



Research

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Microhabitats in the tropics buffer temperature in a globally coherent manner

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Vegetated habitats contain a variety of fine-scale features that can ameliorate temperate extremes. These buffered microhabitats may be used by species to evade extreme weather and novel climates in the future. Yet, the magnitude and extent of this buffering on a global scale remains unknown. Across all tropical continents and using 36 published studies, we assessed temperature buffering from within microhabitats across various habitat strata and structures (e.g. soil, logs, epiphytes and tree holes) and compared them to non-buffered macro-scale ambient temperatures (the thermal control). Microhabitats buffered temperature by 3.9°C and reduced maximum temperatures by 3.5°C. Buffering was most pronounced in tropical lowlands where temperatures were most variable. With the expected increase in extreme weather events, microhabitats should provide species with a local layer of protection that is not captured by traditional climate assessments, which are typically derived from macro-scale temperatures (e.g. satellites). Our data illustrate the need for a next generation of predictive models that account for species' ability to move within microhabitats to exploit favourable buffered microclimates.

1. Introduction

All species have evolved physiological limits to match the environments in which they live; this is a fundamental factor determining the distributions of species. These distributions are predicted to change as a consequence of changing climate [1]: as the world warms species ought to move to cooler climates at either higher latitudes or higher elevations to avoid negative physiological consequences. Indeed, there are now dozens of studies showing that plants, insects, fish, birds and mammals are making such a shift (e.g. [2]). However, there are numerous other studies that have found either no shift or less of a shift than predicted (e.g. [2,3]).

The discordance in these studies may be due to the varying scales at which distribution models are created and those at which organisms actually live (e.g. see macro-scale climate data used by Warren *et al.* [4] and discussion by Gillingham *et al.* [5]). Distribution models are based on macroclimatic data sampled from meteorological observations or satellite data collected at kilometre scales (see [6] for discussion). Such large scales do not consider fine-scale heterogeneity, effectively 'microhabitats' within the 'macrohabitat', which is used by the organisms to evade changing climates, especially over short time scales [7–9]. Finding refuge will be critical as extreme weather events are predicted to increase into the future [10].

There are many forms of microhabitat that could provide refuge from daily, seasonal or other types of short-term variation in climate, such as heatwaves or

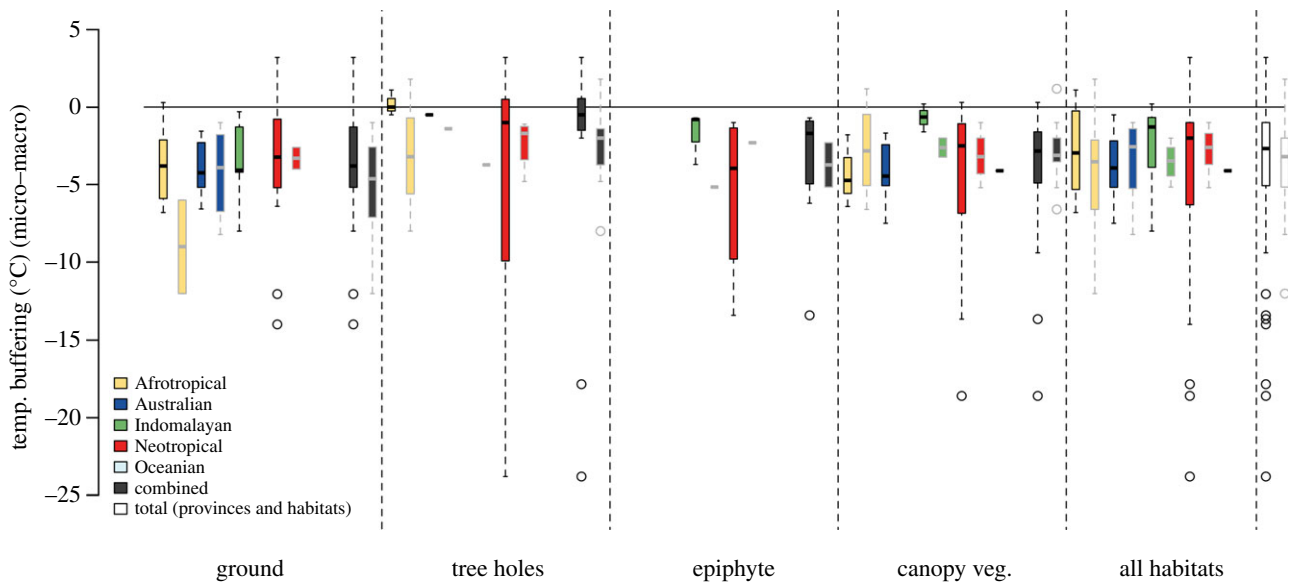


Figure 1. Temperature buffering across habitat types and biogeographic provinces in the tropics. Box and whisker plots with black borders indicate the medians of mean differences between micro- and macrohabitats, whereas plots with grey borders indicate medians of mean differences in maximum temperatures. Data below zero indicate thermal buffering (i.e. microhabitats were cooler than macrohabitat temperatures). ‘combined’ indicates all data combined across provinces for each habitat type, whereas ‘total’ indicates the summary across all provinces and habitats. (Online version in colour.)

drought. These include under rocks and logs, and inside the soil, tree holes or epiphytes, all of which could offer buffered microclimates and act as a mediating force of ambient temperatures at fine spatial scales and expand an animal’s thermal safety margin by several degrees centigrade [9,11,12].

Here, we review the buffering by microhabitats within macrohabitats and thus the potential scale of inflation of species risk from the use of macro-scale temperatures. We do this by asking two questions: (i) How well do different microhabitats buffer temperature; and (ii) Is temperature buffering similar across continents?

2. Material and methods

We collated data on the mean, maximum and variance in temperatures from peer-reviewed literature on micro- and macrohabitat temperatures from the Earth’s tropical regions in ISI Web of Science and Google Scholar. We used only studies that had paired design, i.e. sampled at least one microhabitat and the macrohabitat (i.e. ambient air) temperatures adjacent to the microhabitat. We took data from tables or from graphs (using Digitizeit, www.digitizeit.de to extract data from the graphs). In total, we reviewed 36 studies from 1957 to 2013 from 25 countries (electronic supplementary material, figure S1 and table S1; see Supplementary Methods for more details).

We analysed temperature buffering in microhabitats compared with macrohabitats across microhabitat types, elevation and biogeographic provinces ([13], hereafter referred to as provinces). We calculated temperature buffering by subtracting the mean and maximum macrohabitat temperature from the mean and maximum microhabitat temperature, respectively. We grouped microhabitats by their location: ground (e.g. soil, leaf litter, log), above-ground tree holes, above-ground epiphytes and under-canopy vegetation (i.e. measuring the influence of shade). We defined macrohabitat types as boulder field, grassland, conifer forest, shrubland, savannah, plantation, deciduous forest and rainforest. We used R stats v. 2.15.1 (R Project for Statistical Computing, <http://www.r-project.org>) for all statistical analyses.

3. Results

Thermal buffering was consistent across continents, with all microhabitats reducing macro-scale ambient temperatures (figure 1). Mean temperatures in microhabitats were 3.9 ± 0.5 (s.e.)°C lower and maximum temperatures were 3.5 ± 0.5 (s.e.)°C lower than those in macrohabitats (figure 1). There were significant differences in temperatures across all micro- and macrohabitats (Wilcoxon–Mann Whitney rank sum test; $W = 6913986$, $p < 0.001$). Canopy vegetation had the greatest buffering effect in reducing mean ambient macrohabitat temperatures (−4°C) followed by epiphytes (−3.9°C), ground vegetation (−3.8°C) and tree holes (−3.7°C).

Mean temperature variance was generally lower across all elevations for microhabitats compared with macrohabitats (electronic supplementary material, figures S2 and S3). There was little difference in microhabitat buffering among macrohabitats, with the exception of grasslands. Grasslands contained microhabitats that were warmer than ambient temperatures (electronic supplementary material, figure S4). Microhabitats across all macrohabitats buffered maximum temperatures and were comparable in temperature variance (electronic supplementary material, figures S5 and S6).

Thermal buffering was also evident in the reduction of variance in temperatures. Of the 58 micro- to macrohabitat comparisons of mean temperature variance, 76% of the points fell below the equivalency line—indicating that microhabitat temperatures were buffered (figure 2). The strength of the relationship between micro- and macrohabitat temperatures was contingent on the amount of thermal variability in the system. For example, when macrohabitats had small variances in temperature, microhabitats too had equally small variances. In fact, variance around means ranging from 0 to 10 tracked the equivalency line (linear regression; slope = 0.57) and were highly correlated (Pearson’s correlation; $\rho = 0.65$) (figure 2), suggesting that macro- and microhabitat variance were relatively equivalent. However, this relationship diminished with increasing variances at the macro scale (linear regression;

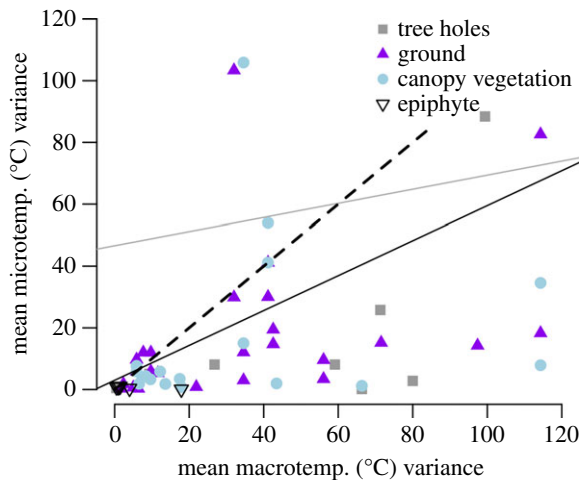


Figure 2. Relative difference in mean temperature variance between micro- and macrotemperatures (macroclimate) displayed by microhabitat type. The dashed line indicates temperature equivalency between micro- and macrotemperatures. Thus, points that fall below the equivalency line indicate higher mean variance within macrohabitats than microhabitats. The black line indicates a regression line for all locations with a macrohabitat variance below 10 ($y = 0.56x + 3$), whereas the grey line indicates a regression line for all locations with a macrohabitat variance above 10 ($y = 0.23x + 47$). The two extreme points above the equivalency line represent temperature variance in a tropical rainforest canopy of Australia and temperature variance within ground microhabitats in a tropical savannah of Zimbabwe. (Online version in colour.)

slope = 0.23 and Pearson's correlation; $\rho = 0.21$) (figure 2). This suggests that variance in macrohabitat temperature changes at a different rate from microhabitat variance, with the effect of buffering by microhabitats becoming greater with increasing macrohabitat variability.

4. Discussion

Microhabitats buffered temperature in a globally coherent manner. Our data suggest that an array of microhabitats distributed across the habitat strata and spanning the four tropical continents strongly buffered temperature relative to ambient environments (figure 1 and electronic supplementary material, figure S1). Temperature may vary by as much as 6–10°C both within and among habitat types [8,14–16] and simply accounting for shade provided by structurally complex rainforest canopies may reduce temperature maximums by up to 6°C in tropical systems of Australia [17] and by approximately 4°C globally (results herein; figure 1). At the extreme, some microhabitats in our study buffered the temperature by over 20°C. Interestingly, microhabitats such

as epiphytes act as air conditioners in the rainforest canopy that stabilize temperature and reduce surrounding maximum ambient temperature [18–20].

Microhabitats in the lowlands performed a superior job in buffering maximum temperatures compared with those in the uplands, but lowlands showed the greatest variance in both micro- and macrohabitat temperatures. Many lowland species live in isolation from major topographic gradients (e.g. majority of the Amazon rainforests) and lack proximate elevation gradients to exploit as temperature warms and as extreme temperature events become more prevalent (e.g. [21]). Therefore, buffered microhabitats may represent the sole means for these species to evade future climates, provided the microhabitat itself remains viable with climate change [8,22].

There is currently widespread use of macroclimate data in modelling species distributions [4], dispersal capabilities [23] and range shifts [2]. But species that have flexible habitat requirements may shift, within or between microhabitats, to exploit favourable buffered microclimates. Our data suggest that this is appropriate for extreme short-term or rapid changes in temperatures, because there are apparently non-uniform shifts in micro- to macrohabitat temperatures, indicating time lags between warming at the macro-scale and corresponding temperature rises at the micro-scale ([12]; figure 2). While species are already moving in response to recent changes in temperature, almost every taxonomic group considered is shifting its range upwards in elevation at a slower rate than expected [2]. One possible explanation for erratic species shifts is that the temperatures used to predict range shifts were measured at scales that do not account for the presence of buffered microhabitats and the slower rates of temperature change within microhabitats compared with macrohabitats. Combined with our illustration of the potential for microhabitat buffering, this suggests that we need a next generation of predictive models that account for species' ability to exploit favourable microclimates, via the inclusion of species physiological limitations [24], trade-offs from using climate refuges for extended periods of time [9] and detailed information about fine-resolution temperature changes and extreme conditions at the microhabitat scale [5,25].

Data accessibility. Data deposited in Dryad, provisional doi:10.5061/dryad.cb051.

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