

ARTICLE

Limits to species distributions on tropical mountains shift from high temperature to competition as elevation increases

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Abstract

Species turnover with elevation is a widespread phenomenon and provides valuable information on why and how ecological communities might reorganize as the climate warms. It is commonly assumed that species interactions are more likely to set warm range limits, while physiological tolerances determine cold range limits. However, most studies are from temperate systems and rely on correlations between thermal physiological traits and range limits; little is known about how physiological traits and biotic interactions change simultaneously along continuous thermal gradients. We used a combination of correlational and experimental approaches to investigate communities of *Drosophila* flies in rainforests of the Australian Wet Tropics, where there is substantial species turnover with elevation. Our experiments quantified individual-level and population-level responses to temperature, as well as the impact of interspecific competition under different temperature regimes. Species' distributions were better explained by their performance at extreme temperatures than by their thermal optima. Upper thermal limits varied less among species than lower thermal limits. Nonetheless, these small differences were associated with differences in the centered elevation of distribution. Low-elevation species were not those with the lowest tolerance to cold, suggesting that cold temperatures were not limiting their abundance at high elevations. Instead, under upland temperature regimes, abundances of these low-elevation species were reduced by competition with a high-elevation species, in both short- and long-term competition experiments. Our results demonstrate that high-elevation species are confined to their current ranges by high temperatures at lower elevations, indicating that their ranges will be highly sensitive to future warming. Counter to expectation, species interactions strongly influenced community composition at cooler, high-elevation sites. Together, these results raise the possibility that tropical communities differ from better-studied temperate communities in terms of the relative importance of biotic interactions and abiotic factors in shaping community

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composition and how the impact of these factors will change as temperatures increase.

KEYWORDS

biotic competition, climate change, coexistence, *Drosophila*, species distribution, thermal performance curve, thermal tolerance, tropics

INTRODUCTION

Temperature has a fundamental impact on the reproduction, survival, growth, and behavior of organisms (Huey & Kingsolver, 1989; Huey & Stevenson, 1979), strongly influencing species' ranges and abundances (Hoffmann & Blows, 1994; Wilson et al., 2005). As a result, estimates of thermal tolerances based on laboratory assays or species' distributions have been used widely to evaluate species' sensitivity to climate change (Deutsch et al., 2008; Kearney & Porter, 2009). Tropical ecosystems comprise many species that live close to their upper thermal limits (Deutsch et al., 2008; Diamond et al., 2012; Huey et al., 2009) and that may not tolerate or adapt to warmer temperatures (Bonebrake & Deutsch, 2012; Kellermann, Overgaard, et al., 2012). The narrow thermal ranges of tropical insects (Khaliq et al., 2014) also mean that they will need to undertake relatively large latitudinal or elevational range shifts to track their climate envelopes as the climate warms, increasing the risk of extinction and community disassembly (Colwell et al., 2008; Sheldon et al., 2011).

Despite high relevance for understanding species' responses to climate change in tropical ecosystems (Corlett, 2012), it remains uncertain as to whether temperature is the major proximate factor setting the position of the "warm" (low-latitude or low-elevation) limits of species' distributions. While there is a strong correlation between species' lower thermal limits and their cold range boundaries (Kellermann, Loeschcke, et al., 2012), upper thermal limits vary less among species (MacLean et al., 2019; Overgaard et al., 2014) and are often higher than the temperatures that these species experience at their warm range boundaries (Sunday et al., 2012). As a result, observed shifts in cold range boundaries often correlate well with predictions based solely on climate models, while shifts in warm range boundaries usually lag behind predictions (Chen et al., 2011; Sunday et al., 2012). A great challenge to predicting changes to warm boundaries in response to warming is the role of biotic interactions, which can constrain or extend ranges (Afkhami et al., 2014; Tingley et al., 2014). The importance of biotic interactions is commonly expected to increase under warmer and more humid climatic conditions (Louthan et al., 2015). However, a recent analysis for 654 taxa found that

biotic factors became less important in determining warm limits with respect to the tropics, while abiotic factors remained consistently important across latitudes (Paquette & Hargreaves, 2021), highlighting geographical differences in the relative influences of abiotic and biotic factors on local thermal gradients.

There remains limited empirical evidence on the proximate factors setting range limits in species-rich tropical communities (Feeley et al., 2017; Jankowski et al., 2013), and most such studies examined only the correlation between thermal traits (i.e., critical temperatures and optimal temperatures) and species' distributions (Amundrud & Srivastava, 2020; Cahill et al., 2014; García-Robledo et al., 2016; Nowrouzi et al., 2018; Pintanel et al., 2021; von May et al., 2017). A significant correlation between tolerance and distribution does not rule out a role for biotic interactions: Differing sensitivities of reproductive performance to temperature can further increase the competitive advantage of tolerant species over less tolerant species, sometimes driving qualitative changes in persistence (Lyu & Alexander, 2022). Additionally, the abundance and distribution of a species may be sensitive to temperature change because of the thermal sensitivities of competitors, hosts, consumers, and other interacting species (Gifford & Kozak, 2012; Merrill et al., 2008; van der Putten et al., 2010). In studies of species' distributions along thermal gradients, niche underfilling has often been used to indicate the influence of biotic interactions (Chick et al., 2020; O'Brien et al., 2017), but biotic interactions, such as competition, have rarely been measured directly. A coupled characterization of fundamental thermal performance and temperature-dependent biotic interactions within a complete guild along an environmental gradient is lacking. Such studies can help unify the long separate concepts of environmental and biotic filters (HilleRisLambers et al., 2012), as well as provide realistic information on thermal sensitivities to pinpoint the components of climate change driving species redistribution and community reorganization (Chen & Lewis, 2023b).

To investigate the roles of thermal tolerances and biotic interactions in influencing species' range limits and structuring communities, we focused on the community of *Drosophila* flies occupying mountain rainforest

habitats in northeastern Australia. These and other tropical mountains provide natural environmental gradients to test the sensitivity of species to temperature (Corlett, 2011), with pronounced changes in species composition with elevation for many taxa (Williams et al., 2003). We hypothesized that species turnover along the elevational gradient would result from thermal constraints at cool, high-elevation sites but from competitive exclusion at warmer, lowland sites. We first quantified species' elevational distributions in the field and then measured thermal performances and competitive outcomes to test the following predictions: (1) Species with relatively low abundance at upland sites ("lowland species") would be the least cold-tolerant, but (2) species with relatively low abundance at lowland sites ("upland species") would not necessarily be the least heat-tolerant. We further predicted that (3) species would be competitively excluded from local assemblages by locally abundant species under the thermal conditions typical at low elevations, but not at high elevations.

METHODS

We collected data on species' elevational distributions in the field, their reproductive performance on thermal gradients, adults' resistance to acute thermal stress (by knockdown assay), and the short-term and long-term outcomes of interspecific competition under low and high temperatures. Figure 1 shows the conceptual forms of data included in this study and the major procedures to obtain them. All statistics mentioned in this section were performed with R version 4.0.3 (R Core Team, 2020). Original data (Chen & Lewis, 2022) and code for analysis (Chen & Lewis, 2023a) are available on Zenodo.

Species distributions along elevational gradients

We used a standardized method to survey the relative abundance of different *Drosophila* species, allowing us to calculate indices of elevational distributions. These indices were used in later sections to test predictions of thermal traits and competitive abilities of species of different distribution types.

Field survey

Relative abundances of various rainforest *Drosophila* species across elevation were estimated by surveying rainforest sites at Paluma Range (18°59.031' S, 146°14.096' E) and Kirrama

Range (18°12.134' S, 145°53.102' E), Queensland, Australia. We sampled three sites on each mountain, at elevations of 70, 350/390, and 730/880 m (subsequently referred to as low, mid, and high elevation, respectively) from 11 March to 12 April 2016. These sites lie within the Wet Tropics bioregion, which has high levels of endemism associated with cool and moist upland refugia (Williams et al., 2003). Abundances of *Drosophila* at these sites peak from March to June. *Drosophila* pupae were sampled using bottle traps baited with fermented banana hanging at the understory level. We set up 15 traps (five traps with exposure times of 12, 15, or 24 days) at each site to collect *Drosophila* offspring of the pupal stage. For each site, all pupae were taken back to the laboratory and mixed, and 182 pupae were randomly deposited in two 96-well plates and then sent for DNA sequencing. Of the total 1092 pupae (from six sites), 716 were successfully identified to species by DNA metabarcoding, with 86–134 pupae at each site (more details in Jeffs et al., 2021). Two infrequent species, *Drosophila serrata* (one pupa) and *Drosophila immigrans* (four pupae), were excluded from analyses.

Distribution analysis

Two methods were used to assess elevational distribution for individual species. First, the probability of detecting a particular *Drosophila* species among other co-occurring *Drosophila* species was modeled as a function of elevation as a continuous variable, mountain (Paluma or Kirrama), and their interaction term in a generalized linear model with a binomial error distribution. For each species, the response variable was 1 if the pupa was identified as the focal species and 0 if it was identified as any other species. Second, since none of the species had a bimodal distribution with elevation, abundance-weighted mean elevation (hIndex) was used as a simple alternative method to quantify distributions. The location of each pupa was assigned a value of 0, 0.5, or 1 if it was collected at low-, mid-, or high-elevation sites, respectively. hIndex was calculated for each species by averaging these values for samples from both mountains. Correspondence between the two measures was tested by Spearman's rank correlation test between the coefficient value for elevation in the regression and hIndex.

Maintenance of laboratory cultures

We additionally collected living flies from several field sites to establish laboratory populations for experimental measurements. To minimize adaptation to laboratory conditions, we maintained each *Drosophila* species by

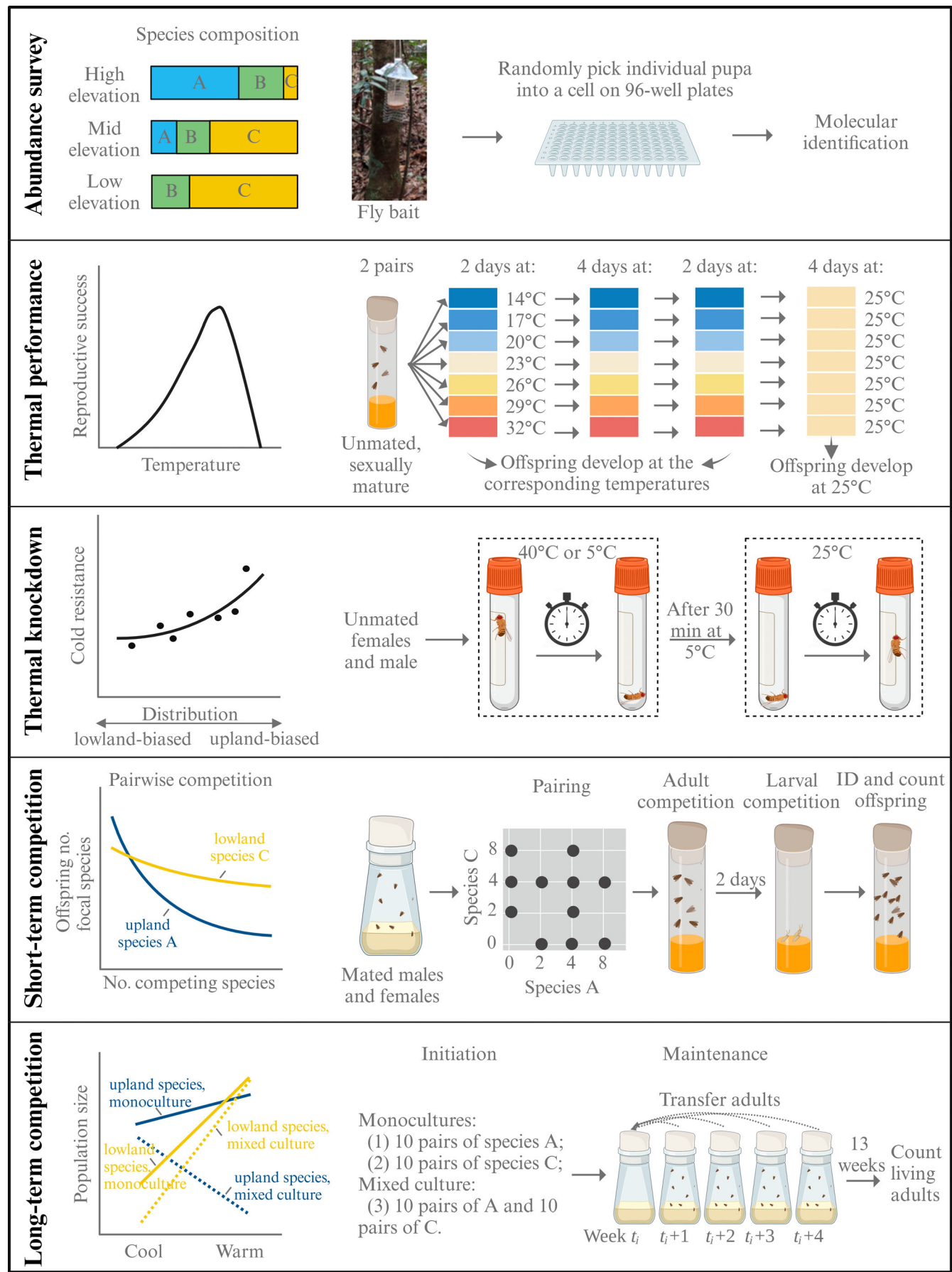


FIGURE 1 Legend on next page.

keeping multiple highly inbred strains (descendants of a single wild-caught female, thus called an isofemale line) collected from high- and low-elevation rainforest sites in 2017 and 2018. Cultures were first established at James Cook University for a short period and then maintained at the Biology Centre, Czech Academy of Sciences. They were maintained at 24°C for approximately 15–30 nonoverlapping generations before being transferred to the Department of Zoology, University of Oxford, in December 2018. These cultures were further maintained at 25°C for another four to seven nonoverlapping generations to acclimate. Cultures and all experiments mentioned below were maintained under a 12 h/12 h light/dark cycle.

To revive the genetic diversity of a population, unmated individuals from several isofemale lines were allowed to mate freely with each other to establish mass-bred lines (MBLs). A MBL is made of four isofemale lines (exceptions are listed in Appendix S1: Table S1). Previous studies found high gene flow between mountains and no local adaptation to elevations (O'Brien et al., 2017; Schiffer et al., 2007). To reflect the average value of traits, the four isofemale lines were from different mountains and elevations if possible (Appendix S1: Table S1). For each species, two independently reared MBLs were maintained for four to six generations to allow genetic recombination and then mixed into a large population. These mass-bred populations were maintained at 25°C until March 2020 and at 23°C thereafter. Measurements taken from these mass-bred populations to compare traits among different *Drosophila* species should not have been influenced by maternal effects, acclimation, or isofemale line effects.

Eight *Drosophila* species (*D. bipectinata*, *D. birchii*, *D. bunnanda*, *D. pallidifrons*, *D. pandora*, *D. pseudoananassae*, *D. simulans*, *D. sulfurigaster*) sourced from the Queensland tropical rainforest plus a laboratory population of *D. melanogaster* (wild type, *Dahomey* strain) were measured for cold resistance, heat resistance, and thermal performance curves (collectively called thermal traits). *Drosophila melanogaster* does not occur naturally at the study sites but was measured as a benchmark for future comparisons. Competitive outcomes under different temperature regimes were assessed for five species (*D. bipectinata*, *D. pallidifrons*, *D. pandora*, *D. pseudotakahashii*, *D. sulfurigaster*). *Drosophila rubida* was not measured because it was difficult to raise to a

large number and to synchronize development time with the other species. The thermal traits of *D. pseudotakahashii* were not measured because its population was contaminated by another species at the time. A new mass-bred population derived by crossing two uncontaminated isofemale lines was constructed later for the competition experiment.

Reproductive thermal performance

We exposed adult *Drosophila* to seven temperatures ranging from 14 to 32°C and measured how their reproductive success changed with temperature. We extracted critical and optimal temperatures for reproduction from the thermal performance curves and examined their correlations with centered elevations of distribution.

Experimental measurements

To prepare adult flies for measurements, fly eggs collected from the population cage were reared at low density (<100 eggs per vial) at 25°C. Emerging adults were separated by sex within 12 h of emergence to guarantee that they were unmated. Rearing was started on different days for different species to synchronize the first day of egg laying (1–4 days after emergence). Two additional vials with five pairs of flies were monitored daily for egg laying. Two days after the first observation of egg laying in both vials, two virgin females and two virgin males were paired in a new vial containing 4 mL *Drosophila* medium (weight/volume concentration: 8% corn flour, 4% yeast, 5% sugar, 1% agar, and 1.67% methyl-4-hydroxybenzoate). Vials were randomly assigned to water baths set at one of seven constant temperatures (14, 17, 20, 23, 26, 29, and 32°C). This range of temperature spans the temperatures our *Drosophila* usually experience in the field. For each species and each temperature treatment, eight replicates were evenly split between two experimental blocks, making up a total of 1512 vials. To measure productivity at different temperatures, vials were submerged with the water level kept above the zone within which flies could freely move. The temperature and relative humidity of vials in each water bath were monitored within two empty tubes placed at the center and the corner. Observed temperatures varied

FIGURE 1 Summary of methods. Five sets of data concerning field distribution of *Drosophila* species, thermal performance curves, physiological thermal tolerance, short-term pairwise competition outcomes, and long-term competition outcomes are included in this study. Conceptual forms of the data and the major experimental procedures are shown. Photo of the field bait was taken by Jinlin Chen. The image was created with [BioRender.com](https://www.biorender.com).

$\pm 0.5^\circ\text{C}$ around the set temperature. Temperatures in the center of the water bath were on average 0.5°C higher than at the corners; the average of the former during the experimental period was used as the corrected temperature in analyses. Relative humidity levels were similar to field conditions, ranging between 80% and 95%.

Flies in the experimental vials were left to lay eggs on fresh food for 48 h (vials from the first and second days). They were then transferred to new food and kept in their corresponding water baths for a further 4 days before being put onto new food for another 48 h (vials from the seventh and eighth days). Vials containing eggs from the two 48-h periods were kept at the corresponding temperature until adults emerged. Productivities for the two periods are shown separately in Appendix S1: Figure S1. We averaged these values to reflect the relative reproductive success in early adult life (within 14 days of emergence).

After 8 days in water baths, all flies were returned to 25°C , a favorable temperature, in new vials with fresh food for a further 4 days before being sacrificed. Their offspring developed at 25°C until eclosion. These adult offspring numbers reflect the recovered reproduction following 8 days of exposure to different temperatures. The numbers of surviving parents were recorded when flies were transferred onto new food on the third, seventh, and ninth days and eventually sacrificed on the 13th day. Offspring numbers were counted 5–7 days after the first emergence was observed. The experiment was conducted from May to August 2019.

Thermal performance curves

A multilevel, nonlinear piecewise model was fitted to describe how reproductive success changed with temperature for all nine *Drosophila* species tested. We used the “Briere2” function (Briere et al., 1999) to describe how reproductive performance (square-rooted daily productivity per female) changed with temperature:

If $T \leq \text{RTmin}_i$ or $T \geq \text{RTmax}_i$, then reproductive performance equals 0. Otherwise,

$$P(i, T) = a_i \times T \times (T - \text{RTmin}_i) \times (\text{RTmax}_i - T)^{1/b_i}, \quad (1)$$

where $P(i, T)$ is the theoretical reproductive performance of species i at temperature T , RTmin_i and RTmax_i are respectively the minimum and maximum temperatures for species i to reproduce, a_i is a scaling factor, and b_i is a shape factor of the curve for species i .

The observed reproductive performance, $P(i, T)$, was modeled assuming a Gaussian distribution of errors as shown in Equation (2). A Gaussian distribution is not

ideal for modeling transformed count data, which are all positive. However, models using untransformed counts with Poisson, zero-inflated Poisson, negative binomial, or lognormal distributions did not adequately converge.

$$P(i, T) \sim \text{Gaussian}\left(\widehat{P(i, T)}, \sigma_{P(T)}^2\right). \quad (2)$$

As SDs, $\sigma_{P(T)}$, tend to get smaller as temperature approaches the critical points (beyond which performance is zero), we assumed seven different $\sigma_{P(T)}$ for our seven test temperatures. They follow:

$$\sigma_{P(T)} \sim \text{Gaussian}(\mu_{\sigma_P}, \sigma_{\sigma_P}^2), \quad (3)$$

where mean, μ_{σ_P} , and variance, $\sigma_{\sigma_P}^2$, are hyperparameters that describe the mean and variance of $\sigma_{P(T)}$.

RTmin_i , RTmax_i , a_i , and b_i are parameters of the “Briere2” function describing the thermal performance curve of species i . We assumed that values of the i th species are samples from Gaussian distributions reflecting distributions of these parameters across *Drosophila* species (Equations 4–7). Their means and variances are also hyperparameters defined by priors. Additionally, the values of a_i and b_i were bounded to be positive. The values of RTmin_i were bounded to be lower than 17°C , and the values of RTmax_i were bounded between 26 and 35°C based on prior knowledge of the range of temperatures within which our species can reproduce:

$$\text{RTmin}_i \sim \text{Gaussian}(\mu_{\text{RTmin}}, \sigma_{\text{RTmin}}^2), \quad (4)$$

$$\text{RTmax}_i \sim \text{Gaussian}(\mu_{\text{RTmax}}, \sigma_{\text{RTmax}}^2) \quad (5)$$

$$a_i \sim \text{Gaussian}(\mu_a, \sigma_a^2), \quad (6)$$

$$b_i \sim \text{Gaussian}(\mu_b, \sigma_b^2). \quad (7)$$

Prior distributions of hyperparameters μ_{RTmin} , μ_{RTmax} , μ_a , μ_b , and μ_{σ_P} are Gaussian distributions with reasonable means (15°C , 30°C , 0, 0, 0) and large SDs (10, 10, 1, 10, 10) compared with the realistic range of these parameters in our species. The prior distribution of the hyperparameters σ_{RTmin}^2 , σ_{RTmax}^2 , σ_a^2 , σ_b^2 , and $\sigma_{\sigma_P}^2$ is inverse-gamma (0.001, 0.001), which is a commonly used noninformative distribution for prior of variance.

The multilevel model was fitted under a Bayesian framework using Markov chain Monte Carlo sampling by the rstan package (Stan Development Team, 2020). The model converged (indicated by $\hat{R} \leq 1.01$), and performance was acceptable in diagnostic plots (Appendix S1: Figure S2). Medians of the posterior distributions for

$RT_{min,i}$, $RT_{max,i}$, a_i , and b_i were used to construct the thermal performance curve of species i . Optimal temperatures for peak reproduction (RT_{opt}) were deduced from known parameters:

$$RT_{opt} = \frac{h + l + \sqrt{h^2 + l^2 - 4b^2 RT_{min} RT_{max}}}{4b + 2}, \quad (8)$$

where

$$h = 2bRT_{max}, \quad (9)$$

$$l = (b + 1)RT_{min}. \quad (10)$$

Testing for associations between reproductive thermal traits and species distributions

Among the tropical *Drosophila* species, the medians of the posterior distributions of RT_{min} , RT_{max} , and RT_{opt} were modeled as a function of hIndex in a linear model with phylogenetic correction. The phylogenetic tree was derived with modification from Finet et al. (2021) (Appendix S1: Figure S3). Productivity at 29 and 17°C and recovered productivity after 29 and 14°C were used as direct measurements of performance at high or low temperatures. These temperatures were chosen because they are known to cause stress to the reproduction of the focal *Drosophila* species and correspond to realistic understory air temperatures during the hottest and coolest months. These productivities were modeled as a function of hIndex and experimental block as fixed effects and species as a random effect in the generalized linear mixed-effect models (assuming errors followed a negative binomial distribution) with phylogenetic correction using the brms package (Bürkner, 2021). Species was included as a random effect to account for repeated measures. *Drosophila simulans* was not found in the standardized field survey of relative abundance, so it was not included in the regressions. It is potentially a lowland-biased species because we only found their isofemale lines from lowland sites when we tried to collect as many isofemale lines as possible from different elevations. Adding *D. simulans* as a lowland-only (hIndex = 0) species to the regression did not change the conclusions.

Thermal knockdown

We measured the physiological tolerance of each *Drosophila* species to extremely cold and hot environments and then examined their correlations with distribution patterns.

Experimental measurements

Resistance to extreme cold temperature was measured as knockdown time for each individual at 5°C and the time for recovering muscle coordination at 25°C after a 30-min extreme cold exposure. The constant temperature chosen for cold stress studies is often around 0°C (Gibert et al., 2001). As tropical species often have significantly weaker cold resistance (Gibert et al., 2001), 5°C was used instead to increase the variation among the tested species after pilot trials. Heat stress was chosen to be 40°C, which follows common practice for *Drosophila* species (Hoffmann et al., 2003) and is expected to capture the between-species variance in heat tolerance over a time scale that is convenient to measure (Jørgensen et al., 2019). After being knocked down by heat (40°C), most flies did not survive. In this case, only knockdown time was used to evaluate resistance to heat. The knockdown experiments were conducted from May to June 2019.

Virgin adult flies (siblings of those used for reproduction measurements) were kept in same-sex groups at 25°C for 9–10 days before knockdown assays. Assays were conducted for male and female flies separately. An observation rack was divided into nine (3 × 3) cells. Each cell was randomly assigned one of the nine *Drosophila* species and held seven flat-bottomed 3 mL glass vials, each with a randomly selected individual of the allocated species. One set of observations in such a setup represents a single block. We repeated measurements for three experimental blocks, and the allocation of species to cells was redrawn for each block. In total, we measured 21 individuals per sex per species. During measurement, the observation rack was moved immediately to the incubator preset at 5 or 40°C. Every tube was examined once every minute, and flies that lost their ability to stand in that minute were recorded (defined as the knockdown time). After exposure to 5°C for 30 min, all flies were in a chill coma. The observation rack was moved to a 25°C room. Flies were left undisturbed, and the time taken until each fly regained its ability to stand was recorded.

Testing for associations between knockdown resistance and species distributions

The knockdown time by heat, knockdown time by cold, and recovery time from cold of each sex were first compared among species using ANOVA. When interspecific variation was observed, they were modeled as a function of hIndex, block, and cell position as fixed effects and species as a random effect in linear mixed-effect models with phylogenetic correction using the brms package.

Species was included as a random effect to account for repeated measures for each species.

Short-term competition

Pairs of *Drosophila* species were reared together in the same vials for one generation to evaluate how interspecific competition affects the observed reproductive success and predicted coexistence patterns under temperature regimes typical of low-elevation and high-elevation sites.

Experimental design

We used incubators set at alternating temperatures mimicking average daytime and nighttime temperatures in February at high-elevation (23°C/21°C) and low-elevation (28.5°C/24°C) sites (Appendix S1: Figure S4). Adults to establish the competition experiment were reared in bottles (30 mL fresh medium) at moderate density (300–500 per bottle) at their testing temperatures. After eclosion, individuals that emerged within 48 h were kept together in mixed-sex containers. Two days after the first observation of egg laying, adults of different sexes were separated and from the following day were allowed to pair and lay eggs in new experimental vials (5 mL medium) for 2 days, without or with another competitor species.

Five species were chosen as representative species for upland-biased, elevation-generalist, and lowland-biased distribution types (see [Results](#) for the definition of distribution types). The six two-species combinations included lowland species versus upland species: (1) *D. bipectinata* versus *D. pallidifrons*, (2) *D. bipectinata* versus *D. pseudotakahashii*, (3) *D. pandora* versus *D. pallidifrons*; lowland species versus lowland species: (4) *D. bipectinata* versus *D. pandora*; lowland species versus elevation generalist: (5) *D. bipectinata* versus *D. sulfurigaster*; upland species versus elevation generalist: (6) *D. pallidifrons* versus *D. sulfurigaster*. Each combination was tested at different founding densities in a factorial design: (four pairs of species A, two pairs of species B: 4A, 2B), (4A, 4B), (4A, 8B), (2A, 4B), and (8A, 4B). We also included monocultures of each species with two, four, and eight pairs. Each density and species combination was replicated 10 times across two or three blocks staggered by 2 days (two blocks for the *D. pandora* vs. *D. pallidifrons* combination; three blocks for the other five pairs). Offspring that successfully developed to adulthood were identified to species and counted. Females of *D. bipectinata* and *D. pandora* were

difficult to distinguish, so their offspring numbers were substituted by doubling their male numbers in this pairwise combination. The experiment of *D. pandora* versus *D. pallidifrons* was conducted from September to December 2020 and the other five pairs from January to March 2021.

Short-term competitive outcomes

We used the Beverton-Holt model to describe the population growth of a single generation of flies on discrete and temporary resources:

$$N_{\text{focal},1} = \frac{R_0 N_{\text{focal},0}}{1 + \alpha (N_{\text{focal},0} + \beta N_{\text{competitor},0})}, \quad (11)$$

where $N_{\text{focal},0}$ is the number of parents, $N_{\text{focal},1}$ the number of offspring of the focal species, $N_{\text{competitor},0}$ the number of parents of the competing species, R_0 the generational reproduction rate, and α a constant defining the form of the density-dependent relationship. β represents the interspecific competition coefficient of the competitor species to the focal species and defines the equivalence between the two competing species.

Offspring numbers of the focal species were modeled assuming a negative binomial error distribution, under a Bayesian framework using MCMC sampling by the rstan package, as described by Terry et al. (2021). Seventeen competition terms (5α and 12β) were each fitted with a Gaussian prior (mean = 0, $\sigma = 1$). Each species' average R_0 across experiment blocks, μ_{R_0} , was fit with a weak Gaussian prior (mean = 20, $\sigma = 10$). R_0 of each species in different experimental blocks was allowed to deviate from its mean μ_{R_0} , following a Gaussian distribution with a SD sampled from a weak Gamma distribution ($\alpha = 2$, $\beta = 0.1$). The overdispersion term in the negative binomial distribution followed a weak Cauchy distribution ($\mu = 0$, $\sigma = 10$). All parameters were constrained to be positive. Parameters were fitted for cold and warm temperature regimes separately. Both models converged (indicated by $\hat{R} \leq 1.01$); their diagnostics are shown in Appendix S1: Figure S5A,B. Raw data and fitted curves of each pair are shown in Appendix S1: Figure S6. Median values of posterior distributions were used as parameters to infer the equilibrium states of each pair. Following Hassell and Comins (1976), we drew zero-growth isoclines for each pair of competing species and examined the placement of the two isoclines. Stable coexistence requires that the two linear isoclines intersect and that the isocline for the species represented by the x-axis has a steeper negative slope than the species shown on the y-axis.

Long-term competition

To validate the long-term population-level outcomes of asymmetrical competition shown in the short-term competition experiment, we raised one lowland species and one upland species in monoculture and mixed-species culture for multiple overlapping generations under temperature regimes typical of low-elevation and high-elevation sites. We then evaluated the long-term effects of temperature and competition on population sizes.

Experimental design

Four monocultures of each species and eight mixed-species cultures were maintained at each temperature regime for 13 weeks, totalling 32 cultures. The cultures were evenly divided into two blocks starting on different dates. Monocultures were started with 10 pairs of individuals. Mixed-species cultures were started with 10 pairs of individuals of each species. This starting density was very low compared to the equilibrium density. Each culture was maintained in a series of five bottles (30 mL fly medium) following Ayala et al. (1973). At the start of each week, adults surviving in the most recent bottle and adults that had freshly emerged in the older four bottles were separately collected, photographed, and transferred together to a new bottle with fresh food. In this way, adult survival and reproduction were recorded separately. As the total population sizes were relatively stable, they were only counted when the populations were terminated after 13 weeks of maintenance. To avoid pseudo-replication introduced by “incubator” effects, the two incubators were switched between temperature regimes every week, with their contents moved accordingly. Trays were shuffled inside the incubator every 2 days. Temperature and humidity were recorded and the temperature regimes were confirmed during and at the end of the experiments. The experiments were conducted from September to December 2020.

Testing temperature and competition effects on long-term population persistence

Population sizes were modeled as a function of temperature regimes, species, presence/absence of competitors, and their interactions, with culture ID as a random effect in a generalized linear mixed-effects model (assuming errors followed a zero-inflated negative binomial distribution) using the *brms* package. The model diagnostic is shown in Appendix S1: Figure S5C.

RESULTS

Field distributions

The numbers of samples found at low-, medium-, or high-elevation sites for each of the nine major *Drosophila* species (accounting for 99% of all samples) are shown in Figure 2. Distributions quantified using regression and by centered elevation (hIndex) were consistent (Spearman's rank correlation $\rho = 0.93$, p -value = 0.0007, df [degree of freedom] = 7). Among the three elevations sampled, the detection probability of *D. bipectinata* and *D. pandora* increased monotonically toward lower-elevation sites, so they were categorized as lowland-biased species with high confidence. *D. pseudoananassae* showed a lowland bias on one of the two mountains and a midelevation peak on the other. *D. rubida*, *D. sulfurigaster*, and *D. birchii* showed no significant change with elevation and were thus defined as elevation generalists. *D. pallidifrons* and *D. pseudotakahashii* were significantly more likely to be found at high elevations and were thus defined as upland-biased species. Coefficients and p -values of the regressions and hIndex values are shown in Appendix S1:

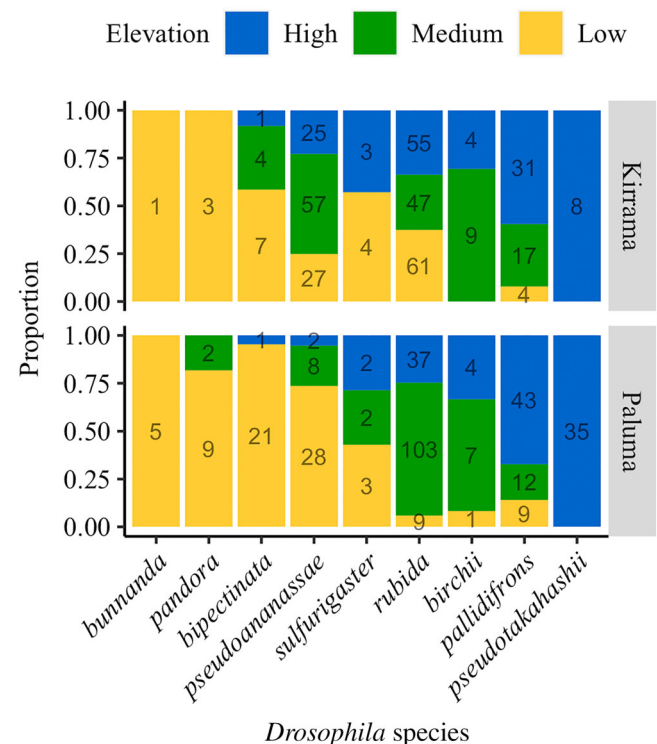


FIGURE 2 Distribution patterns of nine rainforest *Drosophila* species in Kirrama Range or Paluma Range. The proportion of samples found at sites at low (yellow), medium (green), and high (blue) elevations is shown for each species. Numbers on the bars show the counts of samples for each combination of species and site.

Table S2. For *D. bunnanda*, the six records were insufficient for model fitting, but all occurred at lowland sites, and data from a large-scale study suggest that it is a lowland-biased species (Schiffer & McEvey, 2006).

Thermal performance curves

Thermal performance curves of daily productivity per female parent vary among species in terms of the range, optimal temperature, peak productivity, and shape factors (Figure 3; Table 1; see Appendix S1: Figure S2C for original data and fitted curves for each species). The temperature for optimal reproductive performance, RT_{opt} , did not correlate with hIndex (coefficient = 0.09, 95% CI [credible interval] = -2.83–3.01; Figure 3b). Cold tolerances, RT_{min} , varied more among species than heat tolerances, RT_{max} (SD: 2.82 vs. 1.01, respectively). There was no general trade-off between RT_{min} and RT_{max} (Spearman's rank correlation test: p value = 0.10, df = 7; Figure 3c). For example, *D. sulfurigaster* outperforms its upland-biased relative, *D. pallidifrons*, across the temperature range.

Testing correlations between cold tolerance and distribution

RT_{min} values were not correlated with species distribution patterns (Figure 4a; coefficient = -0.41, 95% CI = -4.15–3.43). Similarly, upland-biased species did not show higher productivity at the low temperature, 17°C (Figure 4b; coefficient = -0.27, 95% CI = -3.80–3.05). When exposed to acute sublethal low temperature (5°C), all seven tropical *Drosophila* species showed similarly poor performance compared to *D. simulans* and *D. melanogaster* (Appendix S1: Table S3). Most species did not reproduce during their 8-day exposure to 14°C (Appendix S1: Figure S1B); however, all of them were able to resume productivity once transferred back to 25°C. Species with a higher centered elevation of distribution had slightly but nonsignificantly higher recovered productivity (Figure 4c; coefficient = 0.33, 95% CI = -0.55–1.14). It took longer, but not significantly so, for upland species to regain muscle coordination after chill coma (Figure 4d; male: coefficient = 13.04, 95% CI = -9.31–35.05; female: coefficient = 8.49, 95% CI = -2.18–20.02).

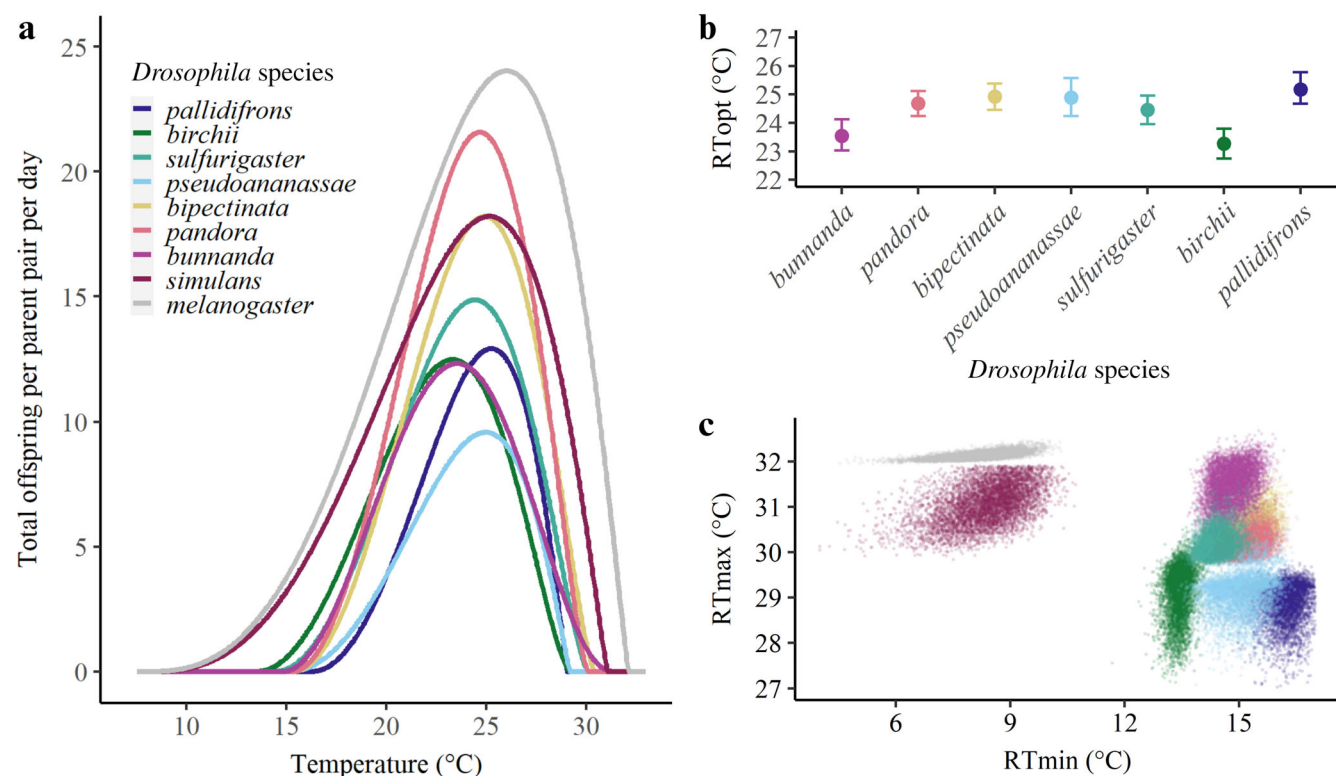


FIGURE 3 Reproductive thermal traits. (a) Thermal performance curves for reproduction of nine *Drosophila* species. The fitted number of adult offspring per pair of parents per day is plotted against temperature. (b) Optimal constant temperatures for reproduction of the seven tropical *Drosophila* species, ordered by their hIndex. (c) Posterior distribution of RT_{max} and RT_{min} values of nine *Drosophila* species. Colors associate with distribution types: The warmer colors indicate species with lower centered elevations of distribution (more lowland-biased); the gray color represents *Drosophila melanogaster*.

TABLE 1 Parameters of thermal performance functions and their 90% credible intervals (CIs) of the nine *Drosophila* species.

Species	<i>a</i> (90% CI)	<i>b</i> (90% CI)	RTmin (90% CI)	RTmax (90% CI)
<i>Drosophila bipectinata</i>	0.0045 (0.0029–0.0059)	1.25 (0.99–1.54)	15.29 (14.56–15.90)	30.47 (30.09–31.12)
<i>Drosophila birchii</i>	0.0033 (0.0022–0.0058)	1.17 (0.95–1.59)	13.45 (13.08–13.79)	29.28 (28.04–29.81)
<i>Drosophila bunnanda</i>	0.0013 (0.0007–0.0023)	0.80 (0.66–1.02)	14.79 (14.17–15.49)	31.51 (30.72–32.10)
<i>Drosophila melanogaster</i>	0.0037 (0.0032–0.0042)	1.73 (1.48–2.04)	8.25 (6.86–9.35)	32.13 (32.03–32.28)
<i>Drosophila pallidifrons</i>	0.0074 (0.0056–0.0101)	1.76 (1.38–2.45)	16.21 (15.50–16.76)	29.06 (28.10–29.39)
<i>Drosophila pandora</i>	0.0052 (0.0037–0.0065)	1.25 (1.03–1.51)	15.26 (14.56–15.80)	30.13 (29.87–30.56)
<i>Drosophila pseudoananassae</i>	0.0053 (0.0034–0.0072)	1.68 (1.19–2.37)	15.07 (14.15–15.91)	29.21 (28.35–29.85)
<i>Drosophila simulans</i>	0.0036 (0.0027–0.0047)	1.70 (1.37–2.28)	8.47 (6.80–9.65)	31.08 (30.34–31.76)
<i>Drosophila sulfurigaster</i>	0.0039 (0.0027–0.0050)	1.25 (1.02–1.51)	14.37 (13.93–14.97)	30.14 (29.85–30.66)

Note: *a* is the scaling factor and *b* the shape factor of the “Briere2” function. RTmin and RTmax are the minimum and maximum temperatures for the species to reproduce.

Testing correlations between heat tolerance and distribution

Species with a lower centered elevation of distribution could reproduce at higher temperatures (Figure 4e; Coefficient between RTmax and hIndex = -3.06 , 95% CI = -5.30 to -0.88). Reproductive performance at 29°C decreased to almost zero among upland-biased species (Figure 4f; coefficient = -5.80 , 95% CI = -9.37 to -2.50). After exposure to 29°C for 8 days, the two species with the highest hIndex could not reproduce when transferred back to 25°C, while four out of the other five elevation-generalist and lowland-biased species resumed reproduction (Figure 4g). Knockdown time at lethally high temperature (40°C) was shorter among species of higher hIndex (Figure 4h; male: coefficient = -6.71 , 95% CI = -13.70 – 0.50 ; female: coefficient = -1.99 , 95% CI = -9.48 – 5.71), indicating these species lose their muscle coordination faster at high temperatures.

Effects of interspecific competition at upland and lowland temperatures

When raised in laboratory conditions mimicking the warmer, lowland sites, reproductive success was highest for the two lowland-biased species, followed by the elevation-generalist species *D. sulfurigaster*. The two upland species could barely reproduce regardless of the presence of competitors (Figure 5; Table 2: proliferation rates $R_0 < 1$). *D. pseudotakahashii*, whose distribution was most constrained to upland sites, had a lower proliferation rate at high temperatures than *D. pallidifrons*. Their competitive effect on lowland species was minimal compared with lowland species’ own intraspecific competition, indicated by low β values (Table 2). The two

lowland species, *D. pandora* and *D. bipectinata*, are expected to coexist stably under lowland temperature conditions, based on their reproductive and competitive parameters.

When raised under cooler, upland conditions, all species could reproduce and sustain their populations (Table 2: $R_0 > 1$ in all cases). Lowland species were strongly affected by the density of *D. pallidifrons*, an upland species (shown by large β values), while upland species were significantly less affected by lowland species. Competition with *D. pallidifrons* under upland conditions was predicted to drive *D. pandora* and *D. bipectinata* to exclusion (Table 2).

In the long-term competition experiment (Figure 6), high temperature drove the upland species *D. pallidifrons* to extinction both in monocultures (except in one replicate where only two adults remained) and when reared together with the lowland competitors. In contrast, the monoculture of the lowland species *D. pandora* remained abundant at both low and high temperatures (temperature effect: 95% CI = -0.26 – 0.12 , overlapping with zero). The presence of *D. pandora* only slightly decreased the population size of *D. pallidifrons* by 27% (median coefficient of competition = -0.32 , 95% CI = -0.14 to -0.49). The presence of *D. pallidifrons* had no significant effect on the population size of *D. pandora* in warm, lowland temperatures (95% CI = -0.28 – 0.06) but reduced *D. pandora* population size by 79% (median coefficient of competition = -1.56 , 95% CI = -1.73 to -1.40) in cool, upland temperatures.

DISCUSSION

Our results do not support the common assumption that cool boundaries to species’ ranges are constrained

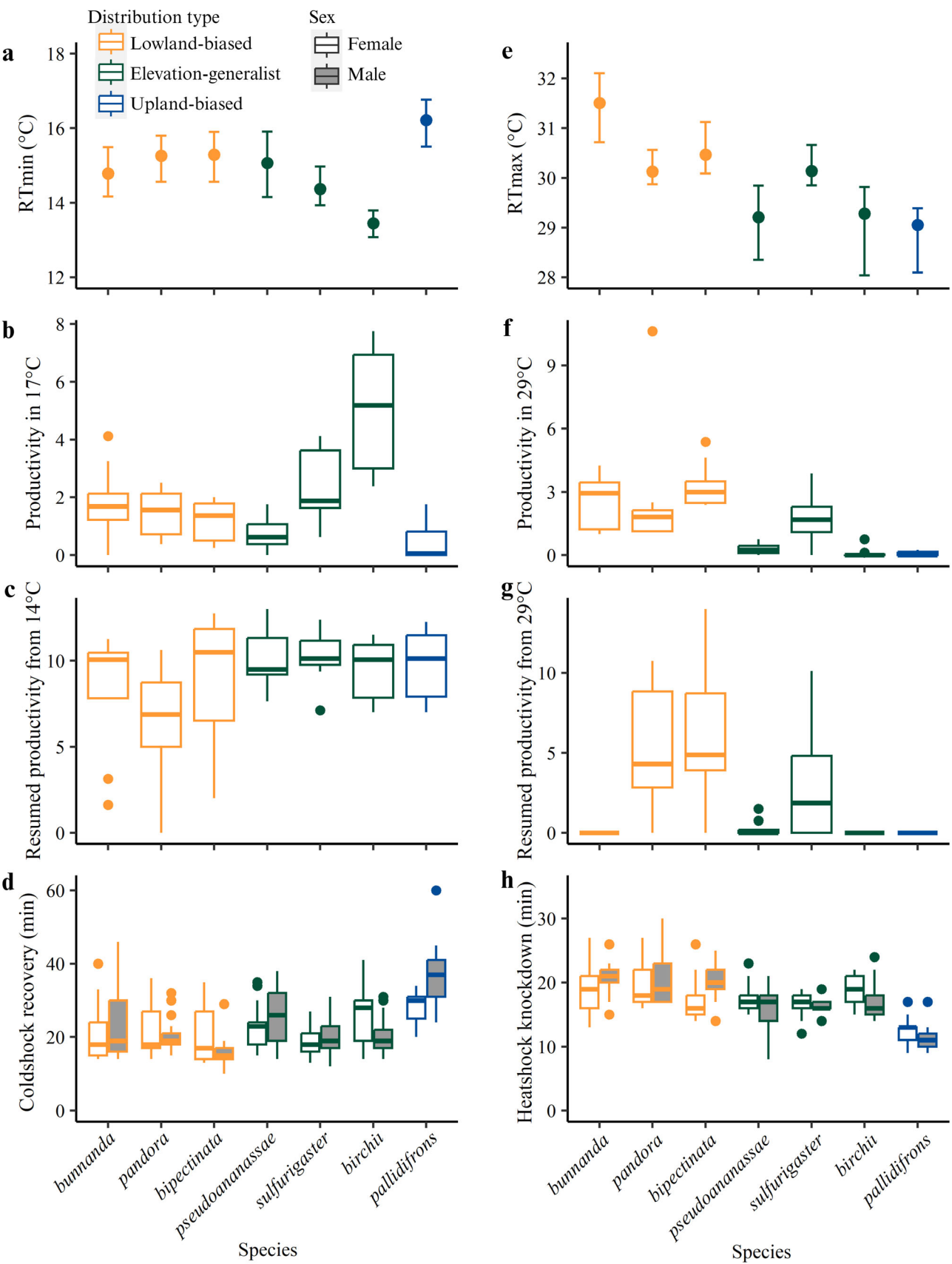


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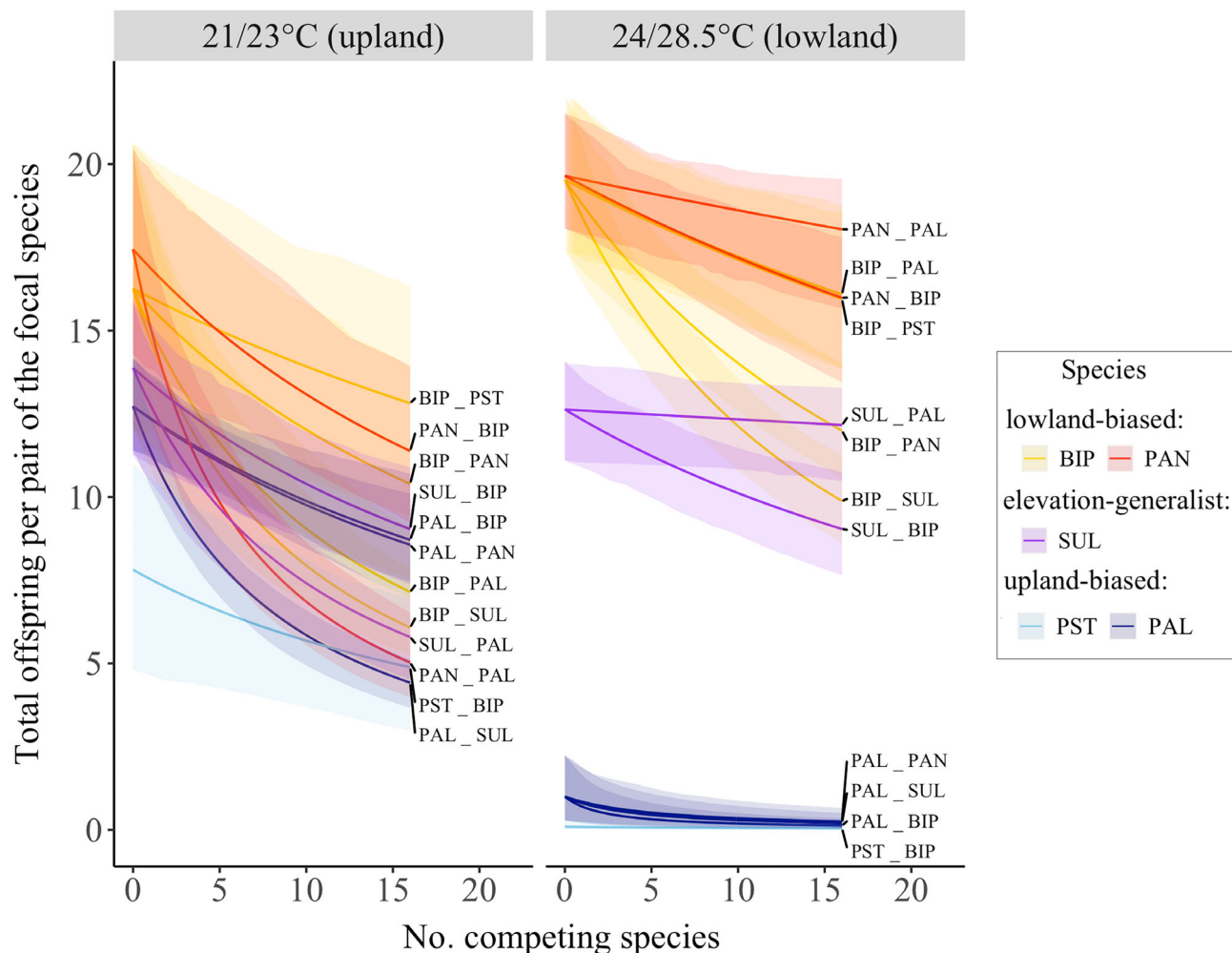


FIGURE 5 Interspecific competition for species pairs under upland (left) and lowland (right) temperature regimes. Each line shows the fitted 2-day productivity per pair of the focal species while changing the number of individuals of the competing species. The identity of the focal species in each pair is indicated by the color of the line (see legend) and by the label (e.g., for BIP_PST, the first code BIP is the focal species and the competitor species is PST). The shaded area indicates the 90% credible interval of the fitted values under the Beverton–Holt model for pairwise species competition. Species abbreviations: BIP = *Drosophila bipectinata*, PAL = *Drosophila pallidifrons*, PAN = *Drosophila pandora*, PST = *Drosophila pseudotakahashii*, SUL = *Drosophila sulfurigaster*.

abiotically (reflecting thermal niches), while biotic interactions (such as interspecific competition) define warm boundaries. Our study adds to a growing body of literature on tropical mountain systems showing significant associations between upper thermal limits and patterns of species turnover with elevation (Amundrud & Srivastava, 2020; García-Robledo et al., 2016; Pintanel

et al., 2021; von May et al., 2017). Notably, this result does not rule out the potential contribution of competition with warm-adapted species to raising warm boundaries to higher elevations. However, the observation that upland species were excluded from the lowest elevations solely by high temperatures experienced on a daily basis implies that further warming will likely drive

FIGURE 4 Reproductive and physiological thermal tolerance of seven tropical *Drosophila* species. Species are ordered by their hIndex, from lowland-biased species (left) to upland-biased species (right). Colors represent distribution types: Orange for lowland species, green for elevation generalists, and blue for upland species. Cold tolerance is represented by RTmin (a), productivity at 17°C (b), recovered productivity after 14°C (c), and recovery time after chill coma (d). Heat tolerance is represented by RTmax (e), productivity at 29°C (f), recovered productivity after 29°C (g), and knockdown time at high temperature (h). Panels (a) and (e) show medians and 90% credible intervals of posterior distribution of estimated parameters. Boxplots in (b)–(d) and (f)–(h) show minimum, 25th percentile, median, 75th percentile, maximum, and potential outliers. In (d) and (h), data for males (shaded) and females (unshaded) are plotted separately.

TABLE 2 Fitted values of parameters (with 90% credible intervals [CIs]) and predicted equilibrium states of pairwise interspecific competition models.

Temperature	Focal species	R_0 (90% CI)	α (90% CI)	Competitor	β (90% CI)	Equilibrium state of focal species
Cool, upland	BIP	11.36 (8.06–15.21)	0.05 (0.02–0.09)	PAL	2.26 (1.4–4.08)	Excluded
				PAN	0.99 (0.47–1.95)	Excluded
				PST	0.47 (0.12–1.09)	Stable coexistence
				SUL	2.95 (1.91–5.25)	Excluded
	PAL	27.94 (19.52–38.66)	0.42 (0.27–0.64)	BIP	0.30 (0.15–0.49)	Dominant
				PAN	0.32 (0.14–0.52)	Dominant
				SUL	1.22 (0.9–1.62)	Unstable coexistence
	PAN	13.68 (10.4–17.85)	0.07 (0.04–0.12)	BIP	0.74 (0.33–1.36)	Dominant
				PAL	3.41 (2.26–5.59)	Excluded
	PST	6.27 (3.4–10.66)	0.08 (0.03–0.19)	BIP	0.79 (0.35–1.76)	Stable coexistence
	SUL	20.96 (14.27–31.13)	0.25 (0.14–0.44)	BIP	0.41 (0.19–0.67)	Dominant
				PAL	1.05 (0.71–1.53)	Unstable coexistence
Warm, lowland	BIP	15.35 (12.51–19.05)	0.07 (0.05–0.11)	PAL	0.29 (0.07–0.63)	Dominant
				PAN	0.87 (0.54–1.35)	Stable coexistence
				PST	0.31 (0.07–0.63)	Dominant
				SUL	1.35 (0.93–2)	Excluded
	PAL	0.99 (0.19–2.37)	0.12 (0.02–0.46)	BIP	6.81 (2.98–22.27)	Unable to establish
				PAN	2.99 (1.52–8.93)	Unable to establish
				SUL	3.98 (1.77–12.83)	Unable to establish
	PAN	17.18 (14.2–21.24)	0.09 (0.06–0.14)	BIP	0.27 (0.08–0.51)	Stable coexistence
				PAL	0.11 (0.01–0.29)	Dominant
	PST	0.65 (0.06–1.95)	1.59 (0.61–2.92)	BIP	0.59 (0.07–2.15)	Unable to establish
	SUL	13.65 (10.26–19.03)	0.15 (0.09–0.24)	BIP	0.37 (0.18–0.62)	Dominant
				PAL	0.04 (0–0.14)	Dominant

Note: R_0 is the reproductive rate (per generation), α a constant defining the form of the density-dependent relationship, and β the interspecific competition coefficient. Species abbreviations: BIP = *Drosophila bipectinata*, PAL = *Drosophila pallidifrons*, PAN = *Drosophila pandora*, PST = *Drosophila pseudotakahashii*, SUL = *Drosophila sulfurigaster*.

contraction of their ranges directly. In contrast, lowland species were not worse than upland species at surviving or reproducing at low temperatures. However, lowland species were outcompeted by one upland species whose distribution was confined to high elevations as a result of intolerance to heat. Another manipulative experiment (Chen & Lewis, 2023b) confirmed that competition, which was sensitive to extreme high temperature, prevented the establishment of low-elevation species in the upland community. This important role of interspecific competition at cold boundaries on elevational gradients (also shown by Gifford & Kozak [2012], Lyu & Alexander [2022], and Rodríguez-Castañeda et al. [2017]) helps to explain the maintenance of species richness and endemism in mountain regions.

Abiotic versus biotic limits of distribution

The idea that contributions of abiotic versus biotic factors might differ for species' warm and cool range boundaries can be traced back to Charles Darwin and remains an area of active debate (Cahill et al., 2014; Hargreaves et al., 2014; Schemske et al., 2009). There is especially mixed evidence on the importance of upper thermal limits in setting warm boundaries (positive relationships: Batista et al., 2018; Duarte et al., 2012; García-Robledo et al., 2016; Kellermann, Overgaard, et al., 2012; Merrill et al., 2008; null relationships: Brandt et al., 2020; Gaston & Chown, 1999; Huang & Ming Chung, 2008; Kimura, 2004; Nowrouzi et al., 2018).

This inconsistency could arise for at least three reasons. First, data available for synthetic studies

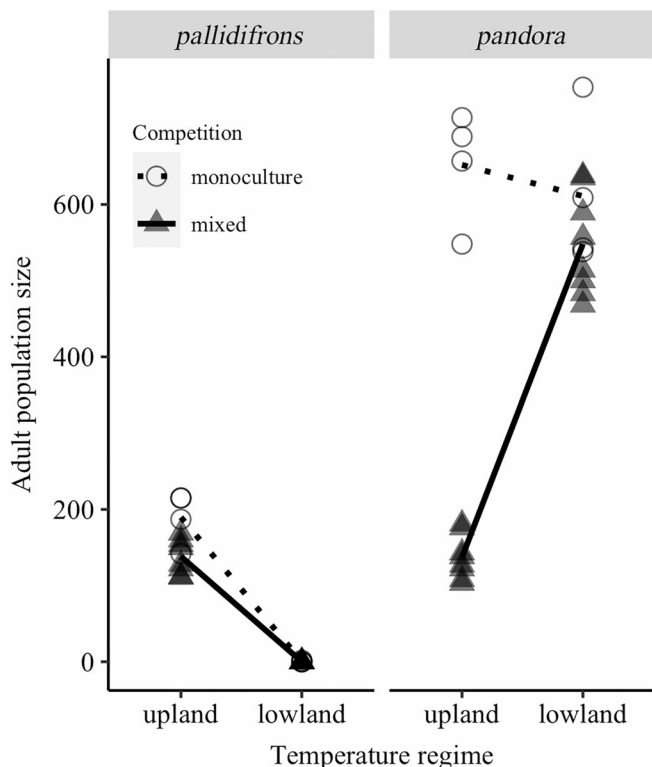


FIGURE 6 Effects of temperature and interspecific competition on long-term population sizes of *Drosophila pallidifrons* (upland species) and *Drosophila pandora* (lowland species). Each point indicates ending population size of each culture (n [monoculture] = 4, n [mixed-species culture] = 8). Dashed (monoculture) and solid (mixed-species culture) lines connect the means of population sizes in the two temperature regimes.

overrepresent systems from temperate latitudes in the northern hemisphere (Feeley et al., 2017; Parker, 2022) and relate largely to cool limits (Cahill et al., 2014). Comparative studies at lower latitudes have shown that local variations in thermal tolerance have a tighter association with environmental variations (Duarte et al., 2012) and that species distribution appears more sensitive to warming (Freeman et al., 2021). Second, mechanisms governing latitudinal or elevational distribution patterns could differ. Studies of CTmin (the critical temperature at which organisms lose their muscle coordination) have found a close relationship between this lower thermal limit and species' latitudinal distributions (Kellermann, Loeschcke, et al., 2012; Overgaard et al., 2014). In contrast, we found that various cold tolerances of our species, including CTmin sourced from the literature, were not indicative of elevational distribution patterns. Third, some of the uncertainty might reflect methodological differences when choosing, defining, and measuring thermal traits.

Different choices of indicators of thermal performance and different experimental methods may explain

why some of our results contrast with some other studies of Australian rainforest *Drosophila*. Overgaard et al. (2014) found no evidence that the upper thermal limits of tropical rainforest *Drosophila* differed among species. Unlike Overgaard et al. (2014), we measured parental productivity by allowing their eggs to develop into adults under the relevant temperature. We observed that many eggs laid at high temperatures never hatched, perhaps as a result of sperm sterilization (Parratt et al., 2021). We also observed different speeds of senescence after exposure to different temperatures (Appendix S1: Figure S1B), which the 3-day period of fecundity measurement in Overgaard's study would not have captured. Nevertheless, both studies highlight the conserved nature of heat tolerance and suggest small thermal safety margins for future warming.

Field experiments on *D. birchii* (O'Brien et al., 2017) found that its single-generation reproduction in monoculture was highest at low elevations. In our experiments, *D. birchii* was one of the most heat-sensitive species, and its populations were unable to persist within a few generations at high temperatures typical of low elevations (J. Chen, personal observations). The single-generation setup of the former study, with lab-prepared mated adults, could not capture the impact of high temperatures prior to sexual maturation. A further possibility is seasonal climatic changes: Our experimental conditions correspond to February temperatures in the field, when the average daily maximum temperature reaches 30.6°C at lowland sites. This is when the rainy season starts, driving an increase in *Drosophila* abundance, and may serve as an annual reset of species' distributions. The field experiments by O'Brien et al. (2017) occurred in conditions in which average daily maximum was no higher than 27°C. As the weather cools, mid- and low-elevation areas will become more suitable for the upland species to colonize. The relative importance of abiotic and biotic factors in affecting species distributions may change seasonally. Spatial and temporal data on species distributions are not yet available for our system but would provide a further test of our conclusions.

Low variations in upper thermal limits

Upper thermal limits vary little among species (Hoffmann, 2010) and have limited adaptive potential (Kellermann, Overgaard, et al., 2012; van Heerwaarden & Sgrò, 2021). Nevertheless, ecologically meaningful variations do exist, especially in tropical regions (Amundrud & Srivastava, 2020; García-Robledo et al., 2016; Pintanel et al., 2021; von May et al., 2017), indicating ecological sorting or adaptation. Consistent with

other studies (Goulet et al., 2017; Hangartner & Hoffmann, 2016), we found that heat tolerance is a systematic trait manifested in critical temperatures, productivities at substerile temperatures, recovered productivities, and locomotive responses. Modest variations in critical temperature may signify ecologically meaningful differences in overall performance under real and variable thermal conditions.

Such small thermal safety margins suggest a severe threat of biotic attrition in tropical lowlands (Colwell et al., 2008; Deutsch et al., 2008; Duarte et al., 2012; van Heerwaarden & Sgrò, 2021). Laboratory-measured critical temperatures are sensitive to experimental conditions, making it difficult to relate the exact values to climatological means or maxima and, hence, the threat of rising temperatures (Sinclair et al., 2016). In this context, our study benefits from a comparative approach, which reveals that upland species are already constrained by high temperatures at low elevations and that a very small difference ($SD = 1^{\circ}C$) distinguishes the upper thermal limits (RT_{max}) of lowland and upland species. Given the low evolutionary potential of heat tolerance (Hoffmann et al., 2013), both lowland species and upland species are likely to be vulnerable to modest temperature increases across the elevation gradient. Thus, lowland biotic attrition and upland range contraction are likely to occur with future warming. This could lead to cascading effects in lowland communities and threaten endemic upland species on tropical mountains such as those in the Australian Wet Tropics (Freeman et al., 2018).

Daily peak temperature as the main abiotic filter

Daily maxima can be more important than mean temperatures in structuring distributions (Lynch et al., 2014). In our study system, the mean temperature during the study season at our lowland sites is around $26^{\circ}C$. At this temperature, all studied species are close to their peak reproductive performance. However, upland and lowland sites differ greatly in the average daily maximum temperature and the daily duration that the temperature reaches or exceeds stressful levels for *Drosophila* reproduction (Appendix S1: Figure S7). In a preliminary experiment where populations were maintained for multiple generations in mixed-species cultures at constant $26^{\circ}C$, *D. pallidifrons* always outnumbered *D. pandora* (J. Chen, personal observations), contrasting with the poor performance of *D. pallidifrons* at $24^{\circ}C/28.5^{\circ}C$. Brief exposure to stressful thermal environments can have fitness costs similar to those incurred under continuously stressful conditions (Saxon et al., 2018). These results highlight

the importance of considering daily temperature variations and extreme temperature events when studying species distributions and projecting responses to climate change (Kingsolver et al., 2013; Ma et al., 2015).

Limitations

Our laboratory environment has low variations in temperature, spatial structure, and diet, limiting the mechanisms organisms use to withstand thermal stress and competitive pressure. Behavioral thermoregulation allows species with distinctive fundamental thermal tolerance to exist in one area but using different microhabitats (Vives-Inglà et al., 2022). This spatial or temporal partitioning can also influence the competition between resource-sharing species (Bestelmeyer, 2008; Porras et al., 2020). Furthermore, competition in reproduction and larval survival may be overrepresented in restricted space inside containers, while differences in abilities to forage, escape, and use alternative resources were not captured. Nevertheless, our thermal performance curves and monoculture experiments showed that lowland species could persist in abiotic conditions outside their observed range. This implies that biotic mechanisms, likely competitive exclusion, play a role in upland community composition. The match between reproduction limits of upland species and recorded air temperature in lowlands implies their lack of ability to mitigate the adverse impact of high temperature on natural populations, such as direct heat stress on larvae on rotten fruits or deficiency in foraging under heat.

Finally, between-population variation and local adaptation (Hoffmann et al., 2002), especially adaptation to abiotic environments at distribution boundaries (Peterson et al., 2019), should not be neglected when studying distributions at large spatial scales (e.g., across latitudes). The relatively restricted spatial scale of our study (within a mountain range), the use of mass-bred lines sourced from different elevations, and the limited plasticity and local adaptation documented for our study species (MacLean et al., 2019; O'Brien et al., 2017) mean that plastic and evolutionary responses to thermal conditions are unlikely to complicate the interpretation of our results.

Conclusions

Tropical ecosystems host an exceptional diversity of endemic species (Laurance et al., 2011). Predicting their sensitivity to climate change is a high priority and requires an understanding of the proximate causes of

current distributions as well as the interactions between thermal tolerance and other environmental factors, both biotic and abiotic. Our study contributes to the growing literature demonstrating that species are sensitive to high temperatures at the warm boundaries of their distributions in the tropics. In particular, we highlight the important role of daily maximum temperatures in structuring communities in tropical lowland sites and the essential role of interspecific competition at upland sites. Our results imply the vulnerability of both upland and lowland communities to increasing temperatures. These results demonstrate that reliable predictions of the sensitivity of species to rising temperatures may not always be achieved using simple correlational approaches; instead, a detailed understanding of multiple thermal traits and interactions with other species may be needed.

AUTHOR CONTRIBUTIONS

Jinlin Chen and Owen T. Lewis both contributed to the development of ideas. Jinlin Chen designed and conducted the experimental work. Jinlin Chen analyzed the results and led the writing of the manuscript. Owen T. Lewis contributed to the writing. Jinlin Chen and Owen T. Lewis both contributed to the revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Chen & Lewis, 2022) are available in Zenodo at <https://doi.org/10.5281/zenodo.6400611>. Code for analyses (Chen & Lewis, 2023a) is available in Zenodo at <https://doi.org/10.5281/zenodo.8059835>.

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SUPPORTING INFORMATION

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

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