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Review

The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change ☆

H. Arthur Woods [a,*], Michael E. Dillon [b], Sylvain Pincebourde [c]

[a] *Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA*
[b] *Department of Zoology and Physiology and Program in Ecology, University of Wyoming, Laramie, WY 82071, USA*
[c] *Institut de Recherche sur la Biologie de l'Insecte (IRBI, CNRS UMR 7261), Université François Rabelais, Faculté des Sciences et Techniques, 37200 Tours, France*

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ABSTRACT

We analyze the effects of changing patterns of thermal availability, in space and time, on the performance of small ectotherms. We approach this problem by breaking it into a series of smaller steps, focusing on: (1) how macroclimates interact with living and nonliving objects in the environment to produce a mosaic of thermal microclimates and (2) how mobile ectotherms filter those microclimates into realized body temperatures by moving around in them. Although the first step (generation of mosaics) is conceptually straightforward, there still exists no general framework for predicting spatial and temporal patterns of microclimatic variation. We organize potential variation along three axes—the nature of the objects producing the microclimates (abiotic versus biotic), how microclimates translate macroclimatic variation (amplify versus buffer), and the temporal and spatial scales over which microclimatic conditions vary (long versus short). From this organization, we propose several general rules about patterns of microclimatic diversity. To examine the second step (behavioral sampling of locally available microclimates), we construct a set of models that simulate ectotherms moving on a thermal landscape according to simple sets of diffusion-based rules. The models explore the effects of both changes in body size (which affect the time scale over which organisms integrate operative body temperatures) and increases in the mean and variance of temperature on the thermal landscape. Collectively, the models indicate that both simple behavioral rules and interactions between body size and spatial patterns of thermal variation can profoundly affect the distribution of realized body temperatures experienced by ectotherms. These analyses emphasize the rich set of problems still to solve before arriving at a general, predictive theory of the biological consequences of climate change.

Contents

☆This article belongs to the Special Issue dedicated to Prof. Ken Bowler for on- going, long-term contributions to thermal biology : What sets the limit? how thermal limits, performance and preference in ectotherms are influenced by water and energy balance.

[*] Corresponding author.
E-mail address: art.woods@mso.umt.edu (H.A. Woods).

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1. Introduction

The recent IPCC report (IPCC, 2014) lays out a stark case that climate change is happening, that the changes stem from human activity, and that the physical effects over the next century will be large. Relative certainty about the physical aspects of change, however, belies significant equivocation about its consequences for the world's organisms—about risks of extinction, about how much species ranges will shift, and about the roles that behavior, acclimation, and evolution may play in blunting impacts at the level of populations and species (Buckley et al., 2013; Deutsch et al., 2008; Huey et al., 2012). In broad terms, the equivocation reflects (i) that climate change at global scales generates more complex, less predictable change at the local scales where organisms live (Pincebourde and Woods, 2012; Potter et al., 2013); and (ii) that responses to local change are filtered through the complex nonlinearities of environment–organism interactions (Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2012; Kingsolver et al., 2011; Pincebourde and Woods, 2012; Williams et al., 2014). These uncertainties are, and will continue to be, key barriers to predicting how soon, and by how much, organisms will be affected. Reducing uncertainty is a high priority because the evidence that populations are affected is now compelling (Bebber et al., 2013; Hughes, 2000; Parmesan and Yohe, 2003; Parmesan et al., 1999; Walther et al., 2002).

Although connections between climate change and ecological shifts are obvious, and even relatively well understood in some systems (Higgins et al., 2013; Kearney et al., 2010), we still lack a framework for understanding those connections in a quantitative, predictive, and mechanistic way (Helmuth et al., 2005; Huey et al., 2012; Williams et al., 2008). A key problem is that the effects of climate change can be manifest via multiple pathways, such that simple one-to-one mappings—between change in a climate variable and in the physiology or ecology of a focal taxon—will rarely if ever occur (Newman et al., 2011). This problem can be visualized in terms of a complex electrical circuit whose elements are arranged simultaneously in series and in parallel. Although, with the right analysis, the behavior of such a circuit may be predictable, it still usually is nonlinear and non-intuitive. In the same way, the climate–organism connection contains many sub-links arranged in series and in parallel. The topology of the links makes the problem difficult; and worse, the properties of nodes and links (thermal physiologies, population growth rates, interaction strengths, etc.) are more difficult to define, and more variable in space and time, than are their analogs in circuits (voltages, resistances, capacitances, wiring, etc.).

One approach is to recognize that two of the major processes are arranged in parallel: (i) climate-related factors that influence ectotherms directly, via their physical effects on individuals and populations, and (ii) factors that influence ectotherms indirectly, via their major biotic partners (i.e., a kind of abiotic versus biotic distinction). Although the rest of the paper focuses on physical effects, indirect, biotic effects may play a dominant role for many animals (Gilman et al., 2010; Tylianakis et al., 2008). Any population is linked, by tens or hundreds of pathways, to other members of its community (host plants, pathogens, competitors, predators, prey). Climate change will alter the strength of those links (Gilman et al., 2010; Post, 2013), sometimes causing the focal species itself to grow, decline, or shift in space. In other words, biophysical analyses like those described below capture only part of the problem.

This paper focuses instead on the direct, physical leg, all in the context of temperature. Clearly, temperature has pervasive effects on large swaths of biology (Kingsolver, 2009). Furthermore, the direct effects of temperature are divisible into smaller steps each of which is relatively amenable to analysis (Fig. 1): (1) macroclimates interact with living and nonliving objects in the environment to produce a complex mosaic of thermal microclimates; (2) mobile ectotherms sample those mosaics by moving around in them; and (3) the physiology of the ectotherms transduces thermal experience into performance (e.g., rates of movement, feeding, metabolism, and growth) (Kingsolver, 2009), which in turn influences demographic parameters (i.e., rates of birth and death) and fitness.

This paper grapples with the first two of these three steps. This emphasis reflects several considerations. First, these two areas contain pressing, open questions in need of general solutions if we are to make progress on the broader problem of predicting organismal responses to climate change. Predicting responses involves both quantifying the available thermal landscapes and understanding the behaviors that organisms use to sample them. Second, significant progress has been made recently in the third area. Using macrophysiological approaches, a set of papers over the past six years has begun to integrate broad-scale climate data with data on thermal physiology (tolerances and performance curves) to predict how future climates will affect organisms (Buckley and Kingsolver, 2012a; Buckley et al., 2013; Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2012; Kingsolver et al., 2013; Sunday et al., 2014, 2012, 2011; Vasseur et al., 2014) and how population fitness will change when climate change has different effects on different life stages (Buckley and Kingsolver, 2012b; Kingsolver et al., 2011).

2. Uncertainty in the microcosmos

Microclimates are spatially-restricted spaces whose conditions are defined by other local objects. Although the existence of microclimates is widely appreciated (Oke, 2002; Willmer, 1982), as are the biophysics connecting their properties to those of local macroclimates (Bakken, 1992; Gates, 1980; Kearney et al., 2014; Porter et al., 2002), the roles that microclimates play in the ecology of small organisms remain understudied (De Frenne et al., 2013; Potter et al., 2013; Sunday et al., 2014). Indeed, forecasting the impacts of future climate change on organisms requires that we understand in a much more general way how microhabitats filter environmental fluctuations, and whether heterogeneity at small scales will be sufficient to allow organisms to find and exploit favorable conditions (Hannah et al., 2014; Kearney et al., 2009; Sunday et al., 2014). Here we discuss patterns of microclimatic variation along three axes—the nature of the objects producing the microclimates (abiotic versus biotic), how microclimates translate macroclimatic variation (amplify versus buffer), and the temporal and spatial scales over which microclimatic conditions vary (long versus short). These three axes define the complexity, heterogeneity, and uncertainty of microclimates in a changing world.

2.1. Abiotic versus biotic microclimates

Along the first axis, microclimates can be categorized as abiotic or biotic according to their main elements. Abiotic microclimates reflect the filtering of environmental conditions by abiotic structures—rocks of different sizes, soils of different compositions, topography of the ground surface, area and depth of water, etc. Biotic microclimates reflect filtering by living organisms or the structures they build. For example, microclimatic profiles under plant canopies are distinct from those of their regional climates because of the effects of shading and transpiration on local energy balances (Nobel, 1999). Biotic microclimates can also be driven by the presence of nearby congeners. For example, exposed mussels living in groups may reach body temperatures that are 4–5 °C lower than identical mussels living alone but experiencing the same macroenvironmental conditions (Helmuth, 1998). Most

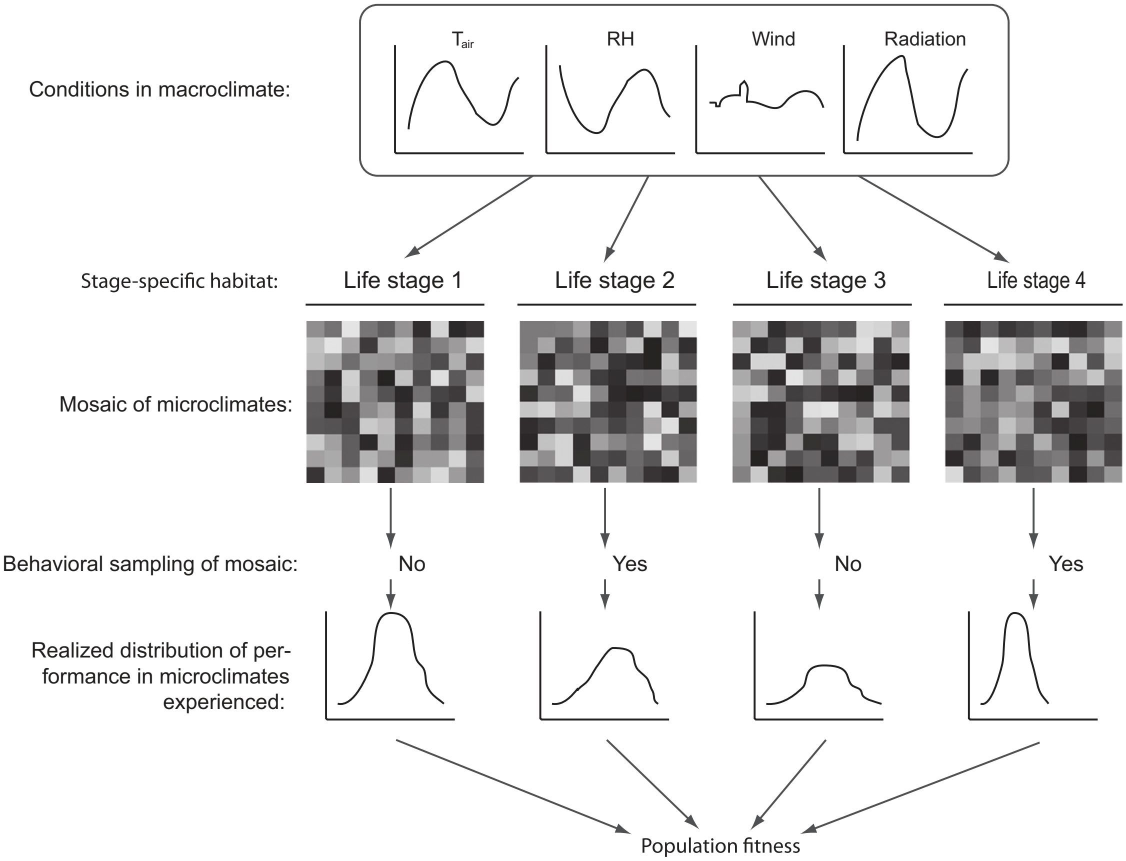

Fig. 1. Diagram of the connections between climate and fitness of a population of ectotherms. The figure emphasizes that ectotherms have different life stages, each with unique microclimates available to it. For example, if the focal species was a metamorphosing insect, life stages 1–4 would represent egg, larva, pupa, and adult, each with its own microclimates. Moreover, some life stages—the mobile ones like larva and adult—may actively sample local microclimatic heterogeneity, whereas the immobile stages do not. The placement of individuals within the range of possible microclimates, and the behavioral rules by which mobile stages sample local heterogeneity, will produce some realized set of performance curves for each stage. Finally, the fitness of the population will reflect the stage-specific effects of microclimates on performance, which can be combined using demographic models.

microclimates combine abiotic and biotic elements, which increases the complexity of local microclimatic mosaics.

Biotic microclimates are less predictable than abiotic ones—because they result not just from the physical relationships determining heat transfer between objects and their surroundings, but also from the ecophysiology of the object. For example, the relative stomatal opening of leaves influences leaf surface temperature, which in turn influences the performance of leaf-dwelling arthropods (Pincebourde and Woods, 2012). The inner structure of fruits such as apples determines the amplitude of thermal conditions available for insects feeding inside (Roberts and Feder, 2000; Saudreau et al., 2009). The heat generated by some thermogenic flowers helps insect pollinators by raising their body temperatures (Seymour et al., 2003). The elevated body temperature of mammals requires sophisticated thermoregulation by their ectoparasites to avoid overheating (Lahondère and Lazzari, 2012). More complex examples involve the high diversity of species that inhabit the thermoregulated nests of social insects (Jones and Oldroyd, 2006). In these examples, attempts to forecast the effects of climate change must account both for direct effects of climate on the focal species and for indirect effects via changes in the physiology and behavior of the biotic components.

Both abiotic and biotic elements can be manipulated by organisms to achieve favorable microclimates. The concept of an "ecosystem engineer", a species that induces changes in its proximate environment (Jones et al., 1997), also applies to organisms that engineer thermal environments. For example, African termite species build nests with sophisticated ducting and air flows that help to regulate internal temperatures (Korb, 2003). In the case of biotic microclimate, one organism can reconfigure or manipulate another to generate specific microclimatic conditions. For example, leaf mining insects feed on leaf tissues from the inside via a structure called a mine. Modified leaf tissues inside mines can cause mine temperatures to depart from both leaf and air temperatures (Pincebourde and Casas, 2006; Pincebourde et al., 2007). Similarly, gall insects reconfigure their vegetal environments, thereby achieving specific temperature patterns (Layne and Layne, 1991). Exploring the effects of climate change on these engineers requires that we identify direct and indirect effects on all parties to the interaction.

2.2. *Microhabitats as buffers or amplifiers of environmental conditions*

Along a second axis, microclimates are defined by the degree to which they amplify or buffer macroclimatic variation. As a null hypothesis, we might expect that microhabitats simply mirror macroscale changes in temperature. More often, however, microclimate temperatures deviate from macroscale temperatures—and the degree of deviation may not scale linearly with macroscale temperature. Thus, the degree of buffering or amplification varies according to the type of habitat. Moreover, the filtering that occurs at high and low temperatures can differ. We illustrate this issue with two examples, one for a buffer and another for an amplifier.

A buffering microhabitat is less variable than ambient air. To illustrate this, we used small temperature data loggers to measure

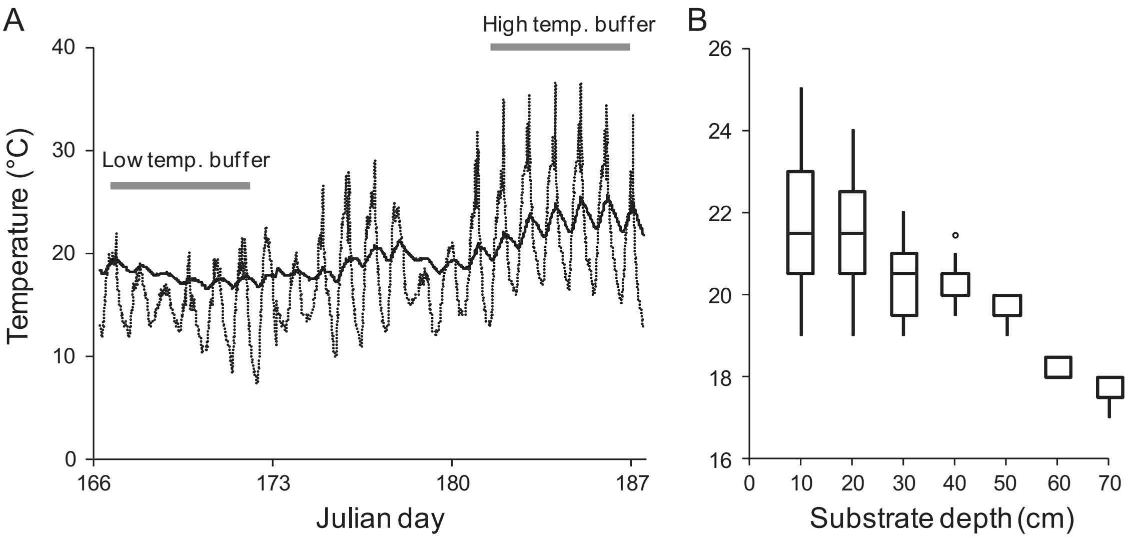

Fig. 2. Example of a microhabitat buffering environmental fluctuations, a temperate pond (near Tours, France). (A) A time series of the temperatures of ambient air (dotted line) and pond water (solid line) during 21 days in spring 2013, both measured at 20-min intervals. Water temperature was taken at the surface of the pond substrate (30 cm depth). The relative position of the two curves indicates when the pond microhabitat buffers the lowest air temperatures (i.e., water is warmer than air) and when the pond buffers the highest air temperatures (i.e., water is colder than air during daily heat peaks). (B) Box plots of pond water temperatures taken at the surface of the pond substrate along the slope from the pond border to the center, across a range of depths. Temperatures were taken every 20 min for one month in spring 2013.

water temperature every 20 min at the bottom of a pond, at the surface of the mineral substrate (depth 30 cm) near the pond edge, throughout spring and summer of 2013 (Fig. 2). The water temperature at 30 cm depth fluctuated much less than did ambient air temperature. The pond microhabitat buffered both high air temperatures during the warmest periods and low air temperatures during the coldest (Fig. 2A). For example, aquatic macroinvertebrates experienced a range of less than 7 °C over the 21-day period shown in Fig. 2A while air temperature varied by more than 25 °C. Nevertheless, thermal stability does not imply spatial homogeneity. To quantify this aspect, we also recorded the water temperature near the bottom of the pond along the slope from the border toward the center, and therefore as a function of depth. The aquatic thermal environment was more stable, and colder, at a depth of 70 cm compared to depths less than 30 cm close to the pond edge (Fig. 2B). Therefore, aquatic organisms living at the surface of the substrate can still thermoregulate over small distances by swimming or walking on the slope, with the caveat that factors other than temperature (predators, food, oxygen, etc.) may influence behavioral decisions.

Finally, the same microhabitat can buffer or amplify macroclimatic change, depending on abiotic and biotic context. We illustrate this point using two leaf examples. First, we measured the temperature of apple leaves in a temperate orchard (near Tours, France) every 5 min using fine thermocouples (type T, 0.2 mm in diameter; TCSA, Dardilly, France) connected to a weather station (CR10X, Campbell Scientific, Leicestershire, UK). Apple leaves exposed to solar radiation were often warmer than ambient air (Fig. 3A). Therefore, the daily maximal leaf temperature regularly exceeded that of ambient air. In addition, leaf temperatures at night were often slightly lower than air temperature, especially on clear nights when leaves received little thermal radiation from the sky. In other words, the leaf surface amplified low environmental temperature at night, depending on level of cloud cover. The second example examines leaves embedded in canopies. We used thermography to follow surface temperatures of leaves of a single shrub (*Clusia nemorosa*) at the top of a tropical inselberg in French Guiana (Trinité reserve). At the canopy scale, the thermal environment can be quite heterogeneous for small ectotherms living at the leaf surface. Thermography shows that canopies are complex mosaics of temperature patches (Fig. 3B and C). The temperature distributions shifted during the day, driven by fluctuations in air temperature (Fig. 3D), but the range of the temperature excess (i.e., the degrees above ambient for a given patch) increased as the sun approached its zenith (Fig. 3E). Amazingly, although these *Clusia* canopies showed high thermal heterogeneity (range of >20 °C), most of the patch temperatures were above ambient air temperature (Fig. 3E). This suggests that organisms on tropical tree leaves will have limited opportunities to escape the heat during global warming because of the amplifying nature of their leaf microhabitats. Competition for the few remaining cold spots can also be expected to increase. By contrast, leaves of other plants, especially those at subtropical and temperate latitudes with ample water available to them may buffer high temperatures by transpiring away heat at high rates (Helliker and Richter, 2008; Linacre, 1967; Potter et al., 2009).

2.3. Spatial and temporal extent of microclimates

A third axis that usefully describes microhabitats is the scale over which they vary in space and time. Generally, scales of variation can be short or long. However, what *short* and *long* mean depends on context and, in particular, on the body size of the focal organism—i.e., a spatial scale of 1 m may be long for a 1-mg ant but short for 1-kg lizard. Temporal scales too have meaning primarily in relation to body size—because larger bodies have slower rates of living and integrate processes over longer time scales. In the context of temperature, larger bodies have more thermal inertia; their temperatures change more slowly (Stevenson, 1985a).

Microclimatic patterns should therefore be analyzed relative to the integration time of the focal organism (see next section). For example, leaf surfaces can show short-term but large increases in temperature when suddenly exposed to direct solar radiation for a few seconds or minutes (Vogel, 2009; Way and Pearcy, 2012)—so-called sunflecks, which are common during cloudy conditions (see also the high frequency fluctuations in Fig. 2A). Therefore, maximum temperature cannot be readily compared to thermal tolerance thresholds that are usually measured in (at best) 1-h temperature trials (Chown and Nicolson, 2004) or during ramping experiments (Terblanche et al., 2011). More broadly, temperature tolerance depends on both the temperature experienced and the duration of exposure (Rezende et al., 2014). Practically, fine-scale

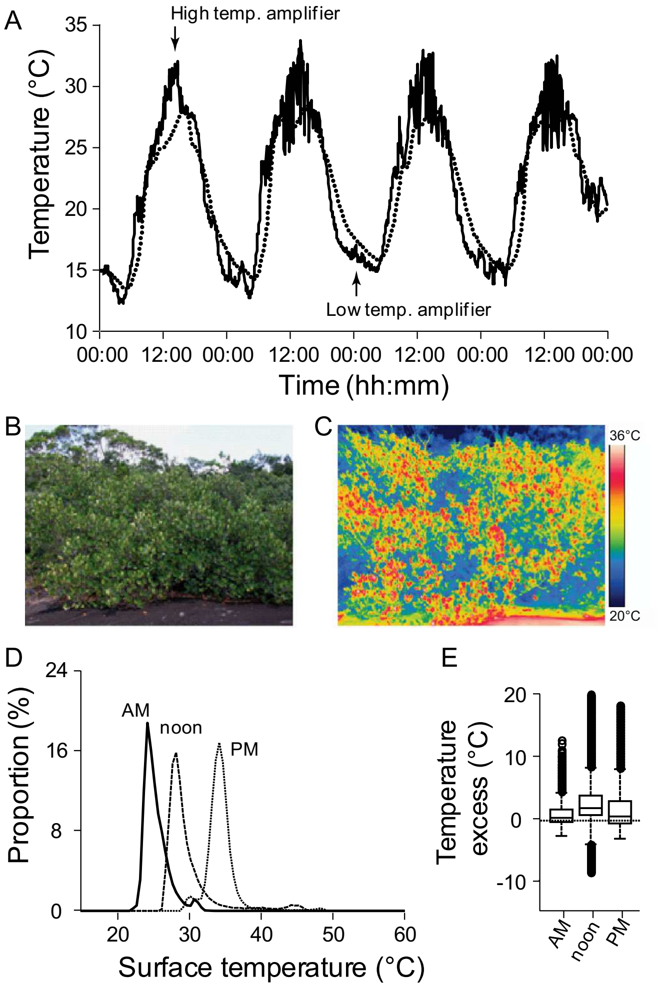

Fig. 3. Example of a microhabitat amplifying or buffering environmental fluctuations depending on context. (A) A four-day time series of the surface temperature of an apple tree leaf (solid line) and of ambient air temperature (dotted line) within a temperate apple orchard. The leaf surface is warmer than air at midday but usually colder at night under a clear sky. (B–E) Leaf surface temperature patterns in a tropical location. *Clusia nemorosa* shrubs (B), located at the top of an inselberg in French Guiana, were followed by thermography (C). Infrared images were taken 3 times per day, in the morning, at midday and in the afternoon. Vegetation surface temperature for each pixel was extracted to graph the density distributions (D). The temperature excess (deviation between leaf surface temperature and ambient air) of each pixel in each image was also calculated to standardize for air temperature. The box plots of these temperature excesses (E) show the relative portion of the vegetation surface that was warmer than ambient air (positive values) and colder than air (negative values).

temporal resolution of temperature sampling is known to influence our capacity to model the ecological impacts of climate change (Dillon et al., 2010), particularly for species that have little or no capacity to buffer environmental changes using behavior (Kearney et al., 2012).

Lastly, many species are broadly distributed, and the microclimate mosaics available locally to populations may change significantly across their ranges; species whose ranges cover large spatial extents may also be subjected to a greater total diversity of microclimates. Such geographic diversity stems from large-scale differences in the combinations of biotic and abiotic factors contributing to local microclimatic diversity. In general, the amplitude of microclimate fluctuations is expected to vary with latitude. For example, thermography of alpine landscapes showed that, in the temperate zone, the diurnal amplitude of leaf surface temperatures was twice as large as the amplitude of changes in air temperature; in the subarctic zone, it was four times as large (Scherrer and Körner, 2010). An intertidal example: the body temperature of the California mussel, *Mytilus californianus*, varies with latitude in a complex way due to the local influence of tide cycle and various abiotic factors (Helmuth et al., 2006; Mislan et al., 2014). All else being equal, areas with complex topography are expected to generate more fine-scale heterogeneity, and in particular higher maximal surface temperatures (Ashcroft and Gollan, 2012), although vegetation may dampen the strength of the influence of topography (Lenoir et al., 2013). Nevertheless, there is no general theory for predicting *how much* microclimatic diversity changes geographically, or how total diversity scales to range size.

3. The potential power of behavioral filtering

Maps of microclimate temperatures do not give organismal temperatures directly because organisms subsample by moving (Bogert, 1949; Kearney et al., 2009). Indeed, movement is a key action by which animals interact with their thermal environments (Bartholomew, 1964; Huey et al., 2002; Stevenson, 1985b). Movement often will be the first line of defense against thermal extremes, and the means by which animals attain body temperatures that they prefer.

For example, despite large diurnal fluctuations in air and ground temperatures in their Chihuahuan Desert habitat, horse lubber grasshoppers (*Taeniopoda eques*) sustain stable daytime body temperatures of about 35 °C (Whitman, 1987). They do so using a suite of behaviors that includes basking in the sun and pressing their bodies to the ground during the mornings (when they would otherwise be too cold) and climbing into bushes and hiding in the shade of stems during midday (when they would otherwise be too hot). In locusts (*Locusta migratoria*), individuals carefully regulate their body temperatures after a meal to control relative extraction of carbohydrates and protein (Clissold et al., 2013; Coggan et al., 2011). Such sophisticated behaviors may be the rule rather than the exception among terrestrial insects (Chown and Nicolson, 2004; Harrison et al., 2012; May, 1979), and behavioral thermoregulation clearly is common among other taxonomic groups (Angilletta, 2009; Blouin-Demers and Weatherhead, 2001; Chapperon and Seuront, 2011; DeNardo et al., 2004; Du et al., 2011; Nice and Fordyce, 2006).

The question is thus not whether behavioral thermoregulation is possible or important but whether ectotherms can use it to buffer (or exploit) changes in their local climates. This question has come to the fore in studies of organismal responses to climate change. In one of the first global analyses of the importance of behavior, Kearney et al. (2009) modeled operative temperatures of a small lizard-like ectotherm distributed across the globe and either sitting in full sun, sitting in deep shade, or shuttling between sun and shade in an attempt to attain a preferred body temperature. Depending on location in the world, and relative amount of available shade, behavior (shuttling) allowed organisms to avoid lethal extremes and to spend significantly greater fractions of their time at the body temperatures they preferred. In another recent study, Sunday et al. (2014) showed that virtual ectotherms (again, 5-g, lizard-like objects) distributed in exposed habitats across the globe, have maximum operative temperatures that often exceed known critical upper and lower temperatures. They infer from these patterns that most ectotherms *must* use behavioral thermoregulation (i.e., shade-seeking during midday when habitats are seasonally warmest) to avoid lethal extremes. For thermoregulating ectotherms, this implies that the spatial and temporal heterogeneity and spatial structure of thermal landscapes are as important as mean temperatures (Caillon et al., 2014; Sears and Angilletta, in press); for biologists, this implies that it is critical to

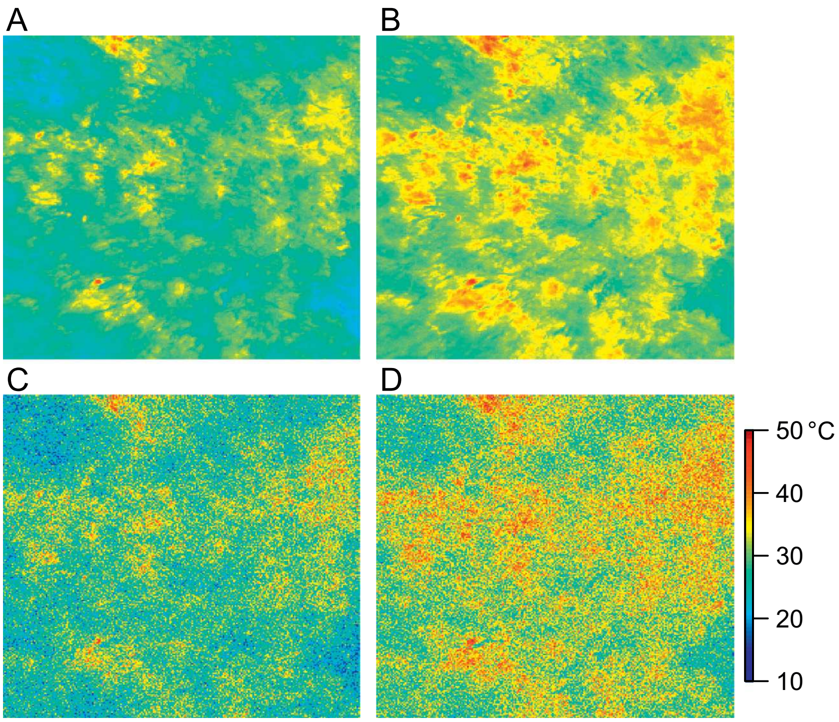

Fig. 4. Thermal landscapes on which virtual ectotherms were released. (A) The original infrared image of mixed grasses and forbs along the banks of the Loire River, taken from about 2 m height. The other panels are manipulations of the original image: (B) every pixel 4 °C warmer, (C) total variance increased by 2 °C, and (D) both effects (shift in mean and variance) combined.

characterize spatial and temporal distributions of available microclimatic temperatures (Potter et al., 2013).

Despite indications of behavior's buffering power, its quantitative importance in different taxa, and across body sizes and biomes, remains poorly understood, especially in relation to climate change. Here, we present two approaches to this issue. First, we present preliminary results from an individual-based model that analyzes how different behavioral rules affect realized thermal experience. These rules reflect simple ways that ectotherms could move among thermal patches within well-defined mosaics. Second, we present a conceptual model for how small ectotherms can exploit highly predictable environmental gradients created by other, larger objects in their environments.

3.1. *Individual-based modeling*

Here we use simulations to examine the relationships between several key traits of organisms, characteristics of microclimates, and more general descriptions of climate-buffering behaviors. As in most simulations, the goal is to strike a balance between capturing sufficient detail and keeping it simple. In particular, we include parameters that, if not already available, are readily measured for diverse taxa. The key questions are, first, to what extent can behavior buffer the realized thermal experience of ectotherms moving through mosaics of microclimates, and, second, how strongly does realized thermal experience depend on changes in mean and variance of landscape temperature?

We model movement on a thermal landscape, which is an image taken with an infrared camera (Flir B335, FLIR Systems, Wilsonville, OR, USA) of a mix of grasses and forbs along the banks of the Loire River near Tours, France in June, 2012 from about 2 m height (Fig. 4A). We make the simplifying assumption that square pixels have sides of length equal to the body length of a virtual ectotherm. Although thermal images at resolutions fine enough to reflect the body sizes of most ectotherms are rarely available (Potter et al., 2013), scaling the thermal landscape to the size of the ectotherm makes sense physiologically and enhances our ability to extract general principles from simple models (Dillon et al., 2012). In the simulations, the boundaries of this thermal landscape were such that organisms moving off an edge reappeared on the opposite side, giving a periodic landscape. In all simulation runs presented here, 100 virtual individuals were tracked across the landscape for 500 time steps.

We first generated a behavioral null model with organisms taking simple random walks on the thermal landscape. The position of an individual at time t is defined as (x_t, y_t), where

$$x_t = x_{t-1} + x_d$$

$$y_t = y_{t-1} + y_d$$

and

$$x_d = d_{max}*N(0, \sigma^2)$$

$$y_d = d_{max}*N(0, \sigma^2).$$

This model approximates Brownian motion because movement at successive steps is both uncorrelated (direction moved is independent of the previous directions) and unbiased (the direction moved is random) (Codling et al., 2008). At each time step, distance moved to the right or left (x_d) and up or down (y_d) is determined by multiplying the maximal possible distance moved (d_{max}) by a draw from a normal distribution with mean 0 and variance $\sigma^2 = 1/3$ (such that 99% of individuals would not exceed the maximum distance). Here d_{max} is estimated from empirically determined maximum walking speeds of *Drosophila* (Fig. 6A; Dillon et al., 2012) with the assumption that pixels on the thermal landscape were equivalent to body lengths (see above). Not surprisingly, the realized body temperatures of small individuals moving by Brownian motion closely matched the distribution of

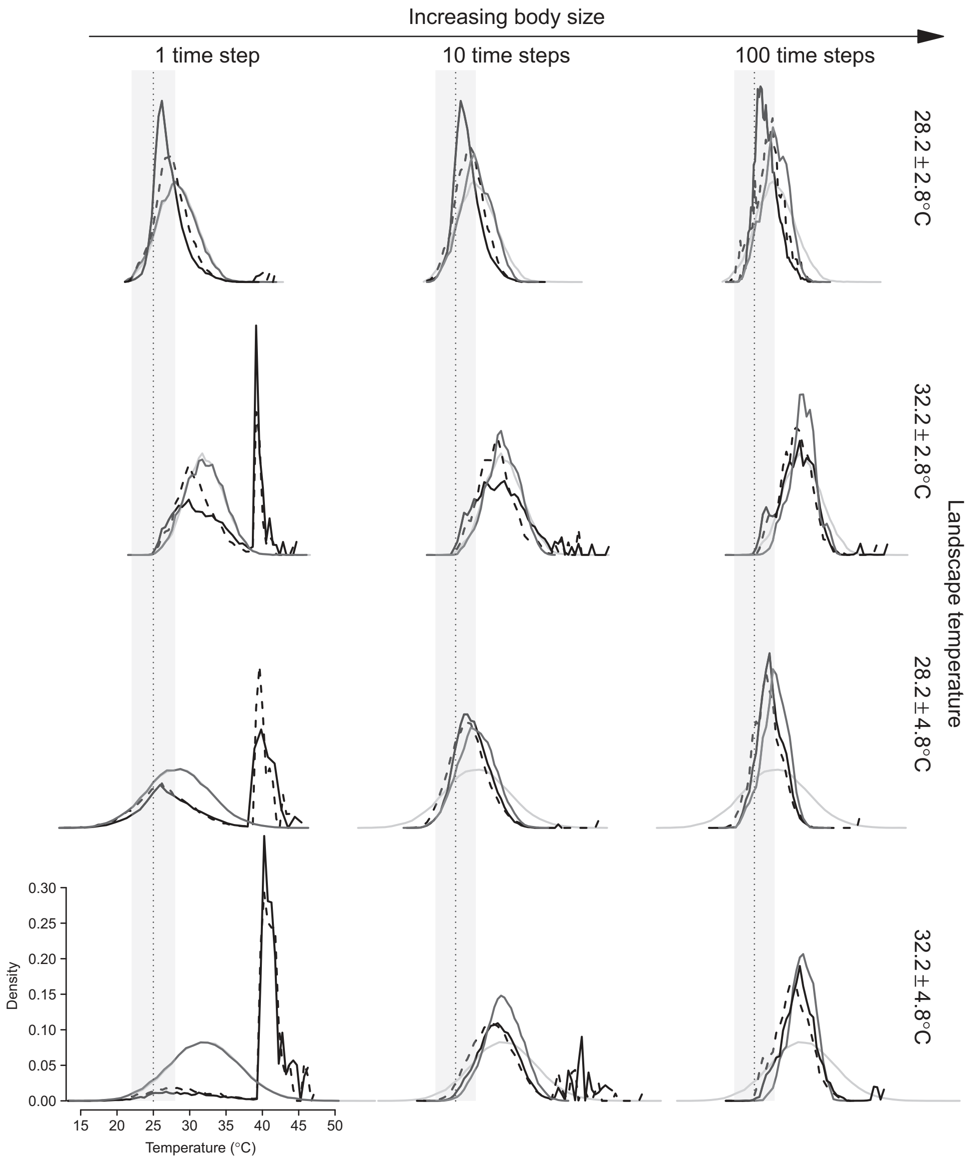

Fig. 5. Thermal distributions of virtual ectotherms after 500 time steps on thermal landscapes. Rows correspond to the different thermal landscapes (see Fig. 4) on which the ectotherms moved. Columns correspond to ectotherms of different size—they integrate body temperature over, from left to right, 1, 10, and 100 steps. Maximum speed at each time step was based on body temperature (see Fig. 6A) and thermal preference followed the temperature curves of Fig. 6B. In each panel, the light gray line represents the landscape temperature distribution, the dark gray line represents the null distribution of simulated organisms moving by Brownian motion, the solid black line represents simulated organisms with precise thermoregulation (see solid black line in right panel of Fig. 6B), and the dashed black line indicates organisms with less precise thermoregulation (see dashed line in Fig. 6B). The shaded rectangles encompass temperatures within 3 °C of the preferred temperature (25 °C) indicated by vertical dotted lines (also shown in Fig. 6B).

landscape temperatures (Fig. 5, left column, light gray landscape lines are largely hidden by dark gray lines from the null model).

A key assumption in the null model (Brownian motion) is that movement depends neither on temperature nor on the organism's perception of its thermal environment. For living ectotherms, this is not realistic because rate of movement usually depends strongly on body temperature (Angilletta, 2009; Lachenicht et al., 2010; Lailvaux and Irschick, 2007). We incorporated thermal dependence of motion into the random walk model by scaling the maximum distance moved to the temperature of the organism:

$$d_{\max} = f\left(T_{\text{body}}\right).$$

We used data on *Drosophila* walking speed as a function of temperature which takes the shape of a standard thermal performance curve (Kingsolver, 2009) with maximum speeds of about 10 body lengths per second near 30 °C (Dillon et al., 2012; Fig. 6A). Note that short-term exposure to high temperatures can cause flies to move slowly or not at all, likely due to physiological damage.

Second, organisms can alter their behaviors to spend more time in environmental patches yielding body temperatures near those they prefer (Dillon et al., 2009; Angilletta, 2009; Fig. 6B). We modeled this effect as a change in the variance of the normal draw:

$$\sigma^2 = f\left(T_{\text{body}}\right)$$

such that the organism is less likely to move large distances when its body temperature is closer to its preferred temperature. To implement this, we use a generalized thermal preference curve for *Drosophila* (Dillon et al., 2009) in which σ^2 (and thus the probability of moving large distances) increased from a minimum near preferred temperatures to maximum values far from preferred

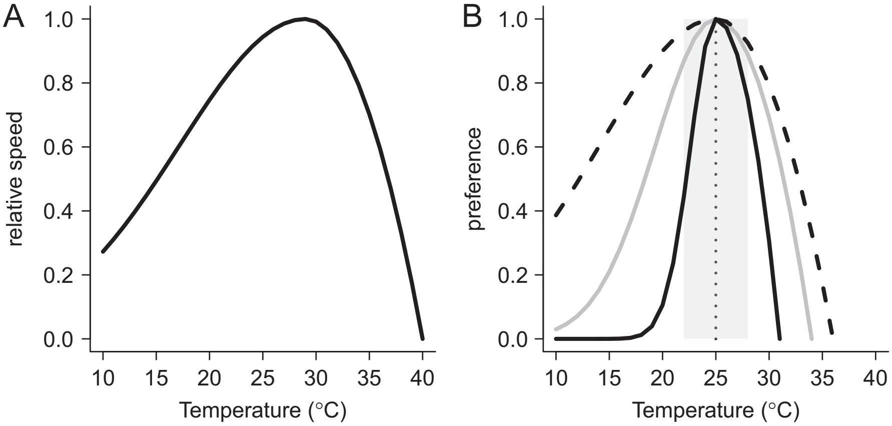

Fig. 6. Relative speed and thermal preference curves of the virtual ectotherms released onto the thermal landscape. (A) Relative speed as a function of body temperature derived from data on walking speed of adult *Drosophila melanogaster*. The thermal dependence of motion was incorporated into the model using this curve, which describes maximum distance moved (d_{max}) as a function of body temperature. (B) Thermal preference of *D. melanogaster* derived from measurements on laboratory thermal gradients (gray), and of virtual ectotherms with high (solid black line) or low (dashed black line) thermoregulatory precision. Thermal preference was incorporated into the model by using these curves to estimate the standard deviation of the normal draw as a function of body temperature.

temperatures (Fig. 6B). Note that this preference curve, like those of diverse organisms, is determined by tracking positions of organisms on laboratory thermal gradients (Dawson 1975; Dillon et al., 2009).

Furthermore, we altered the shape of the preference curve (compare dashed and solid black lines in Fig. 6B) to determine how thermoregulatory precision affects body temperature distributions. In this modified random walk with both preference and thermal dependence of motion, individuals could strongly shift their temperature distributions relative to the thermal distributions of the environment and of the null (Brownian) model (Fig. 5, compare solid and dashed black lines to gray lines).

A third assumption in the null model is that body temperature equilibrates instantaneously with pixel temperature of the landscape surface. In reality, equilibration time depends on body size (Anderson et al., 2007; Dillon et al., 2012; Stevenson, 1985a): small ectotherms have short time constants, such that body temperature always closely approaches the equilibrium local operative temperature; large ectotherms have long time constants, such that current body temperatures carry the imprint of their thermal histories (Helmuth, 1998; Pincebourde et al., 2009). To incorporate body size into the model, we estimated body temperature (T_{body}) in the current time step as the average of environmental (pixel) temperatures from 1, 10, or 100 prior time steps, with body temperatures of larger organisms derived from a larger number of prior temperatures. In these simulations, we assumed that pixel temperature was the only determinant of organism temperature (i.e. these are not operative temperatures integrating radiation, wind, etc.; Bakken, 1992). Because we scale pixel size to match organism size, absolute dimensions of the thermal landscape increase with body size, and we circumvent issues of larger organisms integrating surface temperatures differently in space. This approach does, however, ignore the effect of body size on how embedded organisms are in local boundary layers (Woods, 2013).

Armed with these simple models, we asked how thermoregulatory behavior and body size mediate the impacts of changing climate on realized body temperatures. We altered the original thermal landscape by increasing the mean by 4 °C, increasing the variance by 2 °C, or increasing both together (Fig. 4B–D).

As expected, behavior allowed ectotherms to decouple body from environmental temperature (compare black lines to gray lines in Fig. 5). As surface temperatures warmed, however, behavior was less able to give preferred temperatures (indicated by shaded regions centered around the preferred temperature of 25 °C, the vertical dotted lines; compare top row to bottom three). Because movement speed depended strongly on temperature and declined at very high temperatures (Dillon et al., 2012; Anderson et al., 2007) (see Fig. 6), ectotherms tended to be trapped in areas with prohibitively high temperatures (see peaks near 40 °C in Fig. 5). This effect was pronounced for small organisms in all warming scenarios (bottom three rows), reflecting the increase in the proportion of pixels that were hot enough to be disabling. Because body temperatures of larger organisms were averages of multiple previously experienced environmental temperatures, null distributions of larger organisms were more concentrated near the mean landscape temperature (uncommon temperatures in the tails of the landscape distribution minimally contribute to integrated body temperatures). These results suggest that larger ectotherms may be less susceptible to thermal extremes on the landscape with important implications in the context of climate change: whereas increased microclimate variability profoundly altered realized thermal experience of small ectotherms (compare rows 1 and 3 in Fig. 5), it had little effect on body temperatures of large ectotherms.

When landscape temperatures strongly overlapped preferred temperatures (current climate, top row of Fig. 5), thermoregulatory precision benefited ectotherms (solid black line is closer to 25 °C than is the dashed black line). However, as landscape temperatures shifted away from preferred body temperatures, thermoregulatory precision became a liability (note that black line was slightly right-shifted in bottom rows). Under these simulation conditions, smaller ectotherms will likely get stuck at high temperatures (and die) as climate warms, with increased climate variability having an even larger effect than increased climate mean. Larger ectotherms may avoid heat traps and fare better, particularly if they have shallower (less precise) thermal preference curves; but even then, they will spend little time near their preferred temperatures. This effect arises because, when searching for a given precise temperature, the organism very often keeps moving (because that precise temperature is rare), such that it is more likely to be trapped later in a hot pixel. By contrast, with imprecise thermoregulation, the organism more easily finds temperatures in its preferred temperature distribution. Because it slows down in those pixels, it decreases the probability of later encountering a disabling hot pixel.

The outcomes of the simulations depend of course on the details of the parameters, and on how close the thermal landscape is to the preferred temperature of the organism. Rather than create thermal landscapes de novo with contrived statistical properties, we opted to use an actual thermal landscape. This landscape happened to be warmer on average than the preferred temperature of our simulated organisms, which, for example, may increase the likelihood that the simulated organisms is trapped by lethally hot pixels. More broadly, the results from these simulations depend on the whole parameter set (Figs. 4 and 6), and we did not explore the entirety of parameter space. Nonetheless, the simulations make the general points that the effects of climate change will depend on microclimates, their properties, and how organisms sample them. In particular, the temperature dependence of movement interacts with thermal preference and thermal inertia driven by body size to determine movement patterns and therefore body temperatures of ectotherms across landscapes with different thermal characteristics. Though not examined here, the spatial distribution of temperatures across the landscape (pixel temperatures could range from overdispersed to clumped) may also strongly affect realized body temperatures and performance (Sears and Angilletta, in press) as can fluctuations in pixel temperatures in each time step (Niehaus et al., 2012). A critical next step will be to expand theoretical models to incorporate these diverse effects with the aim of identifying general, mechanistic rules for behavioral filtering, to ground the rules with empirical tests, and then apply these rules to better predict impacts of climate change on ectotherms.

3.2. Sampling predictable gradients created by other, larger objects

Although the energy balance of an ectotherm is strongly influenced by its body size, it can also assume the thermal properties of much larger objects by spending time on or around them. For example, garter snakes (*Thamnophis elegans*) in northeastern California spend substantial fractions of the day in retreat sites under rocks. The thermal conditions in those sites are strongly influenced by rock size (Huey et al., 1989). Thin rocks heat up and cool down fast, such that snakes choosing to retreat under them are subjected to lethal heat at midday and disabling cold at night. Thick rocks, with large total heat capacities and long time constants, have temperatures at their bases that are quite stable but also substantially cooler than the snakes prefer. Intermediate-sized rocks—the ones chosen by snakes disproportionately—have variable but tolerable temperatures, and they give the longest daily exposures to the temperatures that the snakes prefer (Huey et al., 1989). Thus, although the snakes are relatively small (~ 100 g) they can assume the advantageous thermal properties of objects much larger than themselves by retreating under rocks of a particular intermediate size (20–40 cm thick).

In addition, small ectotherms can exploit highly stable and predictable *gradients* of conditions adjacent to much larger objects. One such object is the Earth's surface itself, which can, under some conditions, sustain very steep temperature gradients over the first few centimeters of air away from the surface (Geiger et al., 2009). For example, *Cataglyphis* ants forage in the Sahara Desert during the day, and they avoid overheating in part by using their long legs to raise themselves off the desert floor. By lifting themselves 4 mm off the surface, they encounter air temperatures that are about 10 °C cooler than surface temperature itself (Gehring and Wehner, 1995). If they nonetheless approach their critical thermal maximum, they can climb onto small clods of sand or pebbles so that they push their bodies farther into cool overlying layers of air (Wehner et al., 1992). In the opposite direction from the surface, a highly predictable thermal gradient extends into the soil, and many organisms thermoregulate by moving vertically within the soil (Kadochová and Frouz, 2013). Local objects can also provide steep temperature gradients that can be exploited by slight repositioning of the body. Using operative temperature models, Bakken showed (Bakken, 1989) that lizards perched on tree limbs and trunks could modify their body temperatures by >4 °C simply by elevating their bodies 1 cm off the surface. Similar examples occur at smaller spatial scales. *Manduca* caterpillars heat up over ontogeny as they grow away from their cool leaf substrates (Woods, 2013). An Australian spider lays eggs at a precise location under rocks giving temperatures that are best for egg development (Pike et al., 2012), and spider mites exploit fine-scale temperature gradients across individual apple leaves (Caillon et al., 2014). Here again, the body temperature of these ectotherms is strongly linked to the steep thermal gradient along the object with which they are associated (a rock and a leaf surface, respectively). In general, therefore, we expect that small organisms will exploit the strong gradients that exist between larger objects—living and nonliving—in their environments and the ambient local conditions. These kinds of gradients may be so common and predictable that organisms may have ample opportunity for exploiting them to their advantage.

Finally, ectotherms can exploit the large, essentially binary, step between radiative loads in sunny and shaded microsites. Direct solar radiation plays a critical role in energy budgets (Gates, 1980), and many ectotherms alter their position relative to the sun to adjust the total amount of solar energy absorbed (May, 1979; Whitman, 1987). Shuttling between sun and shade can often be a matter of a few centimeters of movement, which can provide an efficient way for ectotherms to significantly alter their operative temperatures in a given environment. Indeed, several macroecological studies have integrated this dichotomy into models examining global patterns of the coldest and the hottest operative temperatures obtainable by small ectotherms (Kearney et al., 2009; Sunday et al., 2014). In general, the availability of shade will depend strongly on organismal body size and the amount of local vegetation cover (e.g. Kearney et al., 2009). Global data on vegetation cover are now readily available and increasingly fine grained.

4. Challenges and limitations

We focus on two key steps in linking changes in macroclimate to ecological shifts in ectotherm populations: how microclimates emerge from macroclimates and how behavior filters microclimates into realized body temperatures. We discuss these problems with regard to microclimates and body temperatures. Such an approach is reasonable because body temperature has well-defined effects on virtually all sub-organismal processes and ecological interactions, is underlain by a robust biophysical theory, and can be predicted from increasingly fined-grained global datasets. Indeed, new microclimatic models now provide more flexible ways to connect organismal scale processes with macroclimates (Kearney et al., 2014, 2013). Furthermore, sophisticated approaches are now being developed to connect microclimatic patterns, performance and demography of ectotherms across global scales (Hannah et al., 2014). Nevertheless, behavioral buffering, as explored above, has never been integrated into demographic models. Finally, a robust literature already underlies the third step of estimating the effects of changes in body temperature on performance, life history, and fitness (Kingsolver and Huey, 2008; Frazier et al., 2006; Dillon and Frazier, 2013).

All the same, it would be a mistake to conclude that the large problem now rests on a strong footing. First, temperature is only one of many physical variables that will change. Others include water availability and relative humidity, radiation levels (via changes in cloud cover), wind speed, and timing of seasonality, and many of these interact in important ways with temperature (see Bradshaw and Holzapfel, 2001; Diamond et al., 2011; Kleynhans and Terblanche, 2011). Second, as pointed out in the introduction, the problems raised above deal only with different physical effects of climate change—

whereas many of the shifts observed in populations will result from changes to biotic partners (Tylianakis et al., 2008). Other unconsidered dimensions include the roles of evolution, acclimation, plasticity, and senescence in responses to climate change (Bowler and Terblanche, 2008; Terblanche et al., 2005). Third, much of climate biology rests on a limited number of case studies. Conceptually, this problem plagues much of biology. Any one person can study only a sliver of life's diversity; yet the goal is to explain general patterns. Although this problem is academic in many fields, in climate change biology it is pressing and practical: we need predictions now about what will happen to Earth's biodiversity as a whole. Thus, we urgently need more data on a greater diversity of species, and we need explicitly integrative approaches for analyzing it in broader frameworks (e.g., Gaston et al., 2009).

Fourth, and perhaps most seriously, deconstructing the climate–organism problem into a smaller set of more manageable problems reflects a particular approach to biological complexity. The potential problem is the approach's implicit reductionism, which assumes that we can understand a whole by studying its parts. Possibly, the climate problem will defy this assumption and show either weakly or strongly emergent effects (Noble, 2012)—system-level effects that are, by definition, difficult or impossible to predict from processes at lower levels of organization. In terms of the circuit analogy, this means that even with perfect knowledge of resistances, capacitances, voltages, switches, etc. it still may be difficult to predict the output of the circuit from a given pattern of inputs. In terms of climate biology, this means that even when we understand microclimates, and the behaviors and physiological tolerances of each life stage, we still may be unable to predict accurately how a species range will have shifted by the year 2100. Poor predictions could arise because, in studies of each life stage and each physiological effect, we still failed to capture something important about behavioral interactions between organisms and microclimate mosaics; or because we studied components of the system with weak influences while ignoring other important effects—e.g., we studied the effects of temperature when really it is water or the presence or absence of a host plant that exert the greatest control. This prognosis should not be viewed as giving up in the face of complexity, but simply as confronting the limits of what we know, which in this case are severe.

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