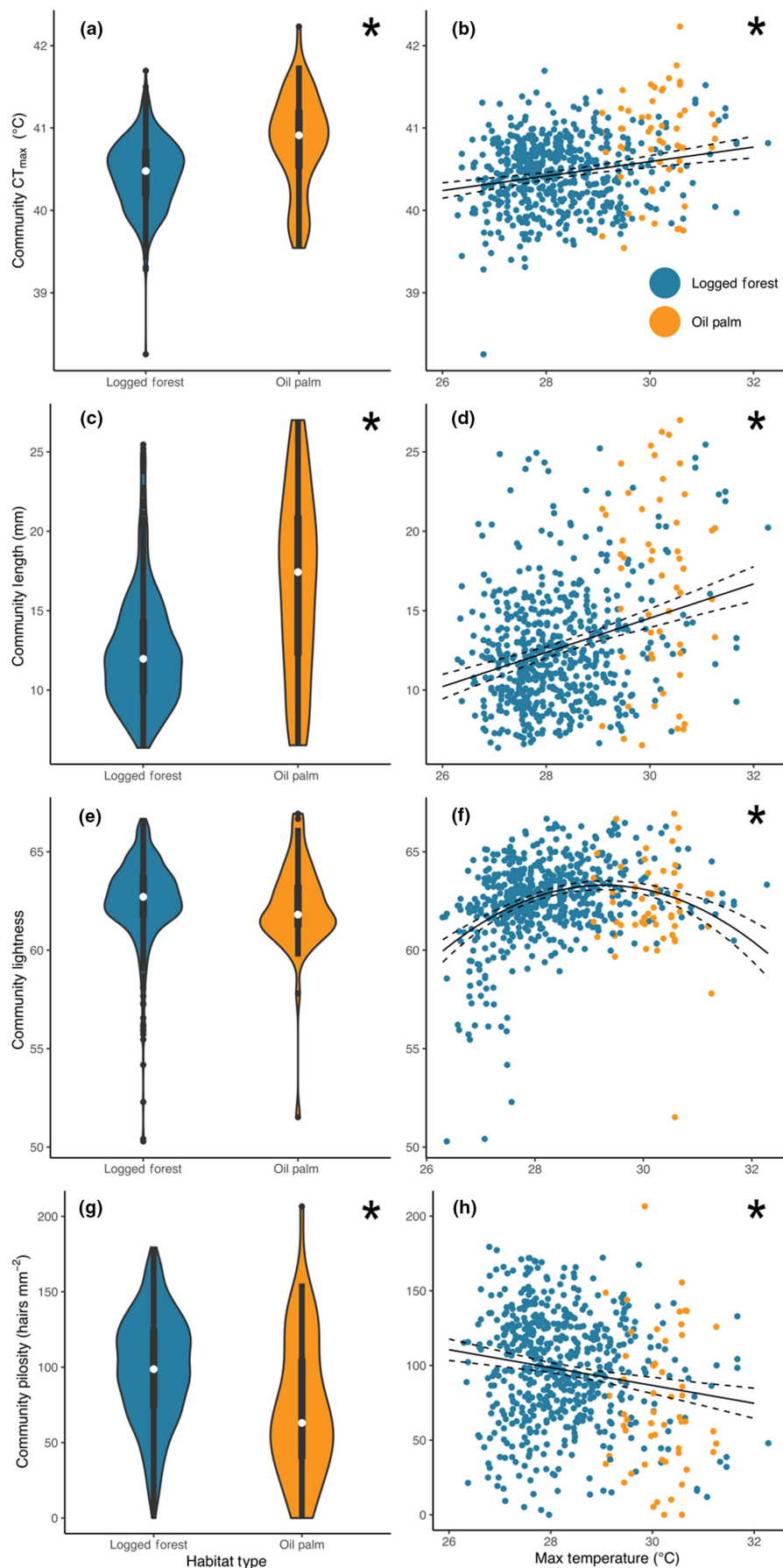
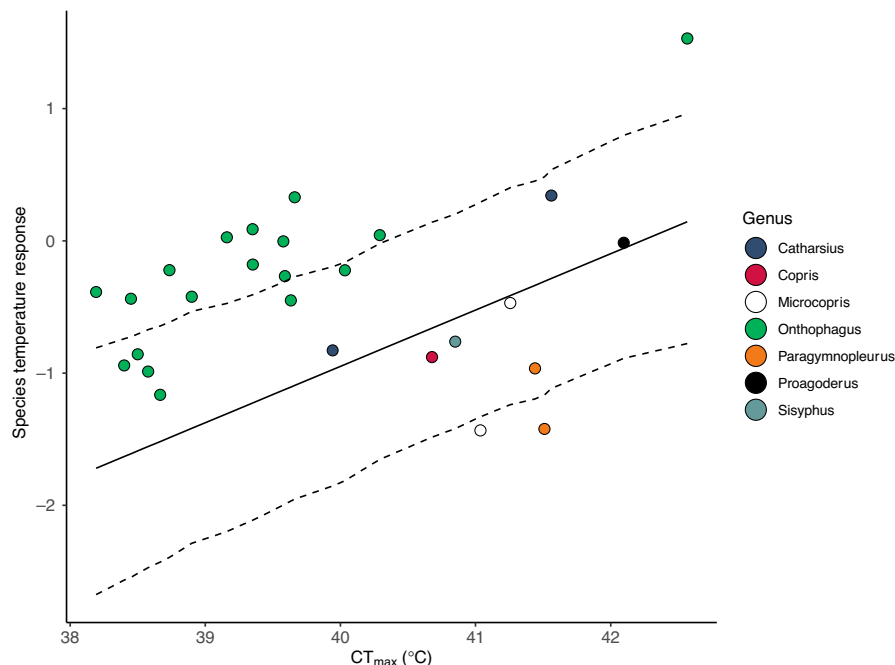


FIGURE 4 Violin plots showing differences in (a) community CT_{max} , (c) community body length, (e) community lightness and (g) community pilosity across habitat types. Mixed-effects models of community traits were constructed with habitat type as a fixed effect, and sampling campaign and sampling site controlled for using a fixed and a random effect respectively. Significance was ascertained through LRTs on the model in question and the respective 'null' model lacking the fixed effect of habitat type (denoted by an asterisk where $p < 0.05$). Scatterplots of (b) community CT_{max} , (d) community body length, (f) community lightness and (h) community pilosity against T_{max} . Mixed-effects models of community traits were constructed with T_{max} as a fixed effect, and sampling campaign and sampling site controlled for using a fixed and a random effect respectively. Significance was ascertained through LRTs on the model in question and the respective 'null' model lacking the fixed effect of T_{max} or lacking the polynomial term in the case of panel f (denoted by an asterisk where $p < 0.05$). A solid line represents the estimated effect of T_{max} with 95% confidence intervals denoted by dashed lines

FIGURE 5 Scatterplot of species temperature responses against CT_{max} , where species temperature responses are the slope estimates of generalised linear mixed-effects models of species abundance (Poisson error-family), as predicted by T_{max} . Thus, a higher species temperature response indicates a more positive association with temperature. The solid line is the mean posterior estimate from a generalised mixed-effects model using Markov chain Monte Carlo (MCMC) techniques to account for phylogeny ($p_{MCMC} < 0.001$). Dashed lines are 95% confidence intervals



old-growth forest to oil palm plantation, there is turnover from communities containing *C. dayacus*, to those containing *C. renaudpauliani*. The physiological differences between these species shown here may drive their niche partitioning, as it does in other sympatric dung beetle species (Verdú et al., 2019). The intraspecific variation in *C. renaudpauliani* CT_{max} also suggests plasticity in their physiology (i.e. a product of acclimation), or landscape-level differences between subpopulations (Rohr et al., 2018). Additionally, *Onthophagus trituber* had the highest CT_{max} of any tunneller, and the second highest of all species, despite belonging to the genus with the lowest CT_{max} . To the best of our knowledge, this is the first *species-level* study to investigate whether critical thermal limits drive responses to temperature change associated with land-use, and is certainly the first study of dung beetle CT_{max} in an oil palm context. The species that showed high physiological differentiation from congeners are noteworthy, as when taxonomic identification is only possible to genus, studies may fail to resolve important drivers of trait distributions, and to accurately predict the responses of taxa to temperature.

Thermal safety margins are the difference between upper thermal limits (here CT_{max}) and the temperature experienced by organisms (Sinclair et al., 2016). As such, given that the highest projected maximum daily temperature (32.3°C at a community sampling point) was below the lowest species CT_{max} (38.2°C), one might naively assume that dung beetles in oil palm landscapes are relatively unthreatened by future and ongoing temperature change. Terrestrial invertebrates, however, are subject to temperatures associated with the substrate they exist upon, experiencing the world at a scale of millimetres (Pincebourde & Woods, 2020). Dung beetles may thus respond closely to hotter temperatures at the soil–air boundary (Blonder et al., 2018). Given that the study landscape has a widespread history of disturbance,

remaining dung beetle communities may also have already passed through an extinction filter, removing the most thermally sensitive species. Additionally, as temperature measured here was a mean of maximum daily values, rather than an absolute maximum, the risk to dung beetle species in climate change scenarios may be greater than assumed using thermal safety margins. Indeed, we found that many species are absent from areas with maximum daily temperatures well below their CT_{max} . It is also important to consider that the detrimental effects of disturbance can be sublethal (van Heerwaarden & Sgrò, 2021), with individual fitness detrimentally affected at temperatures lower than those that might completely inhibit behaviour and ultimately cause death. Gaston and Chown (1999) showed that South African dung beetles at comparable elevations to our study site exhibited CT_{max} values varying from ~40.5 to 51.5°C—a good deal greater than the range reported here (36.9–43.2°C). A low CT_{max} range across species could indicate that tropical forest dung beetles are not particularly varied in their thermal preferences, which may be a contributing factor to their relatively low diversity in anthropogenic landscapes (Fuzessy et al., 2021). Indeed, the CT_{max} values reported here were distinctly lower than those of dung beetles in other biomes (e.g. Gaston & Chown, 1999; Verdú et al., 2019; Machekano et al., 2021), perhaps as a result of the buffering effects of tropical canopies on forest floor thermal maxima (Jucker et al., 2020).

Community-level lightness of dung beetle cuticles was predicted by a quadratic function of maximum daily temperature. These results suggest that the relative importance of the proposed drivers of invertebrate coloration may vary across the temperature gradient (Bishop et al., 2016; Clusella-Trullas et al., 2007; Law et al., 2020). In this study, communities had the darkest cuticles in the most thermally extreme environments, with cuticle lightness peaking at intermediate temperatures. The ability to reflect thermal radiation with a

lighter cuticle may be beneficial as temperatures increase in cooler parts of the landscape (Law et al., 2020), but as the environment becomes more disturbed (with more frequent vegetation gaps), protection against harmful UV-B exposure and/or desiccation tolerance in the form of a darker cuticle may outweigh the benefits of higher reflectivity of thermal radiation (Bishop et al., 2016).

We found that maximum daily temperature increases were predictive of body length at the community level but not the species level, supporting recent global findings by Fuzessy et al. (2021). The fact that greater body size was associated with higher temperatures is perhaps surprising given that smaller animals are thought to have lower equilibration temperatures and shorter equilibration times than larger ones (Clusella-Trullas et al., 2007). Beetles above 2–2.5 g are heterothermic, using abdominal pumping to cool elevated temperatures in the thorax associated with flying (Verdú et al., 2006), potentially mitigating the negative effects of body size. Body size is also correlated with higher vagility (Larsen et al., 2008), meaning that in mosaic landscapes such as ours with patchy mammal populations (Deere et al., 2020) and microrefugia (Williamson et al., 2021), larger-bodied dung beetles may persist on a landscape scale as spatially structured populations or metapopulations.

Dung beetle pilosity decreased with maximum daily temperature across the disturbance gradient, and in plantations compared to logged forests. This was in keeping with previous results in bees (Peters et al., 2016), and suggests that pilosity is associated with cooler temperatures in tropical invertebrates. Pilosity is frequently measured in insect-pollinator studies because of its role in pollen acquisition (Roquer-Beni et al., 2020), but we are unaware of any previous studies on tropical invertebrate hairiness and how it may mediate thermoregulation.

Here, we quantify the often-assumed, but rarely empirically tested, response of species to local-scale temperature changes associated with anthropogenic disturbance (Boyle et al., 2020). Many of the results found here, although significant, had relatively weak effect sizes. This could be due to the temporal mismatch between our dung beetle community samples (taken in 2011, 2015 and 2017/2018) and the airborne LiDAR-derived T_{\max} projections (generated using a 2014 scan). That said, we have attempted to control for this methodological short-coming statistically, and our results were generally robust to analysis of individual sampling campaigns. Alternatively, small effect sizes may be due to physiological (e.g. fertility limits; van Heerwaarden & Sgrò, 2021), morphological (e.g. alternative measures of coloration; Stanbrook et al., 2021) or behavioural (e.g. nesting strategy, that we could not analyse statistically) traits that are more important in determining the response of communities and species to temperature than those presented here. Responses to temperature may also just be complex and cumulative, with many traits contributing to the ability of species to persist in hotter environments, resulting in relatively small effect sizes for any given trait. To understand how species and, ultimately, community patterns and processes, will respond to future temperature change, we must first uncover trait-mediated species responses to existing gradients. As our traits-of-interest predicted invertebrate responses

to local-scale temperature change in dung beetles, we advocate the extension of our methods to additional taxa and contexts to better understand the ubiquity of our findings. Indeed, the traits studied here should be measurable across invertebrate taxa (e.g. Boyle et al., 2020; Law et al., 2020; Peters et al., 2016), and, if shown to be universally important for mediating species responses, could allow ecologists to predict responses of hard-to-survey taxa (Brousseau et al., 2018). In this case, CT_{\max} were particularly critical for mediating dung beetle responses to temperature-related threats, and thus could be vitally important for determining how tropical forest ecosystems will be impacted by climatic warming.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

J.W., E.M.S., S.J.R. and O.T.L. conceived the idea of study. E.M.S. led the community sampling, with support from A.Y.C.C. and E.B. E.M.S., J.W. and J.P. carried out specimen identification. J.W. collected CT_{\max} data. E.T. collected body length, cuticle lightness and pilosity data. T.J. provided temperature data. M.B. constructed the variable rates of evolution models. J.W. conducted all other analyses and wrote the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT

All data are available through the Zenodo data repository. Specifically, dung beetle community data from riparian habitats are available for 2015 and 2017/2018 at <https://doi.org/10.5281/zenodo.3906118> (Slade, Milne, et al., 2020) and <https://doi.org/10.5281/zenodo.3906441> (Slade, Williamson, et al., 2020) respectively. Dung beetle community data from non-riparian habitats are available for 2011, 2015 and 2018 at <https://doi.org/10.5281/zenodo.3906441>.

org/10.5281/zenodo.3247492 (Slade, Bush, et al., 2019), <https://doi.org/10.5281/zenodo.3247494> (Slade, Milne, et al., 2019) and <https://doi.org/10.5281/zenodo.3832076> (Slade, Chung, et al., 2020) respectively. Dung beetle trait data are available at <https://doi.org/10.5281/zenodo.6477719> (Williamson et al., 2022), and thermal projections are available at <https://doi.org/10.5281/zenodo.6477751> (Jucker et al., 2022).

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