



Research

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Higher temperature variability in deforested mountain regions impacts the competitive advantage of nocturnal species

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Deforestation is a major contributor to biodiversity loss, yet the impact of forest loss on daily microclimate variability and its implications for species with different daily activity patterns remain poorly understood. Using a recently developed microclimate model, we investigated the effects of deforestation on the daily temperature range (DTR) in low-elevation tropical regions and high-elevation temperate regions. Our results show that deforestation substantially increases DTR in these areas, suggesting a potential impact on species interactions. To test this hypothesis, we studied the competitive interactions between nocturnal burying beetles and all-day-active blowfly maggots in forested and deforested habitats in Taiwan. We show that deforestation leads to increased DTR at higher elevations, which enhances the competitiveness of blowfly maggots during the day and leads to a higher failure rate of carcass burial by the beetles at night. Thus, deforestation-induced temperature variability not only modulates exploitative competition between species with different daily activity patterns, but also likely exacerbates the negative impacts of climate change on nocturnal organisms. In order to limit potential adverse effects on species interactions and their ecological functions, our study highlights the need to protect forests, especially in areas where deforestation can greatly alter temperature variability.

1. Introduction

Massive and accelerating deforestation is arguably one of the most imminent threats to biodiversity globally [1–3], and increasingly so in mountainous regions around the world [4,5]. Since forests are known to buffer extreme climates and create relatively stable environments for numerous species, deforestation reduces climatic buffering and causes substantial changes in the microclimates that many organisms experience [6,7]. Not only do these climatic changes impact the survival of individual species, they also reshape interactions among species [8]. Ultimately, global warming may therefore exacerbate the climatic effects of deforestation on organismal fitness, further accelerating biodiversity loss [9]. Thus, gaining a better understanding of the detailed mechanisms of how modifications in microclimate influence species interactions, as well as determining how these interactions might scale by assessing the

effects of deforestation on microclimate at a global scale, are particularly urgent priorities for predicting and mitigating the ongoing biodiversity crisis in this changing world.

Deforestation is known to cause increases in both the mean and variability of temperature [10–12]. How changes in mean temperature influence species' physiological performance [13] and spatial distribution [14] are topics that have been well studied. Yet the role of temperature variability on organismal fitness is poorly understood, perhaps because temperature variation not only influences species' physiological performance [15–18], but also greatly complicates interactions among species [16,19]. More importantly, recent theoretical models have suggested that changes in the mean and variability of environmental temperature will have complex and interacting effects on species competition and coexistence [20].

An increase in temperature variability driven by deforestation is largely the result of daytime warming and night-time cooling [21], together leading to a larger daily temperature range (DTR) that will cause species to experience more extreme (either cold or hot) temperatures throughout the daily cycle. Under this scenario, differences between thermal environments directly experienced by coexisting diurnal and nocturnal species will become more pronounced due to the larger difference between daytime and night-time temperatures. Therefore, the effects of deforestation on species with different daily activity patterns may also vary considerably. Past studies have predominantly focused on the effects of daytime warming on diurnal species because they are more likely to experience stressful high temperatures during daylight hours [22,23]. Yet, if species that are active at different times of the day compete for the same resources, such changes in temperature variability may differentially affect the environmental temperature experienced by these competing species. This, in turn, can alter their fitness by modulating competition between them. Yet, surprisingly few studies have documented how increases in climatic mean and variability driven by deforestation affect interspecific competition [16], particularly between diurnal and nocturnal species. To our knowledge, no study has explicitly addressed how increased temperature variability affects the fitness of, and competition between, species with different daily activity patterns.

Here, we first analysed data from a published global microclimate database [24] to assess how deforestation affects daily temperature variability at different elevations at a global scale. Next, we conducted field experiments in forested and deforested habitats along an elevational gradient in Taiwan (Mt. Hehuan, spanning 1170–2903 m above sea level) to investigate how changes in temperature variability caused by deforestation affect interspecific competition between nocturnal Asian burying beetles (*Nicrophorus nepalensis*) and all-day-active maggots of blowflies (*Calliphoridae* spp.). Burying beetles use nutrient-rich vertebrate carcasses as the primary food resource for rearing their young [25]. Since carcasses are precious 'bonanza resources' [26], competition for carcasses with other insect species, especially blowflies, strongly limits the breeding success of burying beetles [27–29]. Previous studies have revealed that interspecific competition between burying beetles and blowflies is mediated at least in part by climate, as blowflies grow and breed faster at warmer temperatures, whereas burying beetles breed more successfully at cooler temperatures [27–32]. Nevertheless, how temperature variability affects competitive interactions between these species exhibiting different daily activity patterns remains unclear.

Finally, to provide a general explanation for the results of the field experiments, we also developed a mathematical model that incorporates both the performance curves and daily activity patterns of competing species to understand the detailed mechanisms by which climate variation influences interspecific competition. Ultimately, our broadscale analysis will help to determine the priority for global forest conservation by focusing on areas where deforestation will have a greater impact on climate variability. In addition, our field experiments provide an understanding of how deforestation affects interspecific competition to varying degrees with changes in elevation. Consequently, we expect our study to have important implications for the conservation of biodiversity in mountain ecosystems across the globe.

2. Methods

(a) Predicting the impact of deforestation on DTR worldwide

To predict the effect of deforestation on DTR, we first used the global land cover database developed by Tuanmu & Jetz [33] to determine the global forest distribution by summing the proportion of four forest types (coniferous, deciduous, evergreen and mixed) in each 1 km grid. Next, we converted the spatial resolution to approximately 15 km (10 arcmin) using the resample function in the R package *raster* to match the microclimate data. Finally, we selected grids with greater than 50% forest cover to estimate DTR in forests and then predict the potential impact of deforestation on DTR.

Next, we estimated the DTR of these forest grids before and after deforestation using temperature estimates for 1 cm above the soil surface with 100% and 0% shade levels for each hour of the day taken from the microclim database [34] at approximately 15 km (10 arc min) spatial resolution. The temperature estimations from this database are from the outputs of the NicheMapR microclimate model [24]. The model considers long-term climatological observations of solar radiation, longwave radiation, hourly interpolation of weather data, vertical air temperature and wind speed profiles, hydric and thermal properties of air, soil heat balance and thermal properties and soil water balance. We estimated the DTRs in July for the Northern Hemisphere and January for the Southern Hemisphere. First, we estimated DTR by subtracting each grid's minimum from the maximum daily temperatures. Next, we estimated the change in DTR due to deforestation (Δ DTR hereafter) by subtracting the DTR before from after deforestation; this allows us to compare the changes across grids with the same units.

To investigate the relationship between Δ DTR and elevation, we obtained elevation data from WorldClim 2.1 [35] derived from the Shuttle Radar Topography Mission (SRTM) elevation data [36] to 10 arc min resolution. We examined the relationship between Δ DTR and elevation using nonparametric local regression (LOESS) analysis. Furthermore, we estimated how changes in daily maximum temperature (ΔT_{\max}) and daily minimum temperature (ΔT_{\min}) correlate to Δ DTR using Pearson correlation coefficients to assess the relative importance of maximum and minimum temperature on DTR.

(b) Thermal performance curves of burying beetles and blowfly maggots

Burying beetles bury carcasses to defend against other insects and only begin to reproduce after burying the carcass. Therefore, we established the thermal performance curve (TPC) of burying beetles based on their speed of burying a carcass. In contrast, we

obtained the TPC of blowfly maggots from the results of a laboratory experiment conducted in a previous study [37]. Since the use of carcasses by blowflies largely entails maggot feeding, we considered two measurements to establish the TPC of maggots, egg hatching rate and maggot survival rate, which may relate to the number of maggots on the carcass and their foraging efficiency.

We used the function described previously [38,39] to represent the nonlinear and low-temperature skewed properties of the TPC:

$$P(T) = \begin{cases} \exp\left(-\left(\frac{T - T_{\text{opt}}}{2\sigma_p}\right)^2\right), & \text{when } T \leq T_{\text{opt}} \\ 1 - \left(\frac{T - T_{\text{opt}}}{T_{\text{opt}} - CT_{\text{max}}}\right)^2, & \text{when } T > T_{\text{opt}} \end{cases} \quad (2.1)$$

where T is temperature, σ_p is the shape parameter determining the curve's steepness at the lower end, T_{opt} is the temperature with optimal performance and CT_{max} is the upper critical temperature.

To obtain the TPC for burying beetles, we experimentally tested the burial performance of beetles in the following temperature treatments: 8°C ($n = 16$), 10°C ($n = 18$), 12°C ($n = 25$), 16°C ($n = 20$), 20°C ($n = 18$) and 22°C ($n = 21$). For each experiment, we prepared a nursing box for beetles using a 20 × 13 × 13 cm (length × width × height) plastic container filled with potting soil. We released one male and one female from our laboratory-reared population maintained under standard conditions (16°C in mean temperature with $a \pm 3.5^\circ\text{C}$ daily cycle) into each nursing box. In addition, we provided the beetles with a 75 g fresh carcass of a domesticated feeder rat. Next, we placed each nursing box in a growth chamber for the temperature manipulation. Since we conducted the experiments sequentially with three growth chambers, we randomized the combinations of temperature treatments and growth chambers to prevent any potential chamber-specific effects. We monitored the experiments daily to determine whether beetles successfully buried the carcass. We considered the inverse of the time it took beetles to bury the carcass as an index of beetle performance. For those experiments in which beetles failed to bury the carcass, the performance was equal to zero (i.e. one divided by infinity). We identify the beetles' T_{opt} by regressing beetle performance against temperature using nonparametric local regression (LOESS) and finding the temperature that maximizes performance. Finally, we estimated CT_{max} and σ_p using a nonlinear regression model with the R function *nls*.

We obtained the TPC for blowfly maggots by considering the experimental results from a previous study. Specifically, Yang & Shiao [37] measured adult locomotion, egg hatching rate and maggot survival rates in response to temperature treatments of *Chrysomya pinguis*, the most abundant blowfly species in the mountains of Taiwan. Here, we considered the egg hatching rate (P_{hatch}) and the maggot survival rate (P_{survive}), with the following relationships to temperature, obtained from regression models in [37] from their experimental results:

$$\sin^{-1}\left(\sqrt{P_{\text{hatch}}}\right) = -0.3660 + 0.6223T - 0.1521T^2 \quad (2.2)$$

and

$$\sin^{-1}\left(\sqrt{P_{\text{survive}}}\right) = -0.4480 + 0.5977T - 0.0943T^2 \quad (2.3)$$

In the equations, P_{hatch} and P_{survive} are arcsine-square-root transformed to resolve the problem of non-normality in ratio data when constructing the models [37].

Next, we calculated the joint performance and rescaled it to the range between 0 and 1 by using the following formula:

$$P_{\text{maggot}} = \left(\frac{P_{\text{hatch}} \times P_{\text{survive}}}{\max(P_{\text{hatch}} \times P_{\text{survive}})}\right)^{1/2} \quad (2.4)$$

We calculated T_{opt} for blowfly maggots (the T value which maximizes P_{maggot}) using the R function *optimize*.

Finally, we determined CT_{max} and σ_p iteratively testing every combination of CT_{max} (from 20 to 40°C) and σ_p (from 0.1 to 7) to find the best combination that minimizes the residual mean square error (RMSE) between equations (2.1) and (2.4).

(c) Effect of deforestation on the mean and variability of temperature at a regional scale

To understand how deforestation affects the mean and variability of daily temperature, and subsequently modulates species competition, we adopted a space-time substitution approach [40–42] to conduct field experiments along an elevational gradient in natural forest and cultivated land on Mt. Hehuan, Taiwan (3422 m, main peak at 24°11' N, 121°17' E) from June to September 2011. Mt. Hehuan is located in the central mountain range of Taiwan's subtropical zone. The relatively high temperature and greater than 2000 mm of annual precipitation have resulted in 58% of the island's total area being covered by forest [43]. Our field study area is located below the alpine tree line and was initially covered by primary forest. However, deforestation began after the construction of the Central Cross-Island Highway in 1957, and the Taiwanese government began to establish several highland farms along the highway to house veterans [44]. One such farm encompasses one of our main study sites, the Qingjing Farm on the western slope of Mt. Hehuan that was developed between 1960 and 1966. The foliage cover in the cultivated land results from shrubs, grasses, crops, fruit trees and remnant native trees. In some small cultivated patches, trees at the edges may increase foliage cover.

To monitor how elevation and habitat affect the mean and variability of temperature experienced by burying beetles and blowflies, we selected 14 forest plots and 10 cultivated land plots along the elevation gradient (from 1169 to 2785 m; electronic supplementary material, figure S1). For each plot, we recorded ambient temperature using an iButton datalogger (Maxim Integrated Products, Sunnyvale, CA). The loggers were hung 1.25 to 1.5 m above the ground (within the range of standard heights for weather stations measuring surface air temperatures [45]) in a tree near the experimental apparatus. The loggers were shielded with PVC pipe to prevent direct exposure to solar radiation [46]. Although ground surface temperatures are often higher than air temperatures in open habitats, especially on bare ground, the vertical temperature difference has been suggested to be small at ground level in areas with underlying vegetation [47], as in most of the cultivated areas that we sampled.

Throughout the experiments, we recorded the temperature every 30 min and calculated the mean, maximum and minimum daily temperatures (T_{mean} , T_{max} and T_{min}) and DTR. To confirm the generality of our recorded measurements, we also simulated habitat effects on DTR in our field study area (121.15–121.45°E, 24.04–24.21°N, electronic supplementary material, figure S1) using the R package *Microclima* [24,48], a newly developed package for simulating microclimate at fine temporal and spatial scales. We estimated the DTR of cultivated land (with built-in parameters for cropland) and forest (with built-in parameters for evergreen deciduous forest) throughout the experimental period at a spatial resolution of approximately 1 km (10 arc seconds).

(d) Predicting realized beetle performance with TPCs, daily activity patterns and environmental temperature profiles

We first analysed the daily temperature data from the field and constructed two linear mixed models (LMMs) with temperature as the dependent variable and time of day as an independent

variable. In the first model, we also included elevation, habitat type and their interaction as covariates. In the second model, we included T_{mean} , DTR and their interaction as covariates. Using these two models, we further reconstructed daily temperature profiles for any given combination of elevations and habitat types, as well as T_{mean} and DTR. Next, we calculated the kernel density functions ($F(T)$) for daily temperature (from 00.00 to 23.59) and night-time temperature (from 19.00 to 05.30). We also estimated the performance of each species free from competition by calculating environment-weighted performance ($W(T)$) using the equation

$$W(T) = \int P(T)F(T)dT, \quad (2.5)$$

where $P(T)$ is the performance of the focal species at temperature T_i predicted by the TPC.

To model the influences of different daily activity patterns, we considered the kernel density function for daily temperature as the $F(T)$ for maggots, but the kernel density function for night-time temperature as that for burying beetles, since blowfly maggots continually consume the carcass day and night, but burying beetles are only active at night. Finally, we estimated the realized performance of beetles under competition by maggots by dividing the performance of beetles by the performance of maggots ($W_{\text{beetle}}(T)/W_{\text{maggot}}(T)$).

(e) Field experiment of competition between burying beetles and blowflies

To understand how deforestation modulates competition between burying beetles and blowflies, we conducted a field experiment along an elevational gradient in natural forest and cultivated land on Mt. Hehuan. Since cultivated land was patchily distributed, we conducted field experiments in eight cultivated experimental plots along the elevational gradient (from 1169 to 2785 m; electronic supplementary material, figure S1), as well as in control forest plots close to each cultivated plot. Since we failed to find a large enough control forest plot at one site located at approximately 2000 m, we ended up with only seven forest plots (from 1290 to 2782 m; electronic supplementary material, figure S1). All of these plots were included as parts of the temperature monitoring plots. Therefore, the temperatures experienced by beetles and blowflies were also recorded. We performed 10 replicates of the experiment in each plot, but in one forest plot and one cultivated land plot, we performed only seven and nine replicates due to insufficient area. We also measured foliage cover (defined as the proportion of forest covered by the vertical projection of the foliage) for each experimental site using Gap Light Analyzer (GLA) v.2.0 [49] from a photograph taken with a fisheye lens. All photographs taken for measuring foliage cover are available from Zenodo (<https://doi.org/10.5281/zenodo.7699201>) [50].

We placed a 75 g fresh carcass of a domesticated feeder rat in each experiment as a breeding resource to attract local beetles. We covered each carcass with a metal cage ($21 \times 21 \times 21$ cm) constructed of 2×2 cm wire mesh to keep mammalian scavengers away. Importantly, both blowflies and beetles could freely enter the cage and access the carcass. We checked the carcass every 2 days until either the carcass reached the end of the bloated stage (identified by skin penetration at the trunk part of the carcass due to consumption by maggots [29,51]) or the burying beetles completely buried the carcass. We removed 8 of 146 samples from the analysis of burial success because another burying beetle species (*N. concolor* Kraatz, 1877) buried the carcasses at regions close to the lower elevational range margins of *N. nepalensis*. During each visit, we noted the condition of the carcass and whether beetles were present. In addition, we recorded whether beetles successfully buried the carcasses (i.e. burial probability) as an indicator of fitness, since it is an

important indicator of burying beetles that are successfully defending the resource in the field.

(f) Identifying the primary time of day that burying beetles search for carcasses

We reanalysed the videos taken from the field experiments of Chan *et al.* [29] and recorded the first arrival time of burying beetles on the carcasses. These experiments were conducted along the same elevational gradient and with similar protocols to the present study, except that all experiments were video-monitored, and the carcasses were placed in plastic pots filled with soil to keep the larvae of beetles from escaping.

(g) Laboratory experiment on maggot performance at different DTRs

We conducted a laboratory experiment in which we tested two levels of DTR, 7°C ($n = 17$) and 14°C ($n = 17$), with a mean daily temperature of 16°C. These temperature ranges were selected to reflect those along the natural elevational range of burying beetles, which inhabit forests with a lower mean DTR of 5.3°C and cultivated land with a higher mean DTR of 13.4°C. To minimize the potential for chamber-specific effects, we again randomized the temperature treatments and growth chambers. In each treatment, we housed 100 male and 100 female blowflies in a rearing cage within a growth chamber, with each assigned a specific temperature treatment. We then placed a 75 g carcass of a domesticated feeder rat in each cage and recorded the number of days that it took for the carcass to reach the end of the bloated stage, an index of carcass consumption rate [29,51]. Additionally, we measured the body length of maggots on the seventh day of each experiment as an indicator of maggot developmental rate. We sampled and measured 20 individuals from each rat carcass, except for seven carcasses that yielded fewer than 20 maggots on the seventh day.

(h) Field experiment preventing blowfly competition

To confirm whether competition with blowflies is responsible for the observed impacts of DTR on the burial success of burying beetles, we reanalysed the experimental data of Tsai *et al.* [32], which experimentally prevented blowfly competition in the field. The experiment in the study was conducted along the same elevation gradient on Mt. Hehuan and consisted of a treatment and a control group. The experimental protocol of the control group was similar to the experiment in the present study, except that the carcasses were placed in plastic pots filled with soil to prevent the escape of the beetles' larvae. However, in the treatment group, a pair of burying beetles caught from the surrounding area were released into the plastic pot, and the pot was covered by screen mesh to exclude blowflies. We only considered trials conducted from June to September and compared the effects of mean daily temperature and DTR on the burial success between the treatment and control groups. We also calculated the breeding success rates after carcass burial for both the treatment and control groups to test the validity of using burial success as a fitness indicator for the beetles.

(i) Data analysis

We analysed data from field experiment using LMMs for continuous dependent variables such as temperature and foliage cover. We arcsine-square-root transformed the foliage cover before the analysis. We used generalized linear mixed models (GLMMs) for binary dependent variables (i.e. burial success). Furthermore, we considered the number of days required for beetles to find the carcass as an index of searching efficiency,

and the number of days required for beetles to bury the carcass as an index of burial efficiency. We used cumulative-link mixed models (CLMMs) to analyse the factors affecting these ordinal dependent variables. Julian date was considered as a covariate in all the models. To avoid correlations among explanatory variables due to potential causal relationships (e.g. elevation and habitat affect burial success and the behaviour of beetles by modifying temperature), we modelled the effects of the following combinations of explanatory variables separately: (1) elevation and habitat type; (2) T_{mean} and DTR; and (3) T_{max} and T_{min} . We also calculated variation inflation factors (VIFs) for each model's explanatory variables using the R function *vif.mer* [52] and ensured that all VIFs < 3. We also included in our model nested random effects (plots nested within elevational bands) to account for the potential influence of repeated sampling in each plot, as well as the paired design of two types of habitats at each elevational band. All continuous independent variables were standardized to facilitate model convergence and make regression coefficients comparable. For the laboratory experiments on maggot performance, we tested the difference in carcass consumption rate between treatments using a Wilcoxon rank-sum test, and the difference in body length of maggots between treatments using a LMM with replicate (i.e. carcass) ID as a random factor (since more than one individual maggot was sampled from a carcass). We conducted all statistical analyses using R version 3.3.1 [53] with the package *lme4* [54] for LMM and GLMM, the package *ordinal* [54] for CLMM and the package *emmeans* [56] for the separate tests after significant interactions in the models.

3. Results

(a) The potential effect of deforestation on DTR across the globe

To understand the effect of deforestation on temperature variability, we used the microclimate model of [34] to estimate the potential impact of deforestation on DTR globally. We found that ΔDTR due to deforestation is higher in the tropics (0–23.5°) (figure 1a), especially at lower elevations (approx. 600 m in the Northern Hemisphere; approx. 1000 m in the Southern Hemisphere; figure 1b,c). However, in temperate regions (23.5–66.5°), ΔDTR increases with elevation, indicating a more pronounced influence of deforestation on DTR at higher elevations (figure 1d,e). Furthermore, this trend is more pronounced in the Northern Hemisphere (figure 1d) and less evident in the Southern Hemisphere (figure 1e) due to the lower alpine tree line. Finally, we also found that the variation in ΔDTR was primarily driven by ΔT_{max} (correlation between ΔDTR and ΔT_{max} , Northern Hemisphere: $r = 0.999$, Southern Hemisphere: $r = 0.999$) rather than ΔT_{min} (correlation between ΔDTR and ΔT_{min} , Northern Hemisphere: $r = 0.146$, Southern Hemisphere: $r = -0.193$).

(b) TPCs for burying beetles and blowfly maggots

To predict how changes in temperature variability due to deforestation modulate competitive interactions between burying beetles and blowflies, we determined the fundamental TPCs of both species. First, we measured the burying speed of carcasses at different temperatures in the laboratory to determine the fundamental TPC of the beetles ($T_{\text{opt}} = 16.70^\circ\text{C}$; $CT_{\text{max}} = 23.05^\circ\text{C}$; $\sigma_p = 2.04$; electronic supplementary material, figure S2a; and table S1). We also determined the fundamental TPC of the blowfly maggots ($T_{\text{opt}} = 29.45^\circ\text{C}$; $CT_{\text{max}} = 37.09^\circ\text{C}$;

$\sigma_p = 4.58$; electronic supplementary material, figure S2b) based on the results of a published study [37]. Looking at these TPCs, we can see that the burying beetle is a low-temperature specialist (with a lower T_{opt} and a smaller thermal range than the blowfly), whereas the blowfly is a generalist species that prefers higher temperatures. We note that low-temperature specialist is a relative term and does not mean that the cooler the temperature, the better the organism will perform; after all, all organisms will perform more poorly when the temperature is below their T_{opt} .

(c) Effect of deforestation on the mean and variability of temperature at a regional scale

To understand how changes in temperature variability caused by deforestation affect the competitive interactions between burying beetles and blowflies at different elevations, we examined the differences in temperatures between forest and cultivated plots along the elevational gradient (figure 2a). We first measured the foliage cover (defined as the proportion of area covered by the vertical projection of the foliage) in each sample location, confirming that the foliage cover of cultivated land (0.41 ± 0.10 , $n = 79$) was significantly lower than that of natural forest (0.94 ± 0.05 , $n = 67$) (LMM, $t = 4.27$, $n = 146$, $p = 0.004$; figure 2b). Next, we found that T_{mean} decreased with elevation in a similar manner for both habitat types (LMM, elevation \times habitat interaction, $t = -0.71$, $n = 187$, $p = 0.49$; elevation, $t = -4.92$, $p < 0.001$; figure 2c; electronic supplementary material, table S2a). In contrast, DTR increased with elevation in cultivated land but remained constant in natural forest (LMM, elevation \times habitat interaction, $t = -3.76$, $n = 187$, $p < 0.001$; the separate test for the effect of elevation in cultivated land, $p < 0.001$, and in forest, $p = 0.52$; figure 2d; electronic supplementary material, table S2b). These contrasting patterns occurred because T_{max} , which is mainly influenced by habitat type, was significantly higher in cultivated land than in natural forest (electronic supplementary material, table S2c). In contrast, T_{min} was more influenced by elevation and was lower at higher elevations (electronic supplementary material, table S2d). Thus, although T_{mean} does not differ in forest and cultivated land when controlling for elevational differences, temperature variability is greater in cultivated land than in natural forest. Finally, the results of the *Microclima* model also yielded predictions consistent with the field observations (electronic supplementary material, figure S3).

(d) Predicting realized beetle performance with TPCs, daily activity patterns and environmental temperature profiles

Next, we integrated the fundamental TPCs for burying beetles and blowfly maggots in the absence of competition (figure 3a; electronic supplementary material, figure S2), the daily temperature profiles in forest and cultivated land, and the times of sunrise and sunset at the field site (figure 3b,c), to calculate (i) the environment-weighted TPCs under the real environmental conditions and daily activity patterns (figure 3d,e), and (ii) the realized environment-weighted TPCs under the influence of interspecific competition (figure 3f,g). Without interspecific competition, the environment-weighted burying beetle TPC predicted that under high temperature variation in cultivated

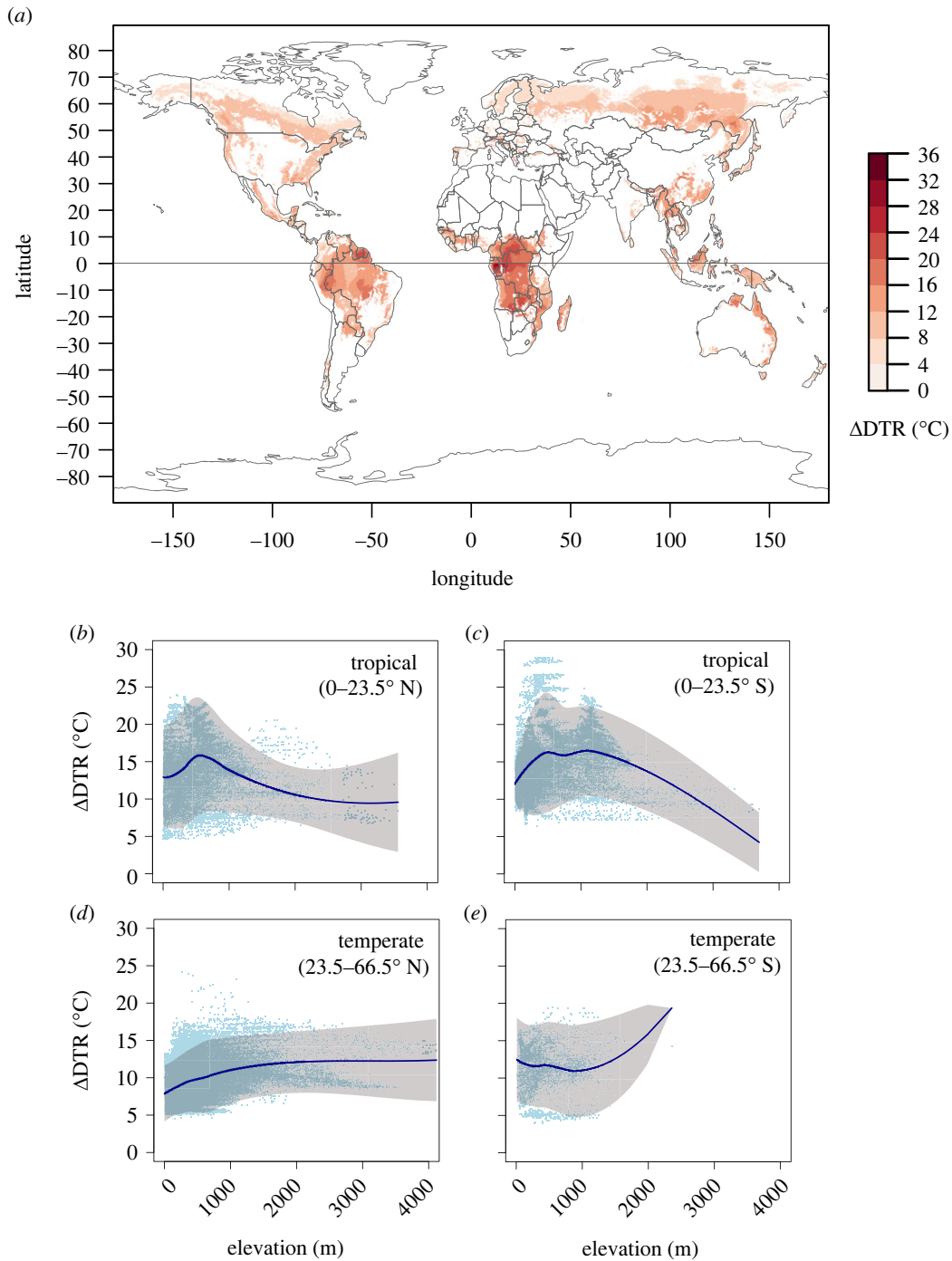


Figure 1. Estimated changes in the daily temperature range driven by deforestation. (a) Map for the estimated changes in DTR driven by deforestation. (b–e) Relationship between changes in DTR driven by deforestation and elevation. In (b–e), lines and shaded areas represent trends and 95% confidence intervals estimated by local regression (LOESS) functions.

land, beetles performed worse at mean temperatures close to their original optimum (16.7°C), but better at the original suboptimal high mean temperature (figure 3*d,e*). Conversely, blowfly maggots performed slightly worse at high mean temperatures close to the original optimum, but slightly better at lower mean temperatures (figure 3*d,e*).

The realized TPC of burying beetles under competition from blowfly maggots ($W_{\text{beetle}}/W_{\text{maggot}}$) yielded three critical predictions. First, the realized performance of burying beetles decreased in environments with DTR in cultivated land at lower T_{mean} compared to environments with low DTR in forest (figure 3*f,g*). Therefore, the negative effect of deforestation on burying beetles was greatest at mid and high elevations (electronic supplementary material, figure S4). Second, in the forest environment with lower DTR, the optimal mean daily

temperature for burying beetles decreased from 16.7 to 14.9°C (figure 3*f*). In contrast, in the cultivated land with larger DTRs, the optimal mean daily temperature for burying beetles increased from 16.7 to 18.3°C (figure 3*g*). Third, the realized performance of burying beetles at the optimal mean temperature in forest (14.9°C) was much higher than that at the optimal mean temperature in cultivated land (18.3°C) (figure 3*f,g*).

(e) Effects of deforestation on interspecific competition between species with different daily activity patterns

Next, we tested the three critical predictions from the above model by examining how deforestation affects the probability

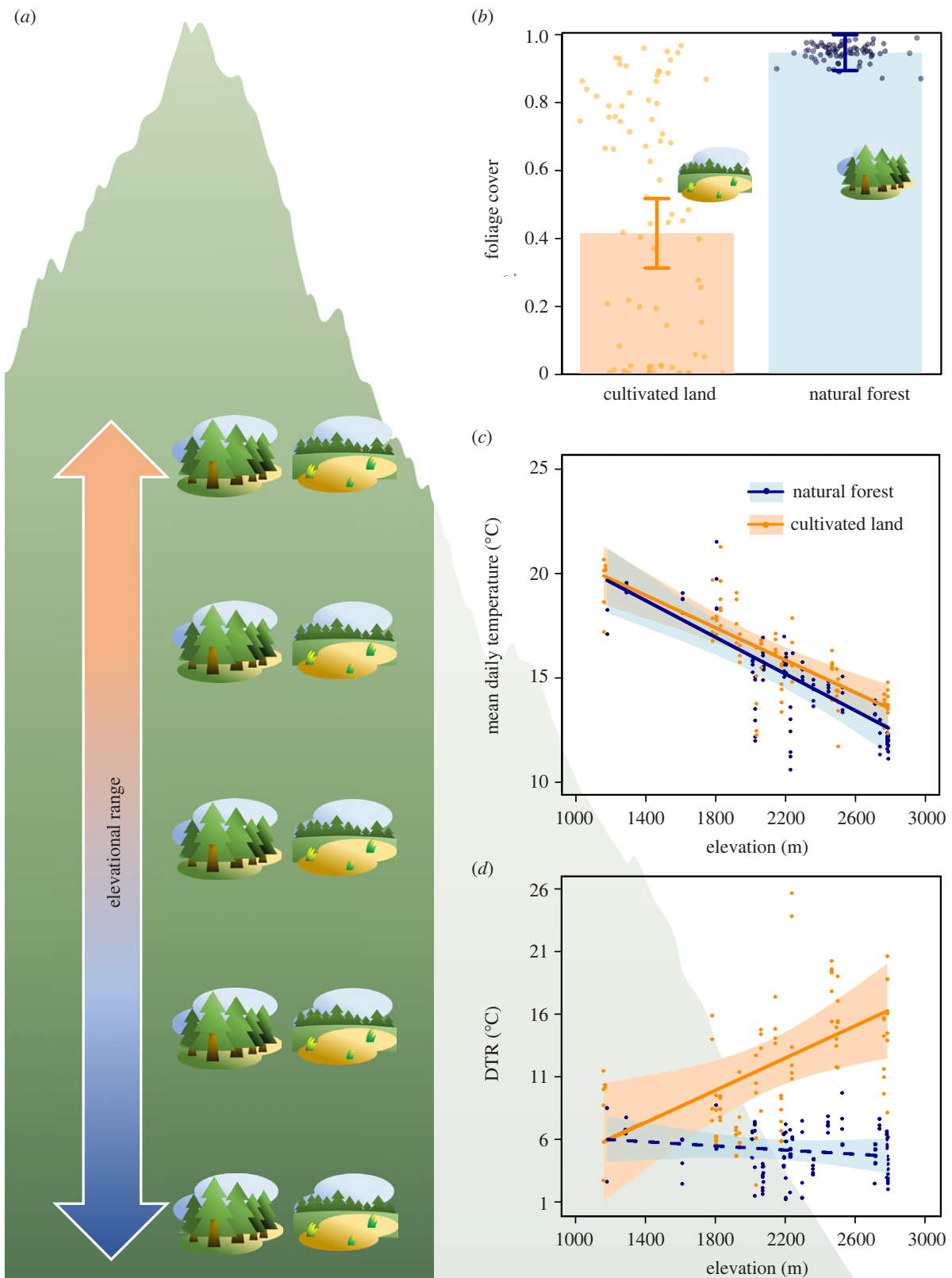


Figure 2. Foliage cover and microclimate between natural forest and cultivated land. (a) The paired design of the field study in forest and cultivated land across the elevational gradient. (b) Difference in foliage cover. (c) Elevational trend of mean daily temperature. (d) Elevational trend in DTR. In (b), dots represent samples, bars represent means, and error bars represent standard errors. In (c,d), lines represent trends (broken lines are non-significant) and shaded areas depict the 95% confidence intervals estimated by GLMMs (see main text for more detail), and dots represent samples (blue for forest samples and orange for cultivated land samples). Note that if two statistics have non-overlapping confidence intervals, they are significantly different (however, if they have overlapping confidence intervals, it is not necessarily true that they are not significantly different).

that the burying beetles successfully secure their reproductive resources (i.e. bury rat carcasses; figure 4a). First, we found that the negative effect of deforestation on the burial

probability of the burying beetles was greatest at mid and high elevations, where the beetle burial probability was lower in cultivated land than in natural forest (GLMM,

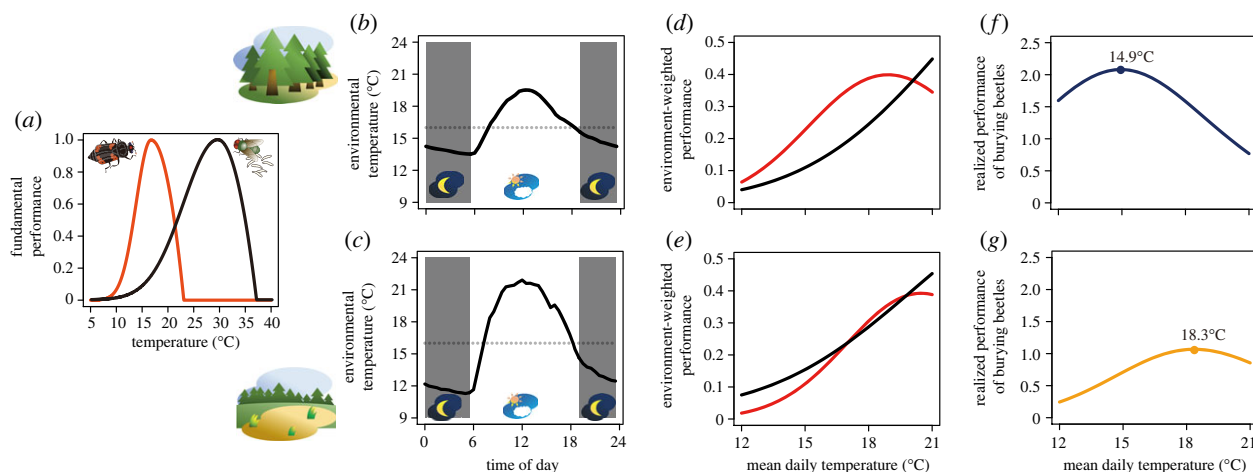


Figure 3. Performance of burying beetles under daily temperature fluctuation and competition from blowflies in natural forest and cultivated land. (a) Fundamental thermal performance curves for burying beetles (red) and blowfly maggots (black). An example for daily temperature profile in (b) forest (DTR = 7°C) and (c) cultivated land (DTR = 14°C). The horizontal dashed lines represent T_{mean} (16°C). (d) Environment-weighted performance of beetles (red) and blowfly maggots (black) in forest. (e) Environment-weighted performance of beetles (red) and blowfly maggots (black) on cultivated land. (f) Realized performance of burying beetles in forest under competition from blowfly maggots. (g) Realized performance of burying beetles on cultivated land under competition from blowfly maggots. The temperatures labelled in (f) and (g) are predicted optimal mean daily temperatures of the beetles in different habitats.

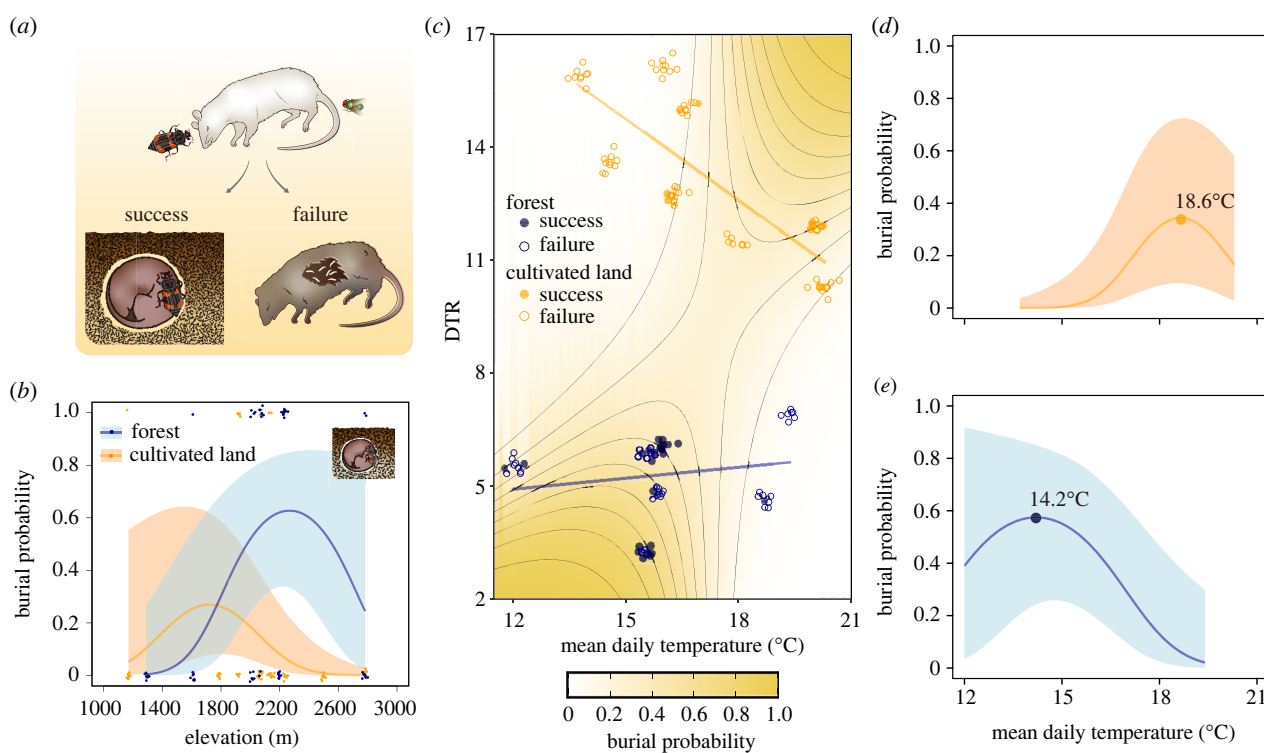


Figure 4. The influence of daily temperature range (DTR) mediating the effect of habitat on burial probability across elevational and temperature gradients. (a) The experimental design. (b) The elevational trend in beetle burial probability in different habitats. (c) The joint influence of mean daily temperature and DTR on burial probability of the carcasses by the beetles in our field experiments. (d) and (e) The influence of mean daily temperature on burial probability in the cultivated land (DTR > 8°C) and the forest (DTR < 8°C). In (c), burial probability is estimated via GLMM. Dots were jittered to avoid overplotting and improve readability. The blue and the orange lines denote the relations between mean daily temperature and DTR in the forest and the cultivated land, respectively. In (b), (d) and (e), lines and shaded areas depict the trends and 95% confidence intervals estimated by GLMM. In (d) and (e), the trends and 95% confidence intervals are predictions along the thermal gradients depicted by the orange and blue lines in (c). The temperatures labelled are the optimal T_{mean} of the two thermal gradients.

Habitat, $Z = 3.40$, $n = 138$, $p < 0.001$; figure 4b; electronic supplementary material, table S3). Interestingly, the negative effects of deforestation were greater at higher elevations, where beetles had a very high probability of successfully burying carcasses in forest but rarely in cultivated land (GLMM, elevation \times habitat interaction, $Z = 2.51$, $n = 138$, $p = 0.018$; the separate test for elevation > 2000 m, $p = 0.01$;

figure 4b; electronic supplementary material, table S3). However, there was no effect of deforestation at lower elevations (the separate test for elevation < 2000 m, $p = 0.43$; figure 4b; electronic supplementary material, table S3b).

Second, in the forest with smaller DTRs, the optimal mean daily temperature for the burying beetles becomes lower than the T_{opt} obtained from the laboratory experiment.

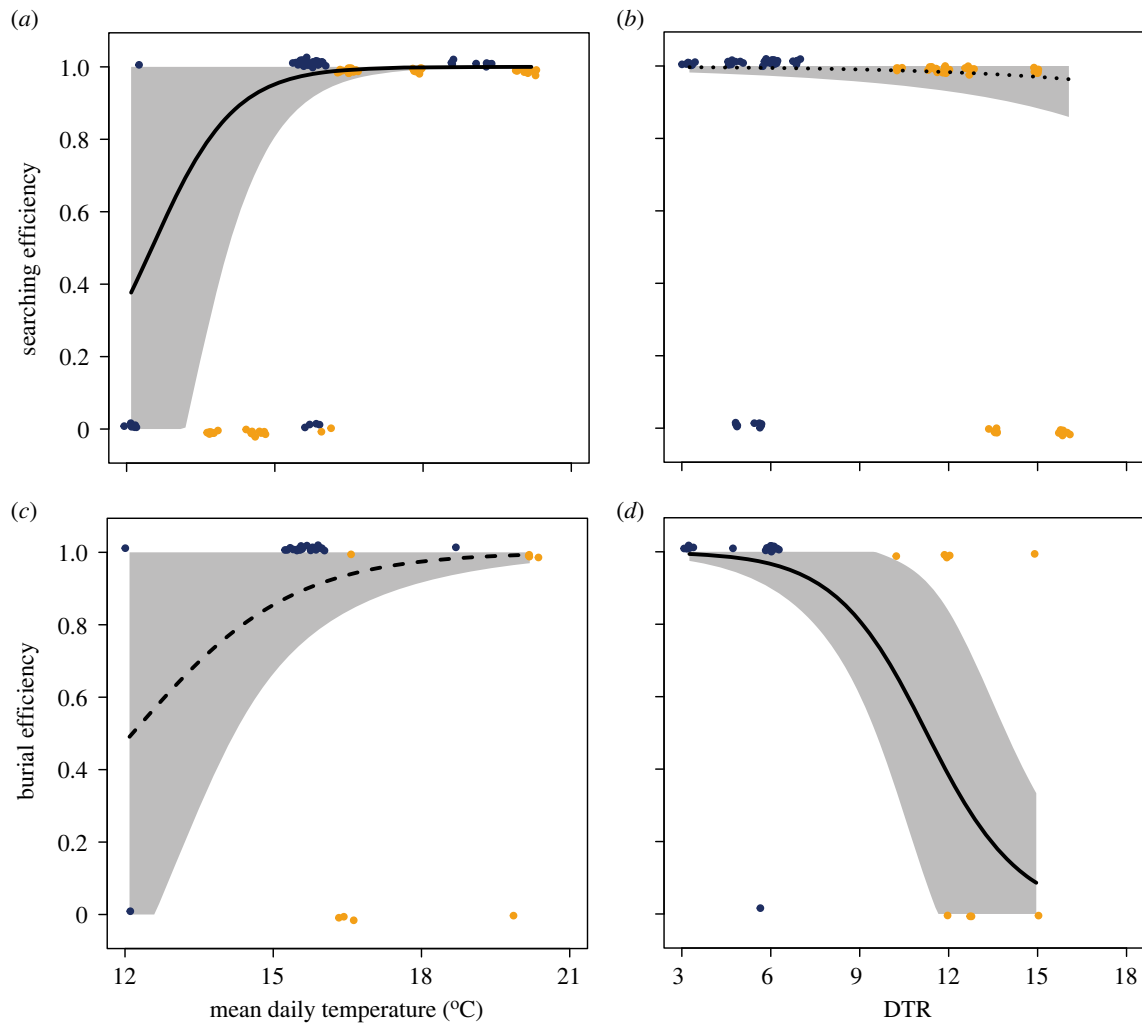


Figure 5. The influences of mean daily temperature and daily temperature fluctuation on the searching and burial efficiencies of beetles. (a,b) The effect of T_{mean} and DTR on searching efficiency of beetles (i.e. probability for beetles to find the carcass in 3 days). (c,d) The effect of T_{mean} and DTR on burial efficiency of beetles (i.e. the probability for beetles to bury the carcass within two days after arriving on the carcass). Lines depict the estimated trends (probability) by CLMMs controlling the effects of all other covariates. The solid lines represent significant trends ($p < 0.05$), the dashed line represents marginally significant tendency ($p < 0.1$), and the dotted line represent nonsignificant relations ($p > 0.1$). Shaded areas depict the 95% confidence intervals estimated by CLMMs. Dots represent samples (blue for forest and orange for cultivated land). Dots were jittered to avoid overplotting and improve readability.

In contrast, in the cultivated land with larger DTRs, the optimal mean daily temperature becomes higher than the T_{opt} . Our analysis of microclimate effects revealed that the interaction of T_{mean} and DTR contributed to the interacting effects of deforestation and elevation on burying beetle carcass burial probability (GLMM, $T_{\text{mean}} \times \text{DTR}$ interaction, $Z = 2.42$, $n = 138$, $p = 0.016$; figure 4c; electronic supplementary material, table S4): the optimal T_{mean} for the burying beetles becomes 18.6°C in the cultivated land (figure 4d) but 14.2°C in the forests (figure 4e), both of which are close to the model predictions (figure 3f,g).

Third, the realized performance of burying beetles at the optimal T_{mean} in the forest (burial probability: 57% at 14.2°C) was much higher than that at the optimal T_{mean} in cultivated land (burial probability: 34% at 18.6°C).

(f) Behavioural mechanisms of how DTR affects competition between burying beetles and blowflies

Previous studies have shown that successful reproduction depends on the beetles' efficiency in finding and burying carcasses [29]. Therefore, we analysed how the thermal environment influences these two behaviors in the field. We

found that the efficiency in finding carcasses improved with increasing T_{mean} (CLMM, effect of T_{mean} on the number of days required to reach a carcass, $Z = -3.07$, $n = 102$, $p = 0.002$; figure 5a, electronic supplementary material, table S5a), but there was no effect of DTR (CLMM, $Z = 1.35$, $n = 102$, $p = 0.18$; figure 5b; electronic supplementary material, table S5a), which may be because that burying beetles search for carcasses mainly in the first two hours after sunset (electronic supplementary material, figure S5) when night-time temperatures have yet to reach their extreme. However, beetle burial efficiency showed a marginally significant tendency to improve with increasing T_{mean} (CLMM, effect of T_{mean} on the number of days required for burying the carcass, $Z = -1.88$, $n = 33$, $p = 0.06$; figure 5c; electronic supplementary material table S5b), but also worsened significantly with increasing DTR (CLMM, $Z = 2.53$, $n = 33$, $p = 0.012$; figure 5d; electronic supplementary material, table S5b). We further analysed how T_{max} and T_{min} affected burial efficiency and found that burial efficiency worsened with decreasing T_{min} (CLMM, $Z = -2.52$, $n = 33$, $p = 0.012$; electronic supplementary material, figure S6a, and table S6), indicating that low night-time temperatures reduce the activity of burying beetles on carcasses. However, burial efficiency also showed a marginally significant tendency

to worsen with increasing T_{\max} (CLMM, $Z = 1.80$, $n = 33$, $p = 0.073$; electronic supplementary material, figure S6b and table S6), which may reflect either a decrease in burying beetle activity or an increase in blowfly maggot development. We found that carcasses decayed faster due to maggot feeding (Wilcoxon rank-sum test, $n = 17$ for each treatment, $p = 0.040$; electronic supplementary material, figure S7a) and maggots developed faster (LMM, $t = -3.06$, $n = 569$ individuals from 34 experiments, $p = 0.005$; electronic supplementary material, figure S7b) when DTR was large. Therefore, a reduction in burying beetle activity and an increase in blowfly maggot competition after the beetles found the carcass together drive the negative effect of large DTR on the beetles' burial success.

(g) Field experiment preventing blowfly competition

To experimentally test whether blowfly competition is responsible for the observed pattern of burial success in the field, we also reanalysed data from a previously published field experiment excluding other insects at the same study sites (see Methods and also Tsai *et al.* [32] for details). We found that burying beetles buried 89% of carcasses at almost all elevations and temperatures ($n = 131$, electronic supplementary material, figure S8a) when insects consisting mainly of blowflies were excluded [32]. The experimental treatment of excluding the competitors eliminated the interactive effect of mean daily temperature and DTR on burial success (GLMM, treatment $\times T_{\text{mean}} \times \text{DTR}$ interaction, $Z = -2.46$, $n = 363$, $p = 0.014$, electronic supplementary material, figure S8 and table S7a). Neither T_{mean} , DTR, nor their interaction affected burial success when competitors were excluded (GLMM, main effects and interaction of T_{mean} and DTR, $n = 131$, all $p > 0.1$; electronic supplementary material, figure S8a and table S7b). In contrast, we still found a significant interaction between T_{mean} and DTR in the control group, which allowed competitors access to the carcass (GLMM, $T_{\text{mean}} \times \text{DTR}$ interaction, $n = 232$, $Z = 2.67$, $p = 0.008$; electronic supplementary material, figure S8b, and table S7c). This result indicates that temperature alone, as well as other microorganisms, have a very limited effect on the burying success of the beetles in the absence of the blowflies. Finally, we also found that burying beetles had nearly 70% reproductive success after carcass burial in both the treatment (82/116) and control (91/130) groups, suggesting that the effect of interspecific competition occurred mainly before carcass burial.

4. Discussion

Our study provides new insights into assessing the potential vulnerability of species to deforestation across the globe. Based on our analysis of the global climate model, we found that deforestation increases environmental temperature variability more in the tropics than in temperate regions, with greater effects at lower elevations in tropical regions but at higher elevations in temperate regions. In addition, our experiments and models for burying beetles and blowflies show that increased temperature variability due to deforestation affects resource competition between the two species with distinct daily activity patterns, thereby impacting their fitness differently. We found that when temperature variability increased, night-time temperatures became too cold for burying beetles, but daytime temperatures increased in favour of blowfly maggots, thereby enhancing the effects of interspecific competition

and imposing a double penalty on burying beetles. To our knowledge, this is the first experimental study demonstrating the effects of deforestation-induced changes in DTR on interspecific competition. Our results suggest that understanding how climatic variability is affected by environmental exploitation is one of the keys to understanding interspecific competition and its effect on species fitness.

Forests maintain relatively stable environments for mountainous species, particularly invertebrates [57], through cooling the understorey when ambient temperatures are hot and warming the understorey when ambient temperatures are cold [6]. Although dense forests can absorb 75–90% of incoming solar radiation [58], in deforested habitats, moisture loss and increased exposure to short-wave radiation (UV and visible light) [59] increase daily maximum temperature. Moreover, at night in forests, long-wave (infrared) radiation from the surface is absorbed and partially reflected by the canopy, resulting in higher night-time temperatures in forests than in open habitats [60,61]. Our results from the global microclimate modelling show that deforestation significantly increases temperature variation experienced by organisms, not just in tropical regions but also in temperate regions at higher elevations. Many previous studies have argued that species inhabiting tropical lowlands are particularly vulnerable to deforestation because forests in these areas suffer from the highest rate of deforestation [62,63]. However, our study suggests that species inhabiting forests in low-elevation areas in the tropics and high-elevation areas in the temperate zone will both be at great risk from deforestation.

Our study also suggests that interspecific competition is a crucial mechanism by which DTR affects organisms, particularly those engaging in exploitative competition for common resources. A primary reason for this is that the resource-utilizing efficiency of a species active during daylight hours will influence the resources remaining for its nocturnal competitor, and vice versa. Previous studies have rarely explored this possibility, suggesting that stressful daytime temperatures due to warming or deforestation influence diurnal species more [22,23] and rarely affect the performance of nocturnal ectotherms that are typically inactive during daylight hours [64]. In contrast to these predictions, our findings suggest that daytime temperature changes can negatively affect nocturnal species by affecting the competitive ability of diurnal species that use the same resources.

Previous studies discussing TPCs have acknowledged the importance of actual environmental temperature on thermal performance (referred to as the probability of performance [39] or the environment-weighted performance [20]). Here, we further point out that it is crucial to understand the critical temporal and spatial environmental temperatures that affect organisms' fitness to calculate environment-weighted performance correctly. In addition, if the fitness of a species is affected by competitors, it is also essential to understand the spatial and temporal distribution of environmental temperatures critical to the competitor species. As shown here, nocturnal burying beetles are more directly impacted by changes to night-time temperatures, whereas blowfly maggots are influenced by changes to both daytime and night-time temperatures. According to our analysis of global mountain temperatures, the daily low-temperature component is less affected by deforestation, but the daily high-temperature component is significantly increased by forest loss. Therefore, we can predict that nocturnal organisms, which do not compete directly with diurnal

organisms, may be less affected by deforestation. Where nocturnal organisms compete with diurnal organisms for resources, however, careful examination of the diurnal temperature effects on the competitors, alongside nocturnal shifts, is necessary to understand the indirect impact of deforestation on nocturnal species.

In summary, our study provides new insights into the synergistic effects of global climate change and land use change on biodiversity. Currently, most studies use species performance curves and climate projections to predict the future distribution of species [38,39,65]. However, our results suggest that deforestation can significantly alter climate variability in addition to its effects on the mean environmental conditions. In turn, this change can drive shifts in species distributions by affecting species interactions. Moreover, such changes have distinct effects on species with different daily activity patterns. When non-temporally overlapping species compete for resources, the potential for indirect effects of climate change on species interactions must not be overlooked. Therefore, our study highlights the importance of considering the potential effects of increased daily temperature variability due to deforestation on the modulation of interspecific competition, even between species with different diel activity patterns. Consequently, conservation efforts should prioritize areas where deforestation may significantly alter temperature variability, such as tropical regions or temperate mountain ranges, to mitigate the potential negative biotic effects. In addition, consideration of changes in temperature variability due to land-use change is also necessary to predict species responses and interactions under ongoing global climate change. Ultimately, our results emphasize the need to study the factors

affecting the spatial and temporal variability of diurnal temperature ranges and to consider the daily activity patterns of different species to better predict climate-mediated biological interactions and species distribution changes under global climate change.

Data accessibility. The published raster layers of global microclimate data are available at: <https://doi.org/10.6084/m9.figshare.878253> [66]. The raster layers of global land-cover data are available at <http://www.earthenv.org>. The published raster layer of global elevational data is available at: <https://www.worldclim.org>. The kml file for the study sites and the photographs taken for measuring foliage cover are available from Zenodo at <https://doi.org/10.5281/zenodo.7699201> [50]. All other data are available in Dryad [67] at <https://doi.org/10.5061/dryad.1m8pk0xv>.

The data are provided in electronic supplementary material [68].

Authors' contributions. S.-F.C.: data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; D.R.R.: methodology, writing—review and editing; I.-C.C.: conceptualization, methodology, writing—review and editing; Y.-M.F.: investigation; H.-Y.T.: investigation; Y.-W.Z.: investigation; S.-F.S.: conceptualization, data curation, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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