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 ± 0.2°C and reduced maximum temperatures by 3.5 ± 0.2°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...
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 $3.9 \pm 0.5$ (s.e.) $^\circ C$ lower and maximum temperatures were $3.5 \pm 0.5$ (s.e.) $^\circ C$ 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 ($-4 ^\circ C$) followed by epiphytes ($-3.9 ^\circ C$), ground vegetation ($-3.8 ^\circ C$) and tree holes ($-3.7 ^\circ C$).

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; $r = 0.65$) (figure 2), suggesting that macro- and microhabitat variance were relatively equivalent. However, this relationship diminished with increasing variances at the macro scale (linear regression;


