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There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change

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Abstract:	Climate warming impacts biological systems profoundly. Climatologists deliver predictions about warming amplitude at coarse scales. Nevertheless, insects are small, and it remains unclear how much of the warming at coarse scales appears in the microclimates where they live. We propose a simple method for determining the pertinent spatial scale of insect microclimates. Recent studies have quantified the ability of forest understory to buffer thermal extremes, but these microclimates typically are characterized at spatial scales much larger than those determined by our method. Indeed, recent evidence supports the idea that insects can be thermally adapted even to fine scale microclimatic patterns, which can be highly variable. Finally, we discuss how microhabitat surfaces may buffer or magnify the amplitude of climate warming.
Author Comments:	

There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change

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Abstract (100-120 words)

Climate warming impacts biological systems profoundly. Climatologists deliver predictions about warming amplitude at coarse scales. Nevertheless, insects are small, and it remains unclear how much of the warming at coarse scales appears in the microclimates where they live. We propose a simple method for determining the pertinent spatial scale of insect microclimates. Recent studies have quantified the ability of forest understory to buffer thermal extremes, but these microclimates typically are characterized at spatial scales much larger than those determined by our method. Indeed, recent evidence supports the idea that insects can be thermally adapted even to fine scale microclimatic patterns, which can be highly variable. Finally, we discuss how microhabitat surfaces may buffer or magnify the amplitude of climate warming.

Introduction

Since Kraus's time, the science of microclimates has been inherently multidisciplinary, involving ecologists, zoologists, botanists, entomologists, physicians, and geographers. As such, this field contains a diversity of key concepts [1]. A general, all-purpose definition is that microclimates are fine-scale climate variations that *deviate* from the background atmosphere, at least temporarily [2, 3]. Here we use the term *deviate* instead of *decoupled* in the original version of this definition [2]. For example, the temperature in a forest understory can deviate strongly from atmospheric temperature [4, 5], but this deviation does not imply a decoupling between the two: a change in atmospheric temperature induces a shift in the temperature of the forest understory. Here, we focus on the main idea that microclimatology provides a way to determine the temperatures experienced by insects in their microhabitats, allowing accurate inference of the impact of climate warming on these microclimate temperatures. We start by providing a simple approach to determining appropriate spatial scales. Then, we highlight to what extent fine-scale microclimates are more variable than local microclimates, which are much more used by entomologists. We distinguish between local microclimates (i.e., air temperature measured in microhabitats) and fine-scale microclimates (i.e., the temperature of surfaces of the various elements composing the microhabitat). We also synthesize the latest findings on how insects are thermally adapted to their fine-scale microclimates. We end by asking the question of what will be the impact of climate change on these fine-scale microclimates and by proposing tentative hypotheses of potential responses.

The spatial scale of microclimates

The notion of microclimate implies the identification of a spatial scale. For atmospheric scientists, microclimate corresponds to horizontal distances of 0.001-100 m while mesoclimate corresponds to 1-200 km and macroclimate to distances >200 km [2]. These divisions, however, are anthropocentric; 100 m will have a different meaning for an aphid and a large reptile. To quantify this effect, we can calculate the ratio [horizontal distance / body size] corresponding to the transitions from micro- to meso- to macro-climate based on the distance limits given above and assuming the body size of human as 1.70 m. We obtain that mesoclimate starts at a ratio of 50 and macroclimate at 12,000. For any body size, we can then estimate the horizontal distance corresponding to each scale as the ratio multiplied by body size (Figure 1). This simple approach makes the point that the scale corresponding to macro-climate for a spider mite (e.g.,

2.4 m) is equivalent to the micro-scale for a lizard (Figure 1). In addition, for most insects, which are less than few mm long, microscale processes occurs at spatial scales below 10 cm (Figure 1). Indeed, for organisms with very small body sizes (<1 mm), the term nano-climate has been used, referring to the climate within surface boundary layers such as a leaf surface or air cavity in the soil [3]. This term was never used by ecologists and physiologists, and indeed this term is no longer needed if we scale microclimates to body size (Figure 1). This method can be applied in any microclimate study to determine the spatial extent at which microscale processes should be analyzed. Most insects have a very small body size and more than 50% of insect species are less than 5 mm [6]. Therefore, the pertinent microscale for most insects is at an area of about 20 cm in length.

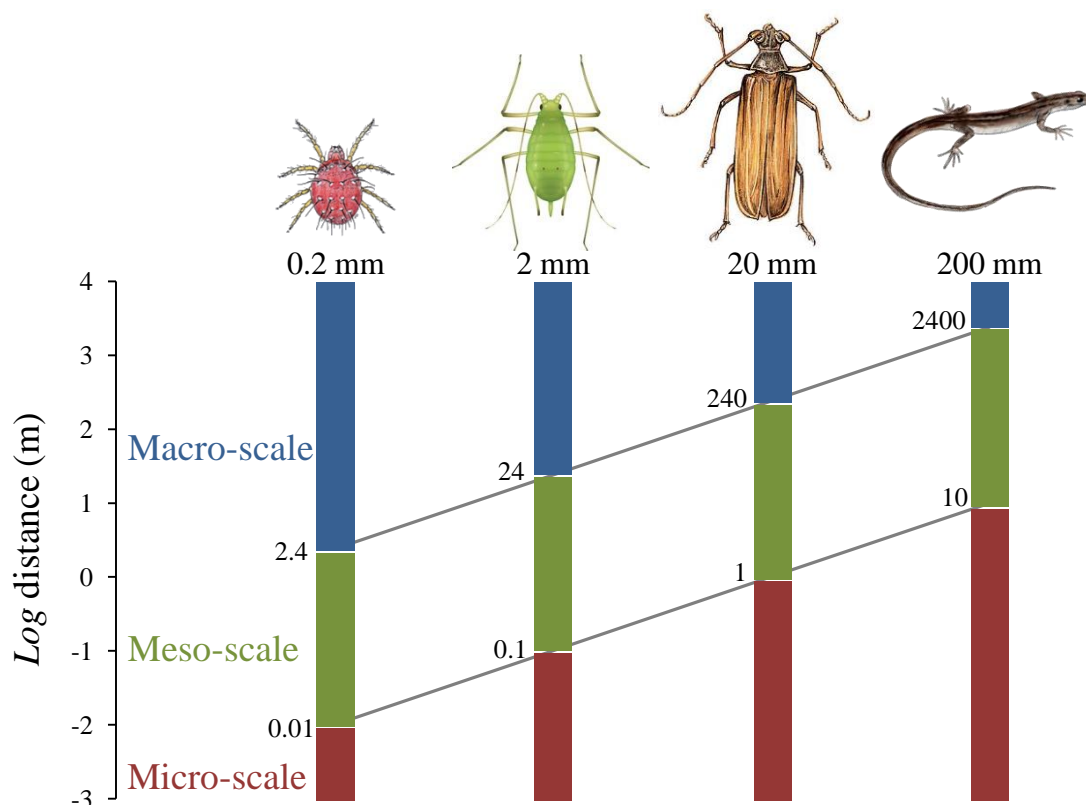


Figure 1. Illustration of the distances corresponding to each type of spatially-scaled climate for various ectotherms differing in body size. The Y-axis shows the log scale of the distance used here as a proxy defining spatial scale. The numbers in the graph provide the actual distances (in meters) delimiting different spatial scales.

So that it will provide a rule of thumb, the approach proposed above is intentionally simplistic. Other layers of complexity can be included. First, the method above focuses on horizontal distances. Most insects, however, can also move vertically through plant canopies or soil layers,

thereby encountering different fine-scale microclimates. Vertical movement thus increases the potential diversity of accessible microhabitats compared to the diversity available just from horizontal movement. The spatial scaling of microclimates defined above may not apply in all directions because species may have different abilities to move horizontally and vertically. Second, when defining relevant spatial scales, speed matters. Insects that run, jump or fly disproportionately faster and further than humans will sample proportionately larger volumes of space in their local microclimates. Additional ratios could be developed that include both relative sizes and relative speeds. Finally, the method above for establishing scale depends entirely on the choice of thresholds for human size and for transitions from macro- to meso- to microclimates. The transitions are necessarily arbitrary, and the literature provides mostly ranges rather than exact values for those scales. For example, by shifting the limit between meso- and microclimate from 100 m to 50 m, we obtain that the microscale is up to only 6 mm for the spider mite instead of 10 cm. The exact values are crucial, however, since the level of heterogeneity embedded in the microscale may differ among spatial scales (see section below).

The thermal heterogeneity blows up at micro-scales

Thermal heterogeneity allows insects to buffer environmental variation or extremes through behavioral thermoregulation [7]. The body temperature of small insects is driven mainly by conductive exchange of heat with nearby surfaces, especially as a small insect is protected from convective heat loss within the surface boundary layer [8, 9]. It is important to distinguish between local microclimates (i.e., air temperature measured in microhabitats) and fine-scale microclimates (i.e., the temperature of surfaces of the various elements composing the microhabitat). Indeed, the so-called local microclimate in the literature corresponds to the meso- or macro-scale for insects.

Local microclimates often are characterized by comparing the air temperature in various microhabitats to air temperature measured at a standard height of 1.5 m above ground in open areas (using appropriate equipment to protect the sensor from solar radiation). For example, shading by the woodland leaf canopy reduced maximum temperatures in the understory by $\sim 5^{\circ}\text{C}$ [5, 10]. In the middle of a sunny day in summer in the UK, woodland air temperatures were lower than grassland and decreased from the canopy-top to the understory [11]. In addition, several studies have focused on topoclimates, which are meteorological air temperatures distributed across the landscape depending on slope and aspect of the terrain,

revealing temperature deviations of 5-10°C among different areas in complex landscape [12-14]. Those local microclimates do not necessarily reflect the temperature experienced by most insects. Instead, local microclimates consist of the *air bath* that encompasses the diversity of local surfaces on which insects live. This air bath may be relatively homogeneous thermally over moderately large extents (at the scale of meters).

The thermal heterogeneity at fine scales, however, is often high. The old literature (1960s to 1980s) is rich in examples indicating the extent to which surface temperatures can deviate strongly from local air temperature (Figure 2). Stoutjesdijk [15] reported a 'snapshot' of surface temperatures measured at the end of winter in Holland. While (meteorological) air temperature was about 12°C, some surfaces reached ~60°C, e.g., decaying grass tussocks, and others were freezing, e.g., humid litter in the shade (Figure 2) (see also [3]). These thermal differences are linked to simple physical processes including the cosine law of illumination [16], evapotranspiration from surfaces [17], and boundary layer effects [18]. The bark surface of trees exposed to full sun can reach extreme temperatures near 50°C for oak when air temperature is near 15°C [19]. A thermal gradient of 30-40°C seen among fine-scale microclimates compares with some of the most extreme known temperature gradients in nature, including geothermal ponds [20] and hydrothermal vents [21].

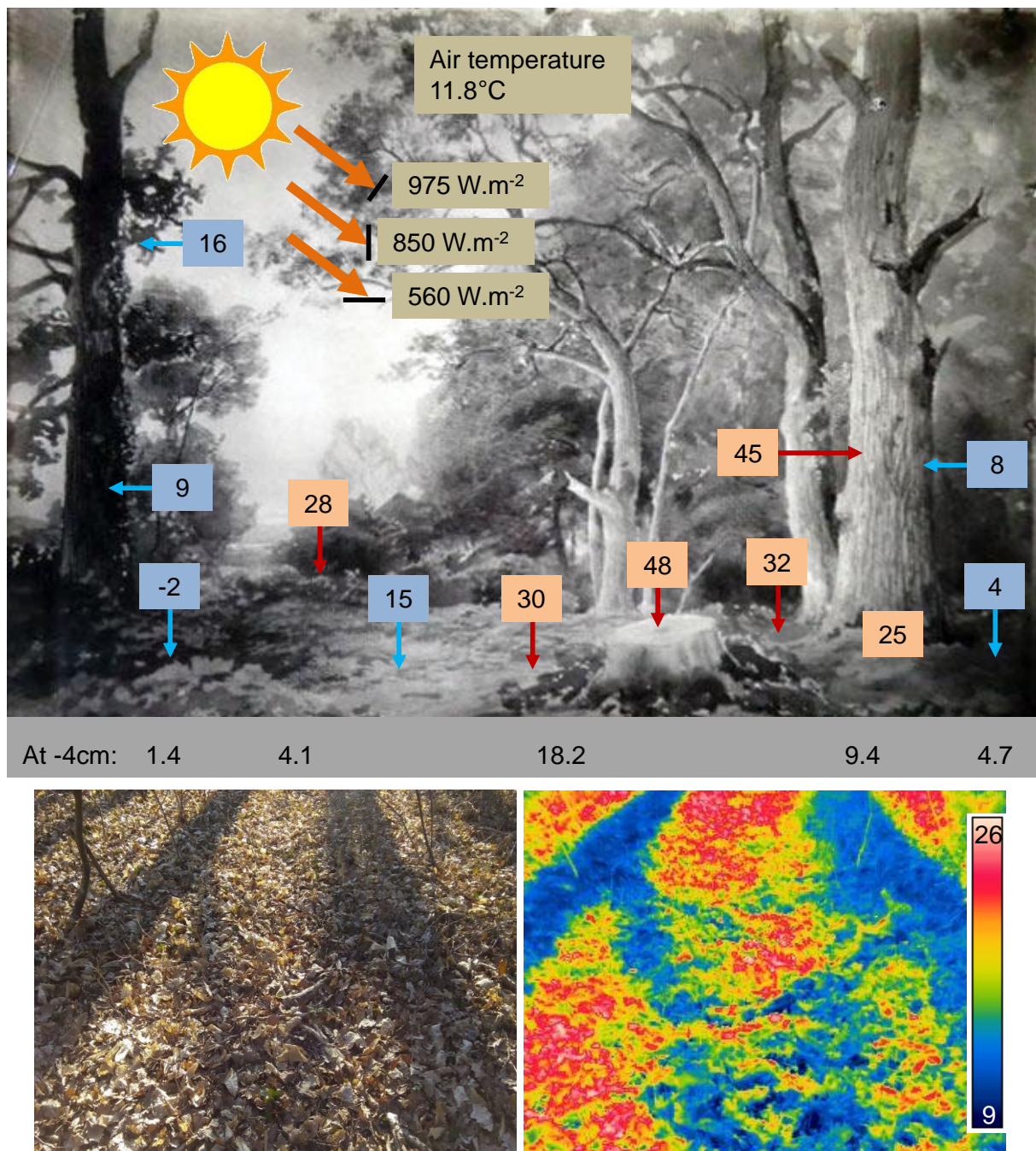


Figure 2. Illustration of the surface temperature deviations across a microhabitat (elements are not to scale). This figure reports a transect across the south-facing edge of a pinewood and adjacent heathland with Juniper shrub (measurements made on 3 March 1976 with an easterly wind of 5 m/s at 10 m height). Numbers are °C. Soil temperature was measured at 4 cm (grey bar at bottom). Adapted and redrawn from [15]. The photograph of the leaf litter and the corresponding thermal image (scale in °C; IR camera FLIR B335, resolution 320x240 pixels, thermal sensitivity 0.05 °C), both taken in an oak forest (near Tours, France, in July 2019), illustrate the temperature gradient within approximately 1 m² of leaf litter.

Fine-scale microclimates are also characterized by large spatial heterogeneity [22, 23]. Nicolai [19] reported 10 °C temperature differences within the surface of rugose trunks, between the

'valley' (depression of the bark surface) and the 'hill' (bumps), which determine distributions of oribatid mites [19]. A similar temperature range ($\sim 10^{\circ}\text{C}$) is observed over a few cm between the undersides of rocks exposed to the sun and the soil substrate in Australia, where the flat-rock spider female finds optimal warm conditions for hunting while the eggs benefit from the cooler environment offered by the substrate [24]. Indeed, A roughly similar amplitude across short distances was observed ($\sim 10\text{-}15^{\circ}\text{C}$) in many different systems including mussels in the rocky intertidal [25, 26], plant crops' canopy surfaces [27], and plant leaves exposed to full sun [28-30]. To conclude, the variety of thermal conditions across fine scales can be high in various ecosystems. This amplitude of variation across fine scales may rival and sometimes exceed the expected thermal variations along geographical extents, as seen for mussel body temperatures, in which variation within 1 m^2 was as great as the variation in mean body temperature observed over ~ 1600 km of coastline [25, 31]. It remains to be determined if movements of insects at fine scales are enough to buffer climate change impacts relative to migrating over geographical extents.

Fine-scale microclimates influences insect thermal traits

For small ectotherms, including insects, the variability of temperature across fine scales can potentially select or generate as much variability in thermal limits or other thermal biology traits as can thermal gradients across much larger spatial scales. Yet, few studies have quantified the inter-individual variation in thermal traits in field populations at fine scales. Variation in critical temperatures (CT_{max}) of $\sim 10^{\circ}\text{C}$ amplitude were recorded at the inter-specific level in a community of ants in the Panama tropical forest [32]. Thermal limits were higher for ants living in the tree canopy where plant surfaces are superheated by the sun. However, plant surfaces in the canopy are both warmer and more variable than those in the understory, thereby selecting for temperature generalists and not specialists [32]. Interestingly, Franken et al. [33] reported intraspecific variation of similar amplitude in the CT_{max} of springtails from a single sand dune site. The sand surface temperature likely varies by $\sim 10^{\circ}\text{C}$ within a meter distance when considering the variations in slope of sand surface at small scale. At an even finer-scale, insect herbivores living at the surface of leaves display thermal limits that match the maximal surface temperature reached by the attacked leaf during extreme heat waves [34]. The transpiration rates of plant leaves respond differently to each herbivore species depending on their feeding mode, thereby generating leaf temperature differences of almost 10°C among herbivore species

on the same host plant. This thermal variability translates into a shift of about the same amplitude in the CT_{max} of the species in the herbivore community on apple [34]. Therefore, understanding the mechanisms generating fine-scale variations in surface temperatures provides a key window into understanding the thermal adaptations of small insects.

Connecting climate change to microclimatic change

The next challenge for ecologists is to predict both the direction and the amplitude of future microclimate change, which will be critical for estimating climate effects on species distributions, population trends, and extinction probabilities [35]. The microclimate models developed so far have been used to predict the dynamics of microclimate temperature and its biological consequence for relatively large insects and reptiles [36] and/or at theoretical spatial scales that are difficult to connect with the fine scale microclimates observed in the natural habitats of most insects [37]. The only study we are aware of that has *directly* and *biophysically* quantified how much of atmospheric warming is transferred into fine scale microclimates comes from the community of intertidal ecologists more than 10 years ago [38]. In this study, a biophysical model of body temperature of California mussels was used to show that a simulated 1°C increase in air or water temperature increased the maximum monthly average of daily body temperature maxima by 0.07–0.92°C, depending on various parameters including the geographic location and the vertical position in the rocky intertidal. Based on climate change scenarios for 2100, Gilman et al. [38] calculated increases in monthly average maximum body temperature of 0.97–4.12°C, again depending on geographic and rocky intertidal locations — warming amplitude values that do not match exactly the atmospheric warming amplitude with locations acting as *buffers* (mussel bodies warming less than the air) or *magnifiers* (bodies warming more than the air). Therefore, the geographic variation in body temperature sensitivity (more a mosaic than a South-North linear gradient) can modulate species' experiences of climate change and must be considered when predicting the biological consequences of climate change. To date, however, similar approaches remain to be applied to insects.

Most studies dealing with the impact of climate change on microclimates provide *indirect* evidence, therefore with less precise and mechanistic quantification compared to the study of Gilman et al. [38]. Nevertheless, these studies provide solid inference that most microclimates will help ectotherms to buffer at least a significant part of the amplitude of global warming (Figure 3). For example, the forest understory buffers atmospheric thermal variations as long

as the canopy remains closed [5, 39]. The maximal temperature within covered forests can be $\sim 5^{\circ}\text{C}$ cooler than adjacent open areas, but this buffering ability depends on the local hydrology and water balance of the trees [40]. This implies that the latitudinal gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate temperature [5]. Similarly, forest microhabitats (soil, logs, epiphytes and tree holes) of tropical forests reduce maximum temperatures by $\sim 4^{\circ}\text{C}$ [41, 42]. Buffering is pronounced in tropical lowlands where temperatures are most variable [42, 43]. A priori, the forest understory buffer may benefit insects by allowing them to survive environmental extremes. Alternatively, this forest buffer may have favored species with moderate to low thermal limits, and with low variability at the population level, thereby causing a high vulnerability to future climate warming.

By contrast, whether and how other microclimates magnify or reduce the amplitude of climate warming is much less investigated. We can make inferences from fine scale microclimate with surface temperatures above air temperature (Figure 3). Many microhabitats are warmer than ambient when they receive solar radiation, including leaves and flowers [9, 44, 45], enclosed structures such as galls and leaf mines [46], the pitcher of some carnivorous plants [47] and at the surface or underneath rocks exposed to the sun [24]. Other particular microhabitats are warmer than the local microclimate independently of solar radiation, such as thermogenic flowers that produce heat during the night [48, 49]. In general, however, the solar energy input is key. Note that these microhabitats can occur within local microclimates that buffer environmental changes (e.g., seedlings receiving solar energy below a canopy gap). In addition, habitat modifications such as logging in forests can shift a buffering effect into an magnifier of maximal atmospheric temperatures simply by allowing how much solar radiation reaches the forest floor [50] (Figure 3). **Quantifying which portion of the amplitude of climate change will be transferred into these microhabitats requires that we analyze how these structures manage the heat radiative energy input at increasing air temperatures.** We foresee three biophysical scenarios that all lead to a decrease in the temperature excess of these structures – in other words, these structures may buffer part of the amplitude of warming even though they are warmer than their local microclimates (Figure 3).

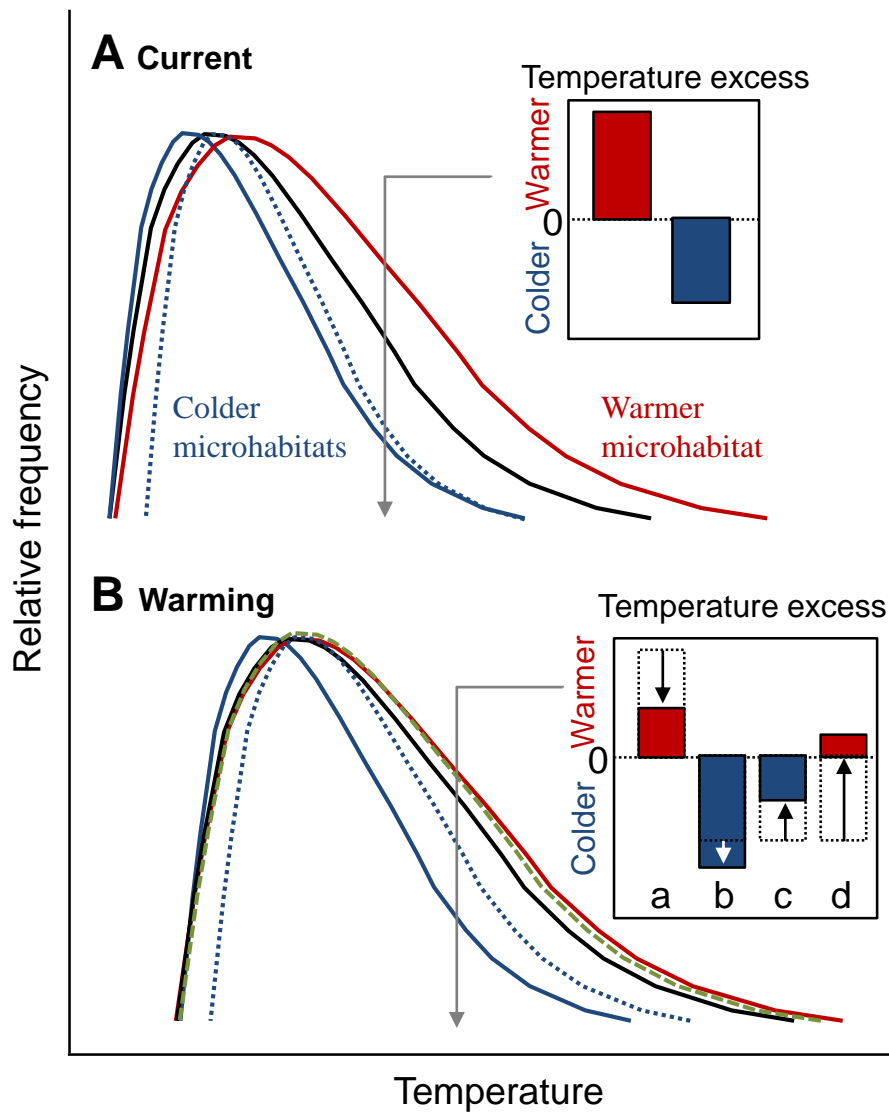


Figure 3. Buffers and magnifiers of climate warming. **(A)** Hypothetical temperature distributions of surfaces for colder (blue) and warmer (red) than-ambient microhabitats, compared to the distribution of atmospheric temperature (black) under current climates. The blue dotted line shows the temperature distribution for a microhabitat that buffers both maximal and minimal air temperatures (i.e., narrower temperature range like the soil forest understory). The inset illustrates the surface temperature excess (i.e., surface temperature minus atmospheric temperature) at the air temperature indicated by the grey arrow and for the two types of microhabitats. **(B)** Hypothetical shift in these temperature distributions with climate warming. Note that both minimal and maximal temperatures are shifting in this schematic. Different scenarii are illustrated (a to d). Warmer-than-ambient surfaces may buffer part of this amplitude of warming (inset, scenario a: the red bar is lower than the dotted bar reporting the temperature excess under current climate), while colder-than-ambient surfaces may buffer (scenario b) or magnify (scenarii c and d) the amplitude of warming. These magnifiers could become warmer than ambient under extreme human-induced disturbance (e.g., logging in forest).

First, the insect may directly cause the temperature excess of its microclimate by building or inducing structures that absorb a high amount of incoming radiation. For example, some leaf mines are better absorbers of near infrared radiation than are intact leaves [51]. This could also be the case for some plant galls [46]. Increasing air temperature around these structures does not change their temperature excess relative to ambient air by the same proportion [52]. However, it remains to determine whether the extended phenotype of these insects is plastic enough to decrease the temperature excess when daily maximal temperatures reach critical values. Second, structures developed by insects may be large enough to generate significant thermal inertia that causes the temperature of the fine scale microclimate to increase at a lower rate than the daily ambient air temperature, resulting in a structure that never reaches its theoretical maximal temperature [8]. Again, this effect is more likely in large structures such as bee (solitary or social) nests, but the great ability for nest thermoregulation in social insects [53] may have overshadowed this thermal inertia effect, which remains to be quantified. Third, a thermodynamic effect may cause the microclimate temperature excess to decrease as air temperature increases. Indeed, the warmer-than-ambient structure loses more radiative energy than it gains from its environment (which is mostly in the shade). This difference is at the power 4 in the heat balance [54], and therefore has more weight in the balance than the increase in convective heat loss as air temperature increases. This thermodynamic effect was nicely illustrated in rocky intertidal mussels [55]. This effect is rarely explicit in studies on the climate effect on the heat budget of ectotherms, but it is implicit in the calculation [56]. In all these scenarios, we focus on shifts of temperature distributions. Nevertheless, any changes in the shape of these temperature distributions (e.g., skewness and kurtosis) should also contribute to the ability to buffer the amplitude of warming.

Conclusions

Studies increasingly call for the inclusion of fine scale weather and climatic data into species distribution models [57, 58] or vulnerability assessments [59, 60] to account for the buffering ability of some microhabitats. Insects of most species, however, live at a much finer spatial scales than conceived even by these models. There is evidence that even within these buffering microhabitats (grasslands, forests), finer scale patches show great thermal heterogeneity, including plant surfaces that are sometimes warmer than ambient air temperature [45, 61, 62]. Productive approaches to incorporating this variation will require (i) measurements of actual

body temperatures *in situ* in relation to the thermal physiology of populations. Such measurements are relatively easier when the microhabitat does not receive direct solar radiation, like for spiders living in subterranean caves [63]. Otherwise, measurements with high spatial and temporal resolutions are required [62]. (ii) A renewed focus on behavioral mechanisms by which insects respond to and exploit the vast thermal heterogeneity that often is available to them [7]. (iii) Developing new biophysical approaches to modeling heat-exchange processes at even finer spatial and temporal scales. Microclimate models provide predictive tools for quantifying the impact of climate change on temperatures experienced by species in their microhabitats [64]. This past decade has seen the emergence of several microclimate models all working at the *local* scale, including the R package *NicheMapR* [65], *Microclima* [66], and other statistical approaches [67, 68]. All of these models open new avenues for microclimate-based macrophysiology [69]. To date, however, only a few models have been developed that capture microclimate heterogeneity detailed above at the finest spatial scales relevant to most insects [52]. In other words, microclimate models still do not extend down to the small scales relevant to most of the biodiversity on Earth, which lies at small body size (the peak of biodiversity has a body size of 3-10 mm in length, likely with more species below than above this range; [6]). We argue that ‘there is plenty of room at the bottom’ [70, 71] and efforts should continue to downscale ecological processes to the most pertinent scale for insects.

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References

- [1] Zellweger F, De Frenne P, Lenoir J *et al.* Advances in Microclimate Ecology Arising from Remote Sensing. *Trends Ecol Evol* 2019; 34:327-341.
- [2] Bramer I, Anderson BJ, Bennie J *et al.* Advances in Monitoring and Modelling Climate at Ecologically Relevant Scales. *Advances in Ecological Research* 2018; 58:101-161.
- [3] Stoutjesdijk PH, Barkman JJ. *Microclimate, Vegetation & Fauna*. Zeist, The Netherlands: KNNV Publishing; 2014.

- [4] De Frenne P, Rodriguez-Sanchez F, Coomes DA *et al.* Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Science USA* 2013; 110:18561-18565.
- [5] De Frenne P, Zellweger F, Rodríguez-Sánchez F *et al.* Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* 2019; 3:744-749.
- [6] May RM. How Many Species Are There on Earth? *Science* 1988; 241:1441-1449.
- [7] Woods HA, Dillon ME, Pincebourde S. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology* 2015; 54:86-97.
- [8] Stevenson RD. Body Size and Limits to the Daily Range of Body Temperature in Terrestrial Ectotherms. *The American Naturalist* 1985; 125:102-117.
- [9] Pincebourde S, Woods HA. Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology* 2012; 26:844-853.
- [10] Suggitt AJ, Gillingham PK, Hill JK *et al.* Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 2011; 120:1-8.
- [11] Morecroft MD, Taylor ME, Oliver HR. Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology* 1998; 90:141–156.
- [12] Zellweger F, Coomes D, Lenoir J *et al.* Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Glob Ecol Biogeogr* 2019; 28:1774-1786.
- [13] Sears MW, Riddell EA, Rusch TW, Angilletta MJ. The world still is not flat: lessons learned from organismal interactions with environmental heterogeneity in terrestrial environments. *Integr Comp Biol* 2019; 59:1049-1058.
- [14] Holden ZA, Abatzoglou JT, Luce CH, Baggett LS. Empirical downscaling of daily minimum air temperature at very fine resolutions in complex terrain. *Agricultural and Forest Meteorology* 2011; 151:1066-1073.
- [15] Stoutjesdijk P. High Surface Temperatures of Trees and Pine Litter in the Winter and Their Biological Importance. *International Journal of Biometeorology* 1977; 21:325–331.
- [16] Oke TR. *Boundary layer climates*. London: Routledge; 1987.
- [17] Jarvis PG. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London B* 1976; 273:593-610.
- [18] Finnigan J. Turbulence in plant canopies. *Annu. Rev. Fluid Mech.* 2000; 32:519–571.
- [19] Nicolai V. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 1986; 69:148-160.
- [20] Dunckel AE, Cardenas MB, Sawyer AH, Bennett PC. High-resolution in-situ thermal imaging of microbial mats at El Tatio Geysir, Chile shows coupling between community color and temperature. *Geophysical Research Letters* 2009; 36.
- [21] Kashefi K, Lovley DR. Extending the upper temperature limit for life. *Science* 2003; 301:934.
- [22] Pincebourde S, Murdock CC, Vickers M, Sears MW. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology* 2016; 56:45-61.
- [23] Pincebourde S, Suppo C. The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity. *Integrative and Comparative Biology* 2016; 56:85-97.
- [24] Pike Da, Webb JK, Shine R. Hot mothers, cool eggs: nest-site selection by egg-guarding spiders accommodates conflicting thermal optima. *Functional Ecology* 2012; 26:469-475.

- [25] Denny M, Dowd W, Bilir L, Mach K. Spreading the risk: Small-scale body temperature variation among intertidal organisms and its implications for species persistence. *Journal of Experimental Marine Biology and Ecology* 2011; 400:175-190.
- [26] Jimenez AG, Jayawardene S, Alves S *et al.* Micro-scale environmental variation amplifies physiological variation among individual mussels. *Proc Biol Sci* 2015; 282:20152273.
- [27] Faye E, Rebaudo F, Carpio C *et al.* Does heterogeneity in crop canopy microclimates matter for pests? Evidence from aerial high-resolution thermography. *Agriculture, Ecosystems & Environment* 2017; 246:124-133.
- [28] Caillon R, Suppo C, Casas J *et al.* Warming decreases thermal heterogeneity of leaf surfaces: implications for behavioural thermoregulation by arthropods. *Functional Ecology* 2014; 28:1449-1458.
- [29] Cahon T, Caillon R, Pincebourde S. Do aphids alter leaf surface temperature patterns during early infestation? *Insects* 2018; 9.
- [30] Saudreau M, Ezanic A, Adam B *et al.* Temperature heterogeneity over leaf surfaces: the contribution of the lamina microtopography. *Plant Cell and Environment* 2017; 40:2174-2188.
- [31] Helmuth B, Broitman BR, Blanchette C *et al.* Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecological Monographs* 2006; 76:461-479.
- [32] Kaspari M, Clay NA, Lucas J *et al.* Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Global Change Biology* 2015; 21:1092-1102.
- [33] Franken O, Huizinga M, Ellers J, Berg MP. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* 2018; 186:311-322.
- [34] Pincebourde S, Casas J. Narrow safety margin in the phyllosphere during thermal extremes. *Proc Natl Acad Sci U S A* 2019; 116:5588-5596.
- [35] Shi H, Wen Z, Paull D, Guo M. A framework for quantifying the thermal buffering effect of microhabitats. *Biological Conservation* 2016; 204:175-180.
- [36] Kearney MR, Deutscher J, Kong JD, Hoffmann AA. Summer egg diapause in a matchstick grasshopper synchronises the life cycle and buffers thermal extremes. *Integr Zool* 2018.
- [37] Sunday JM, Bates AE, Kearney MR *et al.* Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Science USA* 2014; 111:5610-5615.
- [38] Gilman SE, Wetthey DS, Helmuth B. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proceedings of the National Academy of Science USA* 2006; 103:9560-9565.
- [39] Zellweger F, De Frenne P, Lenoir J *et al.* Forest microclimate dynamics drive plant responses to warming. *Science* 2020; 368:772-775.
- [40] Davis KT, Dobrowski SZ, Holden ZA *et al.* Microclimatic buffering in forests of the future: the role of local water balance. *Ecography* 2019; 42:1-11.
- [41] Scheffers BR, Edwards DP, Diesmos A *et al.* Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology* 2014; 20:495-503.
- [42] Scheffers BR, Evans TA, Williams SE, Edwards DP. Microhabitats in the tropics buffer temperature in a globally coherent manner. *Biol Lett* 2014; 10:20140819.
- [43] Montejo-Kovacevich G, Martin SH, Meier JI *et al.* Microclimate buffering and thermal tolerance across elevations in a tropical butterfly. *J Exp Biol* 2020; 223.
- [44] Dyer A, Whitney H, Arnold S *et al.* Bees associate warmth with floral colour. *Nature* 2006; 442:525-525.

- [45] Woods HA, Saudreau M, Pincebourde S. Structure is more important than physiology for estimating intracanalopy distributions of leaf temperatures. *Ecology and Evolution* 2018; 8:5206-5218.
- [46] Pincebourde S, Casas J. Hypoxia and hypercarbia in endophagous insects: Larval position in the plant gas exchange network is key. *Journal of Insect Physiology* 2016; 84:137-153.
- [47] Kingsolver JG. Thermal and Hydric Aspects of Environmental Heterogeneity in the Pitcher Plant Mosquito. *Ecological Monographs* 1979; 49:357-376.
- [48] Pincebourde S, Montufar R, Paez E, Dangles O. Heat production by an Ecuadorian palm. *Frontiers in Ecology and the Environment* 2016; 14:571-572.
- [49] Seymour RS, White CR, Gibernau M. Heat reward for insect pollinators. *Nature* 2003; 426:243-244.
- [50] Mollinari MM, Peres CA, Edwards DP. Rapid recovery of thermal environment after selective logging in the Amazon. *Agricultural and Forest Meteorology* 2019; 278.
- [51] Pincebourde S, Casas J. Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. *Ecology* 2015; 96:986-997.
- [52] Pincebourde S, Casas J. Multitrophic biophysical budgets: Thermal ecology of an intimate herbivore insect-plant interaction. *Ecological Monographs* 2006; 76:175-194.
- [53] Jones JC, Myerscough MR, Graham S, Oldroyd BP. Honey Bee Nest Thermoregulation: Diversity Promotes Stability. *Science* 2004; 305:402-404.
- [54] Campbell GS, Norman JM. An introduction to environmental biophysics. New-York: Springer Verlag; 1998.
- [55] Helmuth B. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecological Monographs* 1998; 68:51-74.
- [56] Kearney MR, Shamakhy A, Tingley R *et al.* Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods in Ecology and Evolution* 2014; 5:273-286.
- [57] Filz KJ, Schmitt T, Engler JO. How fine is fine-scale? Questioning the use of fine-scale bioclimatic data in species distribution models used for forecasting abundance patterns in butterflies. *European Journal of Entomology* 2013; 110:311-317.
- [58] Lembrechts JJ, Nijs I, Lenoir J. Incorporating microclimate into species distribution models. *Ecography* 2019; 42:1267-1279.
- [59] Storlie C, Merino-Viteri A, Phillips B *et al.* Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biol Lett* 2014; 10.
- [60] Lembrechts JJ, Aalto J, Ashcroft MB *et al.* SoilTemp: a global database of near-surface temperature. *Global Change Biology* 2020; n/a.
- [61] Scherrer D, Korner C. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 2010; 16:2602-2613.
- [62] Pincebourde S, Salle A. On the importance of getting fine-scale temperature records near any surface. *Global Change Biology* 2020; n/a.
- [63] Mammola S, Piano E, Malard F *et al.* Extending Janzen's hypothesis to temperate regions: A test using subterranean ecosystems. *Functional Ecology* 2019; 33:1638-1650.
- [64] Kearney M, Porter W. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 2009; 12:334-350.
- [65] Kearney MR, Porter WP. NicheMapR - an R package for biophysical modelling: the microclimate model. *Ecography* 2016; 40:664-674.
- [66] Maclean IMD. Predicting future climate at high spatial and temporal resolution. *Glob Chang Biol* 2020; 26:1003-1011.

- [67] Levy O, Buckley LB, Keitt TH, Angilletta MJ. A dynamically downscaled projection of past and future microclimates. *Ecology* 2016; 97:1888-1888.
- [68] Gunton RM, Polce C, Kunin WE, Orme D. Predicting ground temperatures across European landscapes. *Methods in Ecology and Evolution* 2015; 6:532-542.
- [69] Duffy GA, Coetzee BW, Janion-Scheepers C, Chown SL. Microclimate-based macrophysiology: implications for insects in a warming world. *Curr Opin Insect Sci* 2015; 11:84-89.
- [70] Casas J, De Salvo B. Editorial overview: Plenty of bugs at the bottom. *Current Opinion in Insect Science* 2018; 30:vi-vii.
- [71] Feynman RP. There's plenty of room at the bottom. *Engineering and Science* 1960; 23:22-36.

Highlight of references of special [•] and outstanding [••] interest

- [5] De Frenne P, Zellweger F, Rodríguez-Sánchez F et al. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* 2019; 3:744-749. •• This study shows that the forest floor is buffered from thermal extremes in the same fashion across latitudes and continents. This is the first global analysis of forest understory microclimates.
- [13] Sears MW, Riddell EA, Rusch TW, Angilletta MJ. The World Still Is Not Flat: Lessons Learned from Organismal Interactions with Environmental Heterogeneity in Terrestrial Environments. *Integr Comp Biol* 2019; 59:1049-1058. • This review synthesizes the latest findings on the importance of fine scale thermal heterogeneity for the response of organisms to environmental changes.
- [34] Pincebourde S, Casas J. Narrow safety margin in the phyllosphere during thermal extremes. *Proc Natl Acad Sci U S A* 2019; 116:5588-5596. •• This study shows how fine scale microclimate variations (at the scale of a single leaf) translate into variation in thermal limits of herbivore insects living at the leaf surface. Both microclimate temperature and insect thermal limits vary greatly among species, but surprisingly all species are vulnerable to heat waves.
- [33] Franken O, Huizinga M, Ellers J, Berg MP. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* 2018; 186:311-322. • This study reports the thermal limits of a range of invertebrates living in a sand dune site. It shows that the thermal limits can vary by >10°C at the inter- and intra-specific levels.

[39] Zellweger F, De Frenne P, Lenoir J et al. Forest microclimate dynamics drive plant responses to warming. *Science* 2020; 368:772-775. •• This study shows for the first time that the dynamics of the forest cover, including logging, strongly influences the response of plants living in the understory to climate warming by modulating the forest floor microclimate.

[43] Montejo-Kovacevich G, Martin SH, Meier JI et al. Microclimate buffering and thermal tolerance across elevations in a tropical butterfly. *J Exp Biol* 2020; 223. • This study shows how forest microclimate and the plasticity of thermal limits in tropical butterflies interactively modulate the ability of these species to colonize high vs. low altitude areas.

[50] Mollinari MM, Peres CA, Edwards DP. Rapid recovery of thermal environment after selective logging in the Amazon. *Agricultural and Forest Meteorology* 2019; 278. •• This study nicely describes how logging activities modify the forest floor microclimate and also how long it takes for the original forest buffer to recover.

[57] Lembrechts JJ, Nijs I, Lenoir J. Incorporating microclimate into species distribution models. *Ecography* 2019; 42:1267-1279. • This study is among the rare works that successfully integrate microclimate properties into species distribution modelling for plant species, indicating the large error in distribution predictions when neglecting microclimates.

[62] Mammola S, Piano E, Malard F et al. Extending Janzen's hypothesis to temperate regions: A test using subterranean ecosystems. *Functional Ecology* 2019; 33:1638-1650. •• This fantastic study correlates the microclimate in cave at various depths and the thermal breadth of various cave spiders. This work transposes the Janzen framework to a temperate system for the first time.

[65] Maclean IMD. Predicting future climate at high spatial and temporal resolution. *Glob Chang Biol* 2020; 26:1003-1011. •• Although this is not the first mechanistic model developed to predict microclimates anywhere and anytime, this recent development makes possible to make these predictions at the finest scale possible currently, i.e., at the scale of 1 m².

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Figure 1

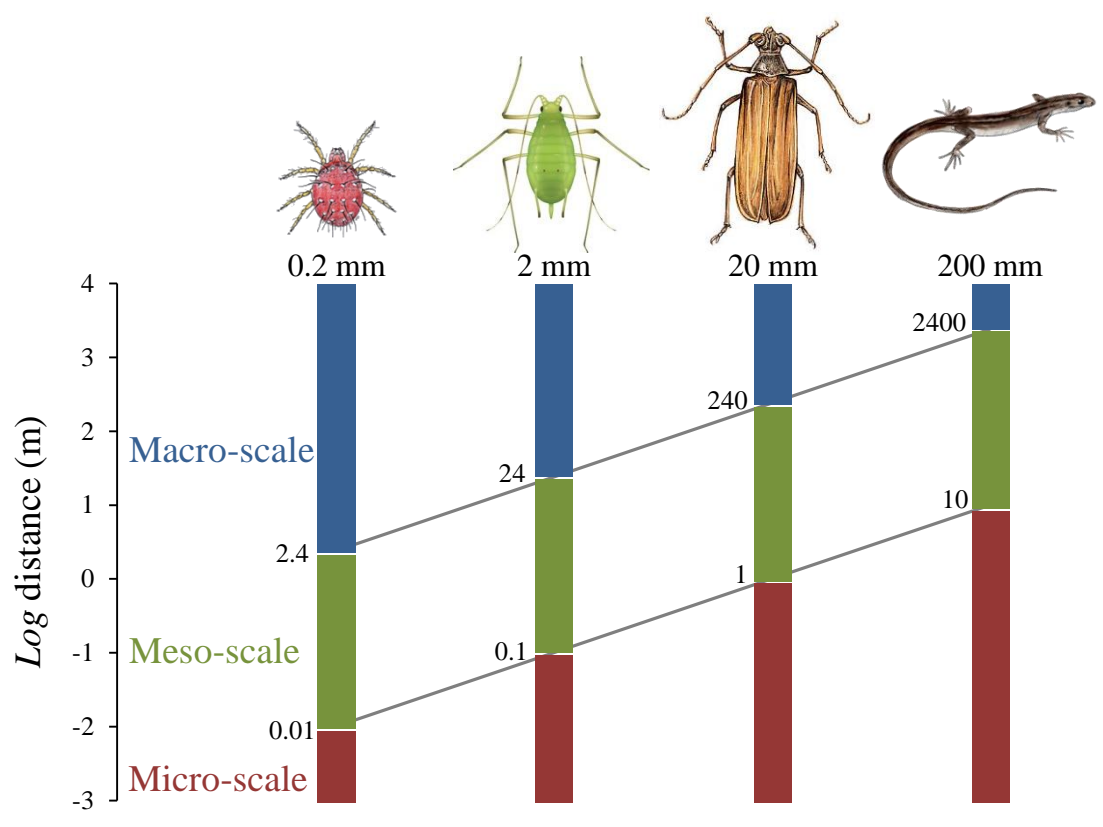


Figure 2

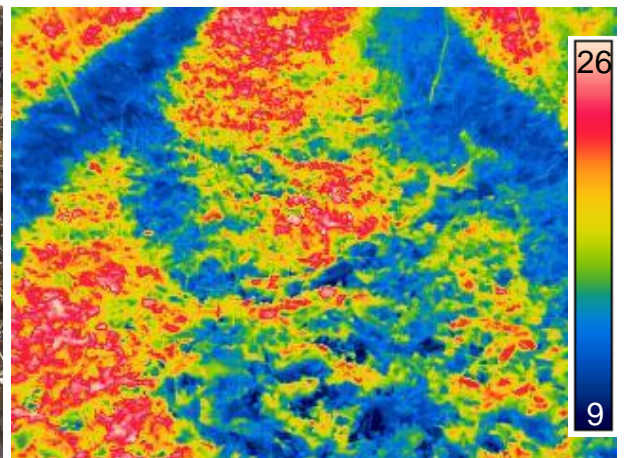
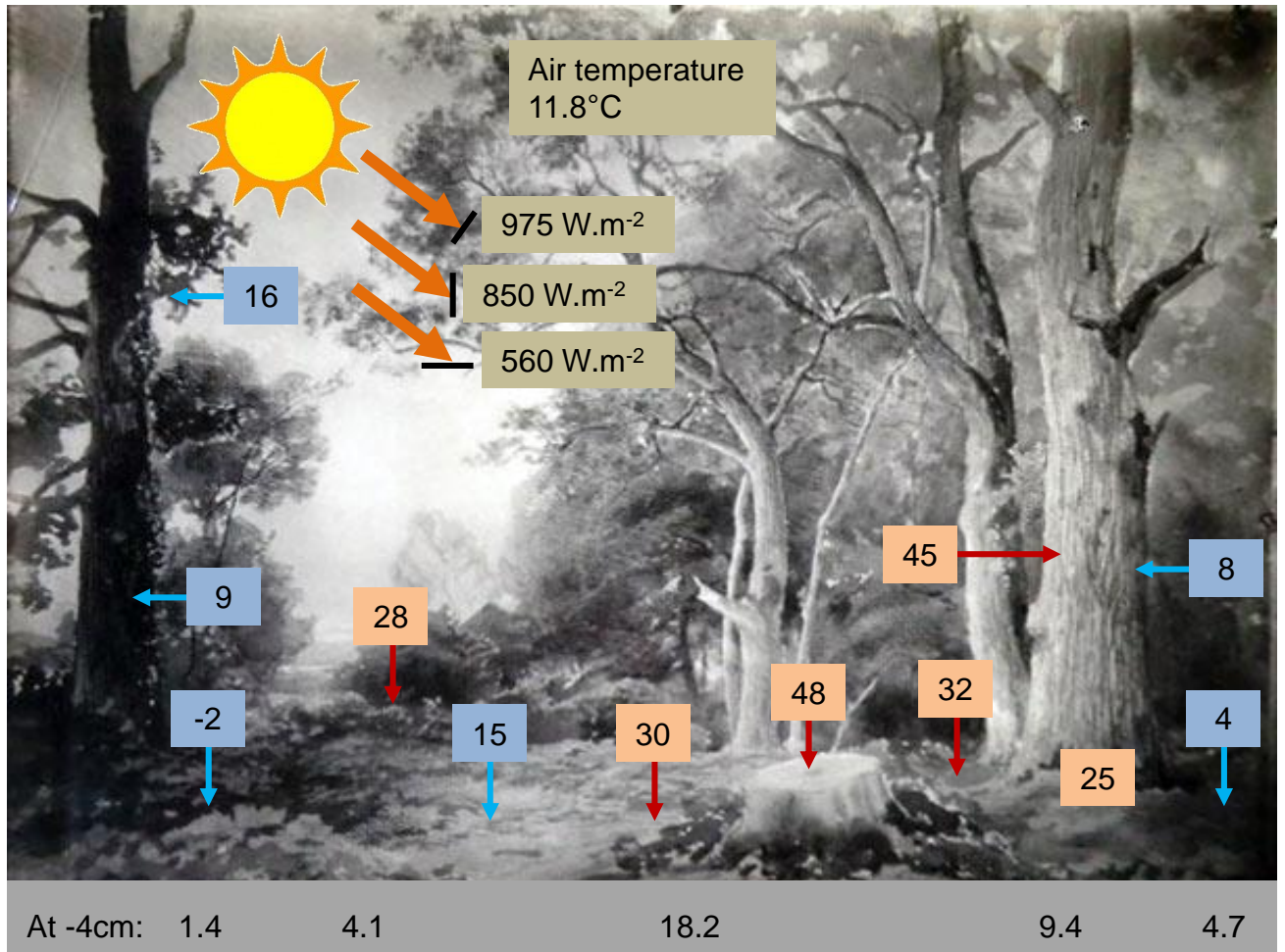
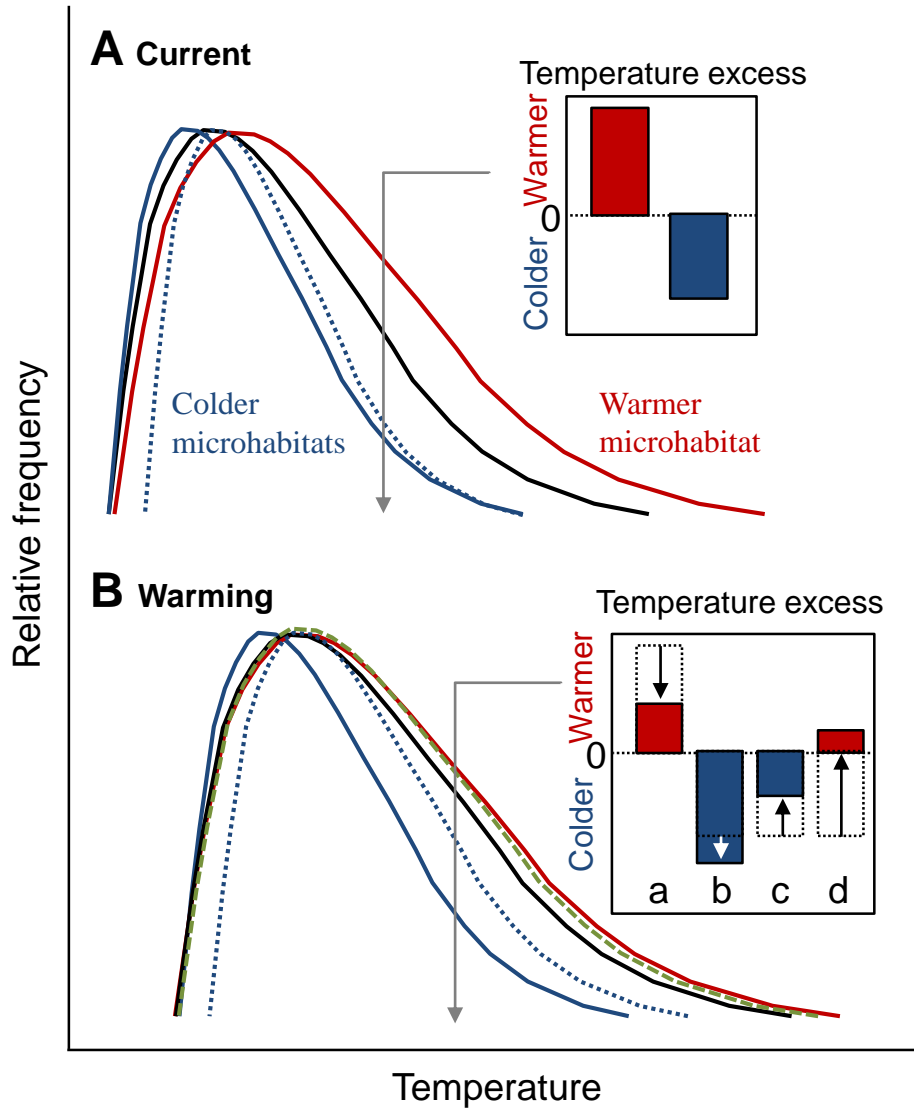
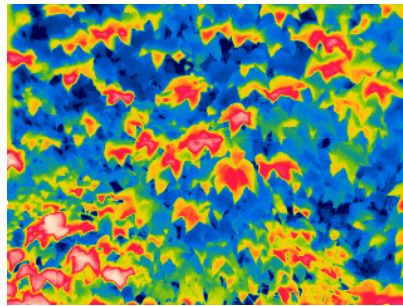
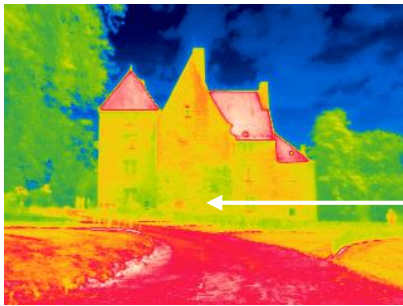


Figure 3



Highlights

- We provide a simple method to determine the microscale pertinent to small insects.
- Fine-scale microclimates can differ from local microclimates that are widely used.
- Temperature variation at fine scales plays a role in thermal adaptations.
- Little is known about the amplitude of microclimate change at such fine scales.
- Some microhabitats may buffer and others magnify the amplitude of warming.



Dear Jérôme,

We thank you and the reviewer for the feedbacks on our MS, and for allowing us to submit a revised version. Below are our responses (in blue) to each comment and question (in black) from both you and the reviewer. We think the changes we made have improved the MS!

Best wishes,

Sylvain & Art

Comments from the Editors and Reviewers:

I received one review of the paper and read it myself in the interest of time for this special issue. As you can read, the referee is quite positive and the requests are feasible, rapidly. I concur with this assessment but would like the authors to think about their Figure 1 a bit more. Indeed, this Figure might become a classic, so special care is not a waste of time. It is actually surprising that no one before came up with a similar construction. It is built on the assumption that the scaling used for humans (the ratio of 1.7 m height to 100 m for defining microclimate for example) can be applied to other organisms and explains for example why you end up with 1 cm for a mite for the extent of microclimate. What's about if the original scaling for humans was not that good? you have yourself work on the surface heterogeneities of apples leaves and showed the extraordinary differences of temperature according to orientation at a much smaller scale than 1 cm. Building a different scaling law - for example in thinking in terms of enzyme kinematics or growth speed- is probably asking for too much for this paper (?), but I wish you would discuss other possibilities as well.

Reply: This is a good idea! We have added an entire paragraph to discuss further other possibilities or complexities when calculating the spatial scale of microclimates. In this new paragraph (see right after figure 3 in the main text), we include 3 axis of discussion. The two first correspond to the two first points raised by the reviewer below. The third point discusses the importance of choosing the right thresholds when calculating this scaling. To illustrate, we recalculated the limit for microscale for spider mites using a lower threshold between meso and microclimate, inducing a change from 10 cm to 6 mm only. We rather prefer, however, to not include nor refer to scaling laws at the physiological levels because they fall outside the microclimatic context that we define in this MS.

Reviewer 1: This is a great paper that I enjoyed reading and makes a timely contribution to the literature on insect microclimates. Several noteworthy points are brought together into a coherent and succinct article. I only had a few minor points and suggestions for clarification or additional detail and a few minor typographical errors to correct.

P 3 spatial scale. Much attention is given here to horizontal distance. Maybe it is worth mentioning that many insects explore vertical habitat heterogeneity, possibly even to a greater extent than horizontally (I'm thinking here of a mite or ladybird living its entire life on a single tree), implying that the microclimate referred to be climatologists is even more disconnected than typically assumed. I guess it's the frequency distribution of thermal opportunities in both vertical and horizontal space you're interested in when defining microclimates, but it depends on the animal's ability/propensity to move and make use that space.

Reply: Yes, this is an important and good point. We mention these issues in the new paragraph mentioned above after the comment from the Editor.

p. 3 Figure 1 - I like this, it's a clever and intuitively simple way of thinking about these sorts of issues. Playing devil's advocate here a little, the potential criticism of this that someone may raise is that linear scaling may not apply since small insects may be capable of travelling proportionally faster or further (e.g. jump easily much more than their height) than a person in its lifetime. So really emphasizing to the reader that this is a quick 'rule of thumb' approximation will suffice while reminding that a good handle on the biology is always necessary, if you agree?

Reply: Yes, we definitely agree! We report these issues in the new paragraph mentioned above.

p.4 "microhabitats to air temperature measured at a standard height of 1.5 m above ground in open areas." Normally this is shaded air temp, right? Maybe add that detail, if you agree.

Reply: Yes, this is correct. The sensor should be shielded to avoid solar radiation to heat up the temperature sensor. We now end the sentence with: "...(using appropriate equipment to protect the sensor from solar radiation)".

p. 4 "sunny day in summer in UK" - add 'the' before 'UK'

Reply: done.

p. 6. Fig. 2. Add in legend the resolution of the thermal camera for the leaf images? Someone might imply that much of that variability is 'noise' of the IR sensor chip on the camera, at least if it's a low-res model.

Reply: Yes, good idea. We now provide this information in the figure legend: "...(scale in °C; IR camera FLIR B335, resolution 320x240 pixels, thermal sensitivity 0.05 °C)".

p. 7. 'characterized by a large spatial heterogeneity' - delete 'a' before 'large'.

Reply: done.

p. 8 'predict the amplitude of' this sentence seems to imply a little that it will always get worse from an overheating perspective, when in reality its possible "the buffers situation" it gets a little better, as discussed and with examples in the Gilman paper further down that paragraph. Perhaps tweak the opening sentence to alert readers that its both the direction and magnitude of the coupling/decoupling effect that is of interest, if that's what you intended?

Reply: This is a good point. The first (opening) sentence of this section was modified to include both the direction and the amplitude of the climatic changes.

p. 9 'By contrast, whether and how other microclimates magnify the amplitude of climate warming' - a bit like my previous comment. Here too you seem to be implying it can only get worse from a thermal point of view, but can't certain specific situations (various combinations of biophysics and moist substrates) also lead to temperatures getting cooler than they were before? Maybe these processes are too rare to be important, but just thinking about this here.

Reply: We have reformulated the corresponding sentence: "By contrast, whether and how other microclimates magnify or reduce the amplitude of climate warming is much less investigated."

p. 9. - not sure I follow. The thermal flowers in the Seymour paper example are warming up at night, so unclear how this is linked to solar radiation. Perhaps just say that some flower/plant structures warm up, but typically when air temps are relatively cool?

Reply: We admit the sentence was not formulated correctly. The idea is to mention that not all microclimates are linked to solar radiation, and thermogenic flowers are a good example of this. We

have reformulated: "Other particular microhabitats are warmer than the local microclimate independently of solar radiation, such as thermogenic flowers that produce heat during the night [48, 49]. In general however, the solar energy input is key."

p. 9 - last line. Odd grammar. "warming despite even though they are warmer than their" - delete 'despite'?

Reply: Sorry, that was a typo. 'despite' has been deleted.

Fig 3 - cool figure. Maybe just state 'hypothetical' or is it based on some observed data from somewhere, if so give source ref?

Reply: Yes, these curves are hypothetical. This is now mentioned in the figure legend.

Fig. 3 - changing the shapes of these curves by buffering and amplifying in the upper parts likely also has profound effects on a range of other heat stress metrics like return times of heat waves, as well as if measuring amounts of times spent above key thresholds (eg. Accumulated heat injury levels)? Add if you think it worth mentioning.

Reply: This is a good point! We now direct the reader to this point at the very end of the section: "In all these scenarios, we focus on shifts of temperature distributions. Nevertheless, any changes in the shape of these temperature distributions (e.g., skewness and kurtosis) should also contribute to the ability to buffer the amplitude of warming."

p. 11 - 'This thermodynamic effects was nicely' - effect in singular, as used in sentence before and after?

Reply: done.

p. 11 - last line 'Otherwise, measurements with a high spatial' delete 'a'

Reply: done.

p.11 - "To date, however, only few models have been developed that" - add 'a'

Reply: done.