RESEARCH ARTICLE

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Body size determines the thermal coupling between insects and plant surfaces

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Abstract

1. Most studies in global change biology predict biological impacts of warming from information on macroclimates. Most organisms, however, live in microhabitats with physical conditions which are decoupled to varying degrees from those in macroclimates depending partly on organism body size.

2. Small ectotherms of a few millimetres in length live deep in surface boundary layers such that their heat budgets are dominated by different processes compared to larger ectotherms, whose bodies emerge from surface boundary layers. We therefore hypothesized that the body size relative to surface boundary layer thickness generates different patterns of body temperature variation for organisms in the same nominal habitats.

3. We tested this hypothesis in a community of arthropods living on a subalpine plant by combining physical models to acquire high-resolution time series of operative temperatures, thermal imaging to assess the strength of coupling between physical models or arthropod bodies and surrounding leaf temperatures, and a cross-scale approach to infer the temperature distributions available to small ectotherms.

4. The size of the physical model strongly influenced operative temperature dynamics: the bigger, the warmer. Small models were just a few degrees warmer than leaf surfaces, whereas large models deviated from leaf temperature by >10°C.

5. We found similar patterns of body temperature of naturally occurring arthropods. Temperatures of small insects closely tracked leaf surface temperatures even in full sun, whereas larger insects were warmer than leaf surfaces.

6. At the whole plant scale, the thermal diversity of leaf surfaces was high, especially in the sun, typically generating a range of microclimatic temperatures (for small insects) of >10°C. Larger insects instead could move between shaded and sunny portions of the whole plant to vary body temperatures by a larger extent.

7. The bulk of animal biodiversity consists of small terrestrial arthropods, the majority of which are associated with plant surfaces at some point in their life cycles. The distribution of body sizes determines how much thermal diversity is available for behavioural thermoregulation, thereby contributing to their potential response to climate change.

1 | INTRODUCTION

The eco-physiological performance of ectotherms depends strongly on body temperature, and consequently biologists have paid close attention to traits and processes that influence organismal heat budgets. Although we have understood for at least 60 years the main biophysical routes of heat exchange between ectotherms and their environments (Angilletta, 2009; Gates, 1980; Heinrich, 1999), accurately predicting body temperatures in the field still remains challenging. The difficulty arises from a key source of complexity: organisms live in, and move throughout, complex mosaics of conditions that change in both space and time and that they experience in taxon- and size-specific ways (Pincebourde & Woods, 2020; Woods et al., 2015). Although we lack a coordinated framework for incorporating this complexity (but see Kearney & Porter, 2009), developing it should be a high priority, as body temperature is a key variable in analyses of the consequences of climate change for ectotherms (Kearney et al., 2009; Sinclair et al., 2016; Sunday et al., 2014; Woods et al., 2015).

A fundamental factor influencing how organisms interact with their environment is body size, which has two overarching biophysical effects, one temporal and one spatial. First, it determines the ratio of surface area (across which energy is exchanged between the organism and its environment) to volume (in which internal energy is manifest as the molecular motion we measure as temperature). Small organisms, with high ratios of surface area to volume, exchange energy rapidly compared to the total size of their internal pools and their body temperatures can therefore change more quickly (low thermal inertia; Stevenson, 1985a, 1985b). Second, body size determines the spatial scale over which organisms interact with, and integrate, locally available biophysical conditions. Ectotherms are mostly associated with other objects in their environments (soil, rocks and other organisms like plants), and those larger objects therefore dominate organismal heat budgets, especially for small ectotherms (Woods et al., 2015). Although these effects have been explored for diverse organisms (e.g. (Berg et al., 2015; Huey et al., 1989)), we still lack a quantitative assessment of the relationship between body size and the thermal coupling with the surfaces on which organisms live.

Perhaps the best developed theory exploring effects of body size on body temperature is Stevenson's size-dependent, two-layer biophysical model of thermal energy exchange between organisms and their environments (Stevenson, 1985a). Model analysis showed that larger organisms in direct sunlight reach higher steady-state temperature excesses (body temperature minus air temperature), reflecting the decreased importance of convective heat loss relative to solar heat gain. Ectotherms larger than 1 kg, however, have progressively smaller diurnal ranges of body temperature because

of progressively longer time lags to reaching steady state (greater thermal inertia). These predictions are supported by empirical data collated by Stevenson and by other work appearing subsequently (reptiles; Blouin-Demers & Weatherhead, 2001; Franklin & Seebacher, 2003; Garrick, 2008; Bulte & Blouin-Demers, 2010 and caterpillars; Woods, 2013; Nielsen & Papaj, 2015), with other studies showing complex effects of body size interacting with surface boundary layers (Bakken, 1989; Kaspari et al., 2015; Spicer et al., 2017; Tracy et al., 2010) or effects of substrate size itself (Bakken, 1989; Gedan et al., 2011; Huey et al., 1989; Pike et al., 2012). Additional theory related to Stevenson's work has appeared over the past 30 years (O'Connor, 1999; O'Connor & Spotila, 1992; Turner, 1987), but it focuses mainly on a spectrum of relatively large body sizes (> 1 cm). A large portion of global biodiversity, however, lies at much smaller body sizes (May, 1988; Potter et al., 2013).

Theoretically, due to their small size, the body temperature of tiny ectotherms (from <1 mm to several mm in body size, corresponding to a range of μg-mg body mass) cannot deviate much from the temperature of the air immediately around them (Stevenson, 1985a). It follows that the temperature of surfaces and the conditions within the boundary layer can generate important selective pressures for tiny ectotherms. For example, the eggs of *Manduca* moths are laid on the coolest portion of *Datura* leaves to allow their development in otherwise hot desert conditions (Potter et al., 2009; Woods, 2013). Spider mites can select optimal temperatures for development by moving small distances across leaf surfaces (Caillon et al., 2014). In a tropical ant community, species' thermal limits correlate with the conditions in the boundary layers they use, especially on superheated plant surfaces (Kaspari et al., 2015). Therefore, the body temperatures of tiny ectotherms are tightly coupled to the energy budgets of the surfaces they use. Furthermore, the body size at which an ectotherm becomes decoupled from its surface energy budget should depend on the thickness of the surface boundary layer; boundary layer thickness depends primarily on the interaction between the size of an object and environmental conditions like wind (Oke, 1987).

Leaf surfaces host a huge diversity of tiny organisms whose lives are necessarily tightly coupled to the heat budget of another living organism, the plant. Leaf temperatures result from complex interactions between numerous plant properties (size, orientation, transpiration rate, etc.) and microsite conditions (Pincebourde & Woods, 2012). Further effects can arise from arthropod feeding, which may induce modifications in plant transpiration rate that affect temperatures over the entire leaf surface (Cahon et al., 2018; Pincebourde & Casas, 2019). While most 'inert' substrates become superheated surfaces when they are illuminated by sunlight (Kaspari et al., 2015; Pike et al., 2012), transpiring leaves

can reach temperatures lower than expected from equivalent but dry surfaces (Dong et al., 2017; Michaletz et al., 2016; Potter et al., 2009). Moreover, plant leaves display thermal heterogeneity with temperature ranges of 8–15°C over single leaf surfaces when they are exposed to full sun (Leigh et al., 2017; Saudreau et al., 2017). So far, the effect of this within-leaf thermal variation on the heat budget of tiny arthropods has been largely overlooked (Cahon et al., 2018; Caillon et al., 2014). Nonetheless, the vulnerability of the 'little things that run the [green] world' (Wilson, 1987) to climate warming can be assessed by comparing leaf surface temperature patterns and their thermal limits (Pincebourde & Casas, 2019).

We characterized the effects of body size on the thermal experience of tiny arthropods. In particular, we used operative temperature models fitted with thermocouples to log temperatures with high temporal resolution (1 Hz), combined with thermal imaging to assess patterns of thermal variation with high spatial resolution (<1 mm). The physical models allowed us to manipulate size while standardizing all biophysical parameters. This experiment provided empirical data to conceptualize the relationship between body size and its coupling to leaf surface temperature. Then, we tested the validity of this conceptual relationship on a community of arthropods living at the surface of leaves of a subalpine annual plant—a field experiment that included variation in all parameters related to the heat budget of organisms, allowing us to challenge the observed relationship from operative temperature models using natural communities of arthropods. Together, these approaches revealed how body size modulates the thermal landscapes available to small arthropods, a group that dominates the terrestrial biosphere. Furthermore, we determined the thermal limit of the most abundant species in the community to estimate their vulnerability to warming by considering the coupling of body and leaf energy budgets.

2 | MATERIALS AND METHODS

2.1 | Site description

The study site was a ~900 m^2 meadow at the University of Wyoming—National Park Service (UW-NPS) research station, near Jackson Lake in Grand Teton National Park (USA; 43°56′18.1″N, 110°38′31.9″W, 2076 m a.s.l.). As is common in the region, arrowleaf balsamroot *Balsamorhiza sagittata* (Asterales: Asteraceae) and other forbs are interspersed with sagebrush in open meadows surrounded by mixed conifer forests (Figure 1; Knight et al., 2014). *Balsamorhiza sagittata*, a perennial widely distributed across Western North America, was the dominant forb at the time of the study (19–24 June 2018). Plants had largely finished flowering but supported an abundant and diverse arthropod fauna on their leaves that experienced moderate late spring air temperatures and intense solar radiation.

2.2 | Experiment 1: Consider a spherical insect

We first used operative models (Bakken et al., 2014) to quantify the effect of body size on core temperature of objects resting on balsamroot leaves. Our aim was to standardize all the parameters while varying only size, instead of attempting to develop a model mimicking precisely the characteristics of any particular species. We selected a spherical shape to simplify assumptions related to insect body shapes (see O'Connor & Spotila, 1992). In particular, a sphere always intercepts the same portion of incoming radiative energy whatever its position relative to the sun, thus allowing us to standardize the orientation/inclination of the insect at the leaf surface relative to the sun. We made spherical operative models with modelling clay (Kmart, Model Magic) in three size classes (2, 6
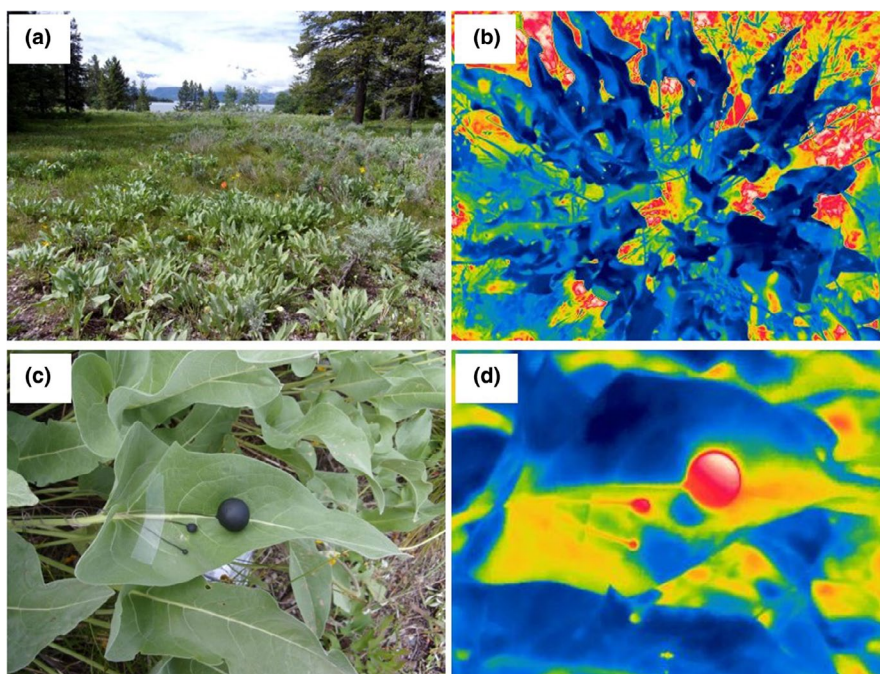
FIGURE 1 The study site (a) was a meadow dominated by arrowleaf balsamroot *Balsamorhiza sagittata* and (b) a thermographic image of a single plant. Operative temperature models ('spheres') were deployed on balsamroot leaves fully exposed to solar radiation (c: photograph, d: thermographic image)

and 15 mm diameter; Figure 1), spanning the typical range of insect body sizes seen at this site and across many environments (Gaston & Chown, 2013). The 2-mm soldered tip of fine-gauge thermocouple (36 gauge, type T, Omega Engineering) was implanted in sphere centres, with the wire held in place by cyanoacrylate glue. The spheres were dried overnight in a drying oven, and spray-painted with matte black paint (Craftsman Specialty Finishes, Ace Hardware) of known emissivity (0.95). We estimated the thermal time constant of the three size classes by individually cooling them to ~5°C in a refrigerator, then removing them quickly and suspending them in still air at room temperature (15°C). We tracked changes in sphere core temperatures via their embedded thermocouples as they warmed to 15°C. From thermocouple traces, we estimated the time required to warm halfway to ambient temperature: 1, 18 and 100 s for small (2 mm), medium (6 mm) and large (15 mm) spheres, respectively.

Spheres were deployed in sets of three (a small, a medium and a large) on individual leaves (Figure 1c) of 11 different arrowleaf balsamroot plants spread across the field site. Spheres were separated from each other by ~3 cm at the (adaxial) surface of a leaf, which was nearly parallel relative to the ground and emergent, so largely unshaded by neighbouring leaves or other plants. Temperatures of each set of three spheres were logged every second for six consecutive days with four-channel thermocouple data loggers (Hobo UX120, Onset). The fourth channel was used to record air temperature from a bare thermocouple (36 gauge, type T, 2 mm soldered tip) positioned within the plant canopy at approximately the same height (20–40 cm) as the set of spheres. The thermocouple wires were so fine that occasional direct sun on them raised their temperature by at most 2°C. The spheres were checked at least four times per day to ensure they stayed in place throughout the 6-day sampling period.

2.3 | Experiment 2: Thermal coupling of spheres and leaf surfaces

We used infrared thermography to determine the extent to which the coupling of sphere core and leaf temperatures depends on sphere size. At the scale of a single leaf, we took thermal images to record simultaneously the surface temperature of the three size-class spheres and the temperature of the leaf surface surrounding the spheres. An infrared camera (FLIR Systems, B335), equipped with a macro-lens (IR LENS 10 mm; FLIR Systems), was used to capture the temperature distribution over the 11 leaves receiving a set of three spheres. The camera was positioned above the leaf surface at a distance of 30 cm, thereby avoiding any effect of the distance on temperature readings (Faye et al., 2016). The spatial resolution was about 0.5 mm and the thermal resolution was 0.05°C. The emissivity of the leaf surface was determined to be 0.95 by comparing temperature readings from thermal images with a direct measurement of leaf temperature using a fine thermocouple. Thermal images were taken several times per day (2–4 times depending on weather). Each time, images were taken following the same order for the 11 plants, and two images were taken per leaf (only one was kept for analysis,

the second was used in the event the first image was blurred). It took <15 min to record all 11 leaves in each session. Therefore, we assumed that the leaf surfaces were exposed to comparable conditions, as long as no clouds passed within a session. Sets of images were taken up to four times per day throughout the 6 days: early morning (around 9:00), morning (between 10:00 and 11:00), around midday (between 12:00 and 13:00) and late afternoon (between 15:00 and 17:00). Infrared images were analysed in ThermaCAM Researcher Professional (FLIR Systems). For each image, the surface temperature of each sphere was taken as the mean temperature of the pixels comprising the sphere, and the leaf surface temperature was estimated as the mean temperature of the 1-cm-wide near-circular area around the given sphere (avoiding the thermocouple). The coupling between a sphere and leaf temperature was quantified by computing the sphere temperature excess relative to the leaf (mean sphere surface temperature minus mean leaf surface temperature).

2.4 | Experiment 3: Thermal diversity at the whole plant scale

Infrared thermography was used at the scale of a whole individual plant (~a meter in diameter) to estimate the level of spatial variance in leaf surface temperature within single plants. Thermal images were taken with another FLIR camera (T540, FLIR Systems) immediately after the images were acquired at the leaf scale (in experiment 2) and following the same order among the 11 individual plants. The camera was positioned above the plant at a distance of about 1.80 m to capture the entire plant in a single frame. Two images were taken consecutively and only one was used (the second was used when the first was blurred). Thermal images were organized using FLIR Tools+ (FLIR Systems). We used masks to extract leaf pixels and exclude non-leaf background pixels. First, a visual image was extracted that corresponded to the same position and dimensions as each infrared image. Those visual images were then processed by hand in GIMP to remove all background parts of the image (e.g. plants other than arrowleaf balsamroot, data loggers, ground and rocks). Those masks were converted into black and white (black pixel values = 0 for all materials except leaves and white = 1 for leaves) before they were combined with the registered infrared image to extract pixel temperatures of leaves only. These extracted pixel temperatures were further processed in R. In particular, we removed pixels having temperatures higher than the 97th quantile, as a way of removing additional extraneous background pixels that usually had much higher temperatures. Finally, the files were vectorized and the values were analysed using density plots of pixel temperatures.

2.5 | Experiment 4: Insect body sizes and body temperatures

Infrared thermography was used to compare the temperatures of diverse insects living on balsamroot leaves with the temperatures of

the leaf surfaces on which they were found. We surveyed all arthropods to obtain the largest body size range possible in this community. The insects were found haphazardly by two observers several times per day during sunny conditions. The two infrared cameras (B335 and T540, FLIR Systems) were used to take an infrared image of any insect observed on exposed leaves. When using the T540 camera, the macro-mode was utilized to capture close-up images of the insects (from a distance of about 30 cm). The macro-lens of the B335 allowed taking images from a distance of about 20 cm. After the infrared image was taken, the insect was collected, assigned a unique code and kept individually in a tube in 70% alcohol. The collected insects were later identified at least to genus and, where possible, to species. Body length, width and height were measured from digital images with embedded scales in ImageJ (Abramoff et al., 2004). Body height was not measurable for some species because their soft legs precluded obtaining realistic values. The infrared images were analysed in ThermaCAM Researcher Professional (FLIR Systems). The body temperature of each insect was taken as the mean temperature of the pixels comprising the insect body (excluding legs and head). The leaf surface temperature was estimated as the mean temperature of the 1-cm-wide near-circular area around the given insect. The coupling between insect and leaf temperature was quantified by computing the insect body temperature excess (mean insect surface temperature minus mean leaf surface temperature). We assumed that the surface temperature of these small insects is a reasonable proxy of their core body temperature.

2.6 | Experiment 5: Thermal limit of insects

We measured the thermal limit of the two most abundant insect species that we found on leaves of the arrowleaf balsamroot: the lace bug *Corythucha immaculata* (Hemiptera: Tingidae) and the caterpillar of *Oidaematophorus balsamorrhizae* (Lepidoptera: Pterophoridae). The aim was to compare their thermal limits with the temperature patterns (both insects and spheres) measured in the field to estimate the vulnerability to warming of these organisms. To determine thermal limits, we measured the temperature at which 50% of individuals died (lethal temperature, LT_{50}) during temperature ramps up to a given experimental temperature (we started by testing the exposure to experimental temperatures of 40 or 42°C which correspond to thermal limits typical for temperate insects; Sunday et al., 2011). For each run, 10 insects were collected on plants in the field, put individually into small tubes containing a cut piece (~1 cm^2) of arrowleaf balsamroot (to provide a perching substrate). The 10 tubes were then immersed in a water bath (Narco Model 220) at 25°C. A fine thermocouple was positioned within one of the tubes to track the temperature increase. After a 15-min acclimation at 25°C, the thermostat of the water bath was set to a given target temperature. The mean rate of temperature increase was (mean ± *SD*) 0.36 ± 0.22°C/min (range: 0.25–0.45°C/min depending on the target temperature). Once the target temperature was reached, the 10 tubes were retrieved from the water bath and placed at room temperature. The

piece of fresh leaf material was replaced to ensure access to food and water. Survival was assessed after 18 hr by gently stimulating the insects with a fine needle. Those that were alive responded by moving. Possible bias due to thanatosis (individuals pretending to be dead), a particular problem with the lace bug, was overcome by marking the position of individuals on a flat surface within small petri dishes. Individuals were considered to be dead if they did not change position over a period of 30 min. A total of 60 and 50 lace bugs and caterpillars, respectively, were measured.

2.7 | Data processing and statistical analysis

In Experiment 1, time series (6 days) of air and sphere temperatures were retrieved for each of the 11 plants from the Hobo loggers and processed in R (v3.3.1). Time series were aligned using functions in the xts package. Analyses focused on spatial variance of the four measured quantities (air temperature and the core temperatures of small, medium and large spheres). The weather conditions varied among the 6 days of measurements: three of them had generally clear sky and sunny conditions while the other 3 days were mostly cloudy. Comparing these two sets of conditions allowed us to infer the influence of solar radiation on the temperature of the sphere models. For each set of weather conditions, we first computed the mean temperature among all leaves at each time step for air and the small, medium and large spheres. Then, we analysed the compound variance (i.e. integrating both spatial and temporal variance) by computing the daytime (9:00–16:00) mean temperature and its standard deviation for each variable.

In Experiment 2, we compared the sphere temperature excess relative to the leaf surface using an ANOVA, with sphere category and daily session as predictor variables and plant ID as a random factor. A post-hoc pairwise comparison (Tukey's Honestly-Significant-Difference Test) was used to compare the different sphere size categories. Graphically, we used boxplots to visualize the differences according to sphere size and daily session (and their interaction term). We also studied the relationship between sphere temperature excess relative to the leaf surface and leaf surface temperature for each sphere category. We applied a LOWESS smoother to visualize the nonlinearity of this relationship and used Pearson correlations to test for the strength of this relationship.

In Experiment 3, the pixel temperature matrix of each individual plant by daily session was converted to a density distribution such that all the distributions from sunny and cloudy days could be compared directly graphically. In Experiment 4, the correlation level between insect body temperature excess and body size was assessed using GLM with morphological data (body length, width and height) as independent variables and body temperature excess of insects relative to leaf surface as the dependent variable. Finally, in Experiment 5, the LT_{50} of each species was extracted from a logistic regression analysis of survival and temperature. We fitted a sigmoid model using TableCurve software (Systat Software) to survival rate as a function of experimental temperature. This nonlinear model

contains four parameters, and the transition centre of the sigmoid was used to estimate the LT_{50} value (Pincebourde et al., 2008).
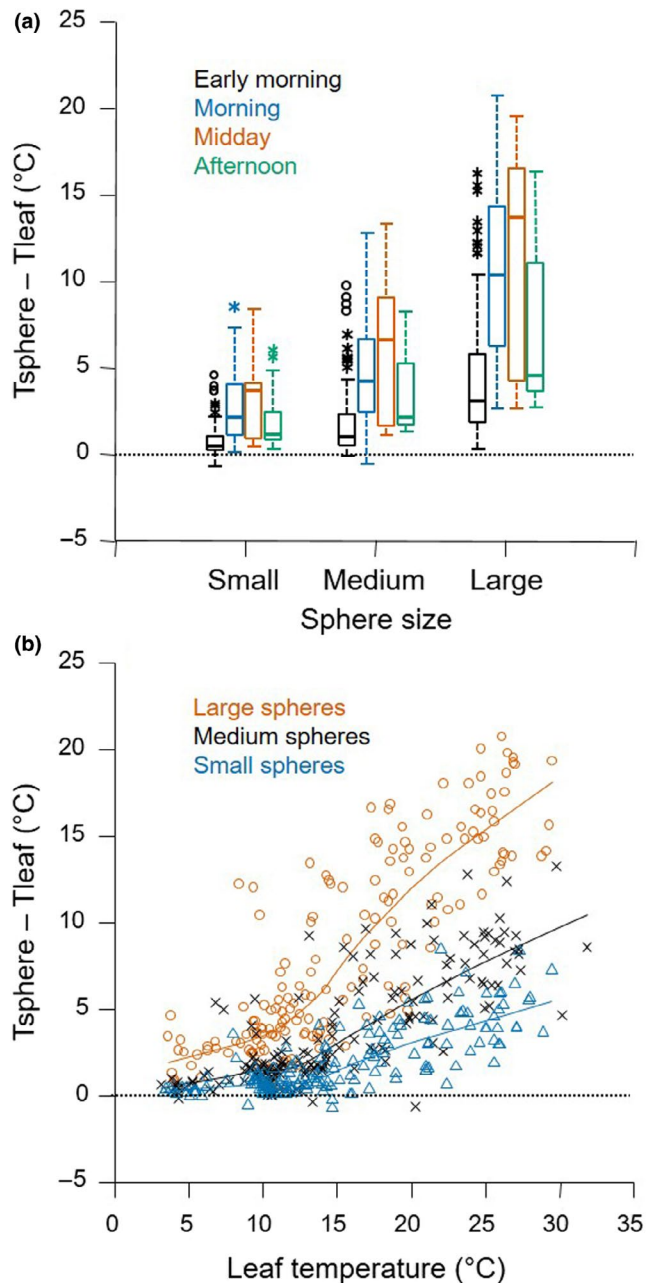
3 | RESULTS

The internal temperature patterns of the different spheres were measured continuously during three cloudy days and 3 days with clear sky (Experiment 1). The comparison between the two weather conditions confirmed the role of solar radiation in driving the difference between sphere and air temperatures (Figure 2). All spheres were warmer than ambient during daytime. Under cloudy conditions, however, internal temperatures of the three sphere sizes were similar and all remained within a few degrees above air temperature except during sun breaks when solar radiation suddenly hit leaf surfaces (which explains that there are more outliers in the temperature distributions under cloudy conditions; Figure 2). By contrast, during sunny conditions, large spheres were up to 20°C warmer than ambient air and up to 5°C warmer than small and medium spheres (Figure 2). As a result, large spheres had a higher daytime mean temperature and standard deviation than small and medium spheres (Figure 2). These differences in temperature patterns were mostly due to an increase in maximal temperatures for large spheres relative to the other sizes (Figure S1).
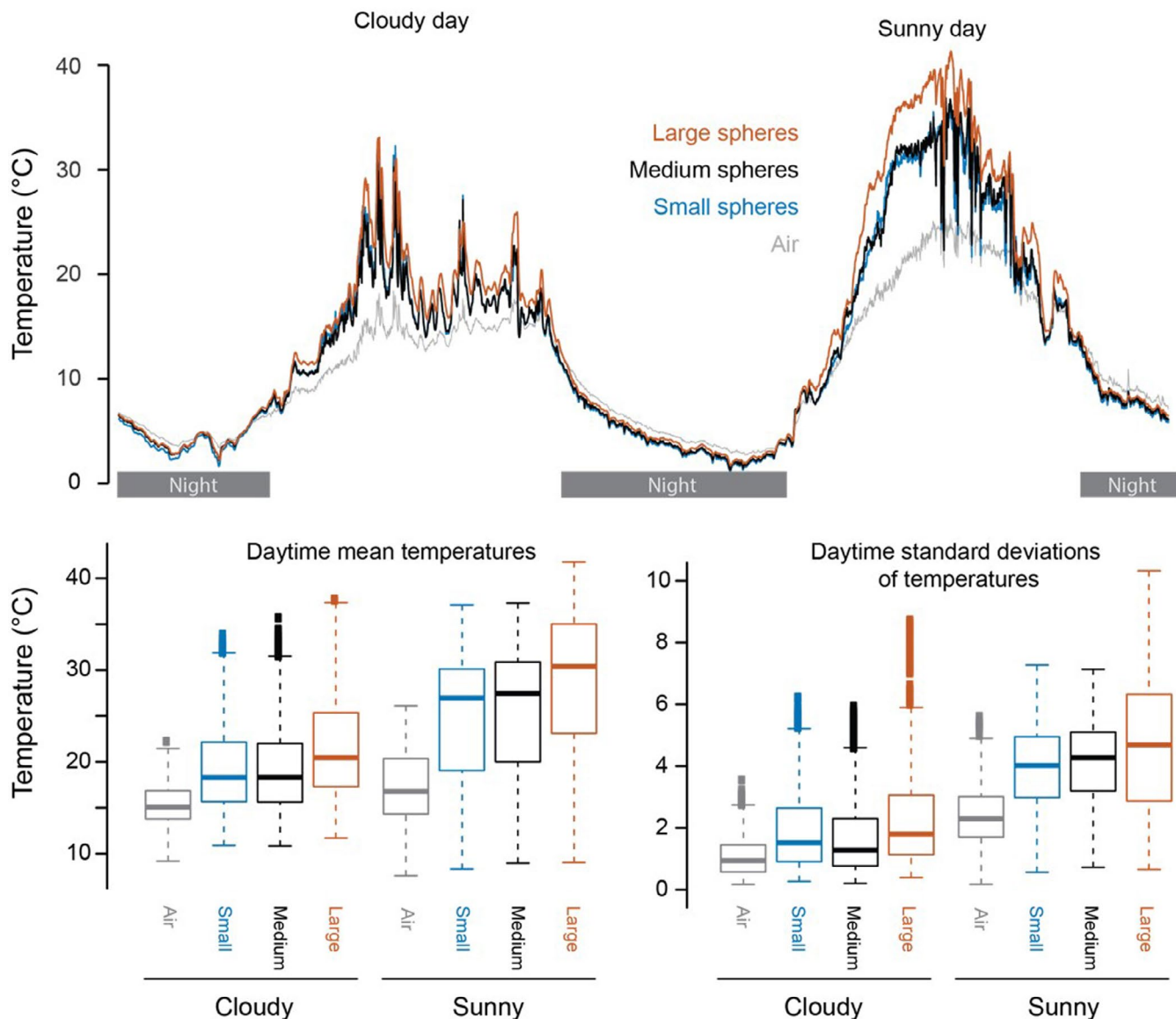
FIGURE 2 Temperature dynamics of operative temperature models ('spheres') on leaf surfaces. Top panel: representative traces for air temperature (grey) and the core temperature of the three size-class spheres (blue: small, black: medium, orange: large) during two typical days (cloudy vs. sunny). Bottom panels: distributions of temperature means (left) and standard deviations (right) for air and the three size-class spheres across the 6 days and for the two conditions (cloudy vs. sunny). The length of each box indicates the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers show the range of values that fall within the inner fences. The squares indicate the values within inner and outer fences

Thermal images of leaf surfaces (Experiment 2) showed that all spheres were warmer than the leaf surface around them, but the sphere temperature excess relative to leaf surface varied depending on sphere size and time of day (Figure 3a; ANOVA: sphere size effect, $F_{2,384} = 109.25$, $p < 0.001$; time of the day or session effect, $F_{3,384} = 38.22$, $p < 0.001$) but not on the individual plant (ANOVA: plant ID effect, $F_{10,384} = 1.26$, $p = 0.25$). The post-hoc test confirmed

that the three sphere size categories differed between each other (Tukey's HSD: $p < 0.001$ for all pairwise comparisons). The early morning session, when solar radiation was low, gave the lowest sphere surface temperature excess for all sphere sizes. Whereas this sphere temperature excess increased little for small spheres later in the day, medium and large spheres had surface temperatures up to 10°C and 20°C, respectively, above leaf surface temperature (Figure 3b). This effect was observed each day with sunny conditions (Figure S2). As a result, the mean surface temperature was up to 49°C, 43°C and 37°C for large, medium and small spheres, respectively, while leaf surface temperature remained below 30°C (Figure S3). To analyse the correlation between air and leaf surface temperature, we extracted the air temperature obtained from the dataloggers (Experiment 1) at the precise time at which the thermal images of leaf surfaces were taken (Experiment 2). Globally, leaf surface temperature followed air temperature (Figure S4; Pearson correlation coefficient 0.84, $p < 0.001$) but variability was important: the leaf temperature excess relative to air temperature was poorly correlated to air temperature (Pearson correlation coefficient 0.23, $p < 0.001$) and it varied between +13°C (e.g. when in full sun) and −7°C (e.g. as soon as the leaf was shaded; Figure S4). Due to the variability in this leaf filtering and integration of environmental conditions, air temperature was a poor predictor of sphere temperatures (Figure S5).

We sampled 31 insect species on the leaves of arrowleaf balsamroot (Experiment 4; total of 177 individuals; Table S1). In this community, body length varied from 2.3 mm to 18.8 mm, with the most abundant species, the lace bug *Corythucha immaculate* (Figure 4f), measuring 3.6 mm in length and less than a millimetre in height (Figure 4h). Body height varied from 0.4 mm to 5 mm, and therefore this insect community encompassed the size of our small and medium sphere models. Across all insects, body temperatures scaled with leaf surface temperature (Figure 4g; Pearson correlation coefficient 0.92, $p < 0.001$), with all insects consistently warmer than the local leaf surfaces (Figure 4a–f). The body temperature of insects living at the leaf surface correlated with all body size metrics, that is, length, width and height (Figure S7; length: Pearson correlation coefficient 0.46, $p < 0.001$; width: Pearson correlation coefficient 0.62, $p < 0.001$), but body height best explained variability in insect body temperature (Figure 4h; Pearson correlation coefficient 0.76, $p < 0.001$). The body temperature excess of insects (relative to leaf temperature) increased gradually with body height for small insects up to 2–3 mm (the size of the small sphere) above which it reached a plateau or increased only slightly (Figure 4h). Small species were <5°C warmer than the leaf surface, whereas large insects were between 4°C and 12°C warmer than their leaf surface (Figure 4h). Overall, the highest body temperature recorded was about 35°C for large bugs (Pentatomidae) and beetles (Cerambycidae). The observed body temperature of true insects was well below the upper lethal temperature (Experiment 4) of the lace bug *Corythucha immaculata* (46.1°C; logistic regression: $R^2 = 0.90$, $F_{3,2} = 32.01$, $p = 0.03$; Figure S6a) and the caterpillar of *Oidaematophorus balsamorrhizae* (45.6°C; sigmoid regression: $R^2 = 0.77$, $F_{3,3} = 11.81$, $p = 0.04$;

FIGURE 3 Surface temperature excess of the operative temperature models ('spheres') relative to leaf surface temperatures: its distribution as function of the session (time of the day) and sphere size (a), and its relationship with leaf surface temperature (b). The increase in leaf surface temperature across the day results from the integration of changes in several environmental variables (in particular air temperature, radiation level and wind speed)

FIGURE 4 Body temperatures of insects sampled at the surface of leaves. (a–f) Infrared images of representative insect species on balsamroot leaves that span a range of body sizes: (a) grasshopper, (b) caterpillar, (c) dipteran, (d) hemipteran, (e) a large coleopteran and a small leafhopper and (f) lace bugs (black arrows indicate the position of each insect). (g) Relationship between insect body temperature and the corresponding leaf surface temperature. The dotted line is the equality line. (h) Insect body temperature excess relative to leaf surface temperature as a function of insect body height. The position on the body height scale of the insects shown in (f) and (d) is indicated for illustration. Vertical grey bars show the size of the small and medium spheres (operative temperature models). The thick line represents a LOWESS smoothing procedure
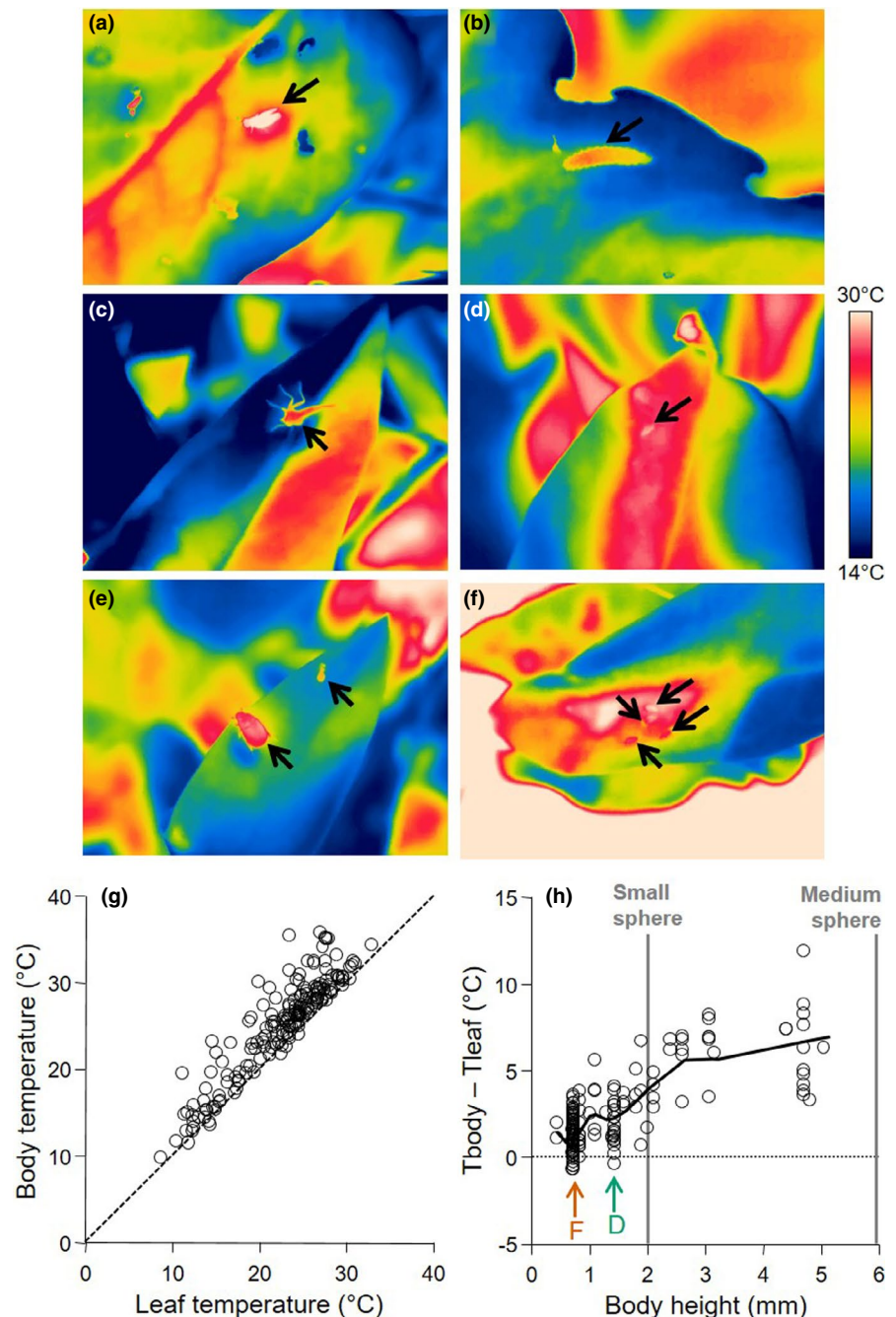

Figure S6b) during our study period (Figure 4g, all body temperatures were all well under 40°C). Nevertheless, the LT_{50} of these small species was approached by the internal temperature of the largest spheres only (Figure S1) and was reached by the surface temperature of large and medium sphere models during the 6 days of the study (Figure S3).

Leaf surface temperature was a reasonable proxy for estimating the temperature pattern of the smallest insect species. Therefore, mapping leaf surface temperatures at fine scale could provide a snapshot of the thermal landscape available for small insects at the microhabitat scale (i.e. the scale of a single plant). The surface temperature distributions that were extracted from thermal images of entire individual plants (Experiment 3) differed strongly between

cloudy and clear sky conditions (Figure 5). The temperature range was >20°C when the plant was in the sun but dropped to only 2–3°C under cloudy conditions (Figure 5). Temperature distributions were mostly unimodal but were more right-skewed under clear sky with a long tail out to high temperatures. Note that the distributions for cloudy and sunny days did not overlap (except for temperature distributions measured during brief clouds), mostly due to relatively low air temperature at our study site (plant surface temperature was close to air temperature under low levels of solar radiation). Although the within-plant thermal distributions are derived from thermal imaging (Figure 5), they do capture small patches in both shade (self-shading) and sun. Therefore, these distributions represent actual microclimate diversity of surface temperatures within an individual
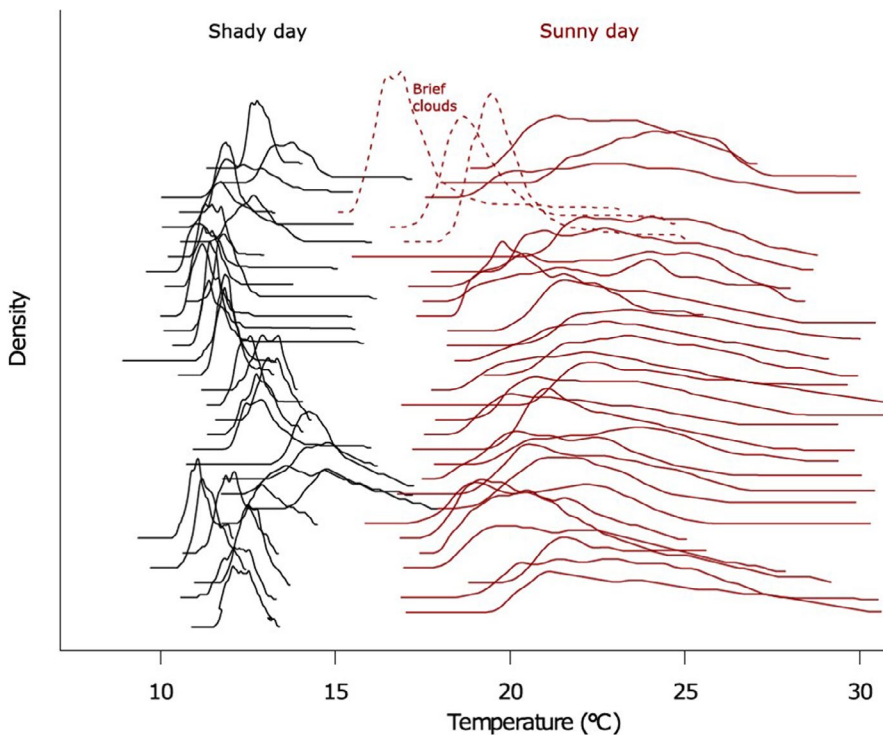
FIGURE 5 Spatial variance of plant surface temperature at the whole plant scale under cloudy (black) versus sunny (red) conditions. Each density plot corresponds to a given individual plant. Dotted distributions show the few plants that were subjected to brief cloud passing over at the precise moment of thermal image capture

plant. A large insect can vary its own body temperature by moving from sunny patches (body temperature 5–10°C above leaf surface) to shaded portions (where body temperature should be close to leaf surface temperature).

4 | DISCUSSION

Most global change biology studies on terrestrial arthropods assume that they experience air temperature and thus neglect the potential influence of microclimatic factors such as wind, radiation and substrate temperature (Pincebourde et al., 2016; Potter et al., 2013; Woods et al., 2015). Recent studies, however, have clearly identified microclimates as crucial mediators of potential responses to environmental change (Lembrechts et al., 2018; Pincebourde & Casas, 2019; Pincebourde & Woods, 2020; Zellweger et al., 2020). Here we show that the range of body temperatures for tiny ectotherms is determined by the thermal dynamics of the leaf surfaces on which they live. By contrast, larger insects are more loosely coupled to the thermal dynamics of the leaf surface both because they emerge from the leaf boundary layer and because solar radiation plays a larger role in their energy budgets (see also Kaspari et al., 2015). As a result, large insects (>2 mm in body height) have higher body temperature ranges than small insects. This difference strongly influences potential strategies for behavioural thermoregulation: the smallest arthropods can exploit small-scale spatial heterogeneity of surface temperature within single leaves or plants, whereas larger insects must thermoregulate primarily by shuttling over longer distances, between local patches of sun and shade.

For small arthropods on arrowleaf balsamroot leaves, body temperature is intimately linked to leaf temperature. The thermal environment of these organisms therefore reflects numerous drivers of the leaf heat budget, including climatic variables (radiation load, air temperature, wind speed, etc.) and plant ecophysiological parameters (transpiration rate, leaf size and shape, etc.; Gates, 1980; Pincebourde & Woods, 2012). Insect herbivores can also induce changes in leaf transpiration rates, which alter leaf surface temperatures (Pincebourde & Casas, 2019). This effect, if it happened in our study system, is included in the temperature ranges we report because we surveyed leaves in the field that showed obvious feeding damage from insect herbivores. Taken globally, our results indicate that leaf temperatures raise arthropods to higher temperatures than ambient air. Nevertheless, body temperature patterns (both measured and inferred) remained below the thermal limits of the two most abundant insects we found, at least during the period of our study. The thermal limit of these species may be surpassed in most microclimates later in the season when air temperatures are higher by several degrees. Finally, we also highlight that the spherical operative temperature models were practical to illustrate the effect of size in a standard way, but arthropods in general have varied body shapes—they are often compressed dorsoventrally—that likely affect their energy budgets to some extent, in particular by determining their body height relative to the leaf boundary layer thickness. Our results indicate, however, that the otherwise unusual metric of body height, which is related to the compression of the body, better explains the energy budget of an organism compared to other metrics like width.

Leaves of *B. sagittata* can be up to 15°C warmer than ambient air when they are exposed to full sun but cooler than ambient in cloudy conditions. This plant has high maximal stomatal conductance and transpiration rates, which contribute to large variations in the leaf temperature excess relative to ambient air (Geller & Smith, 1982). At higher elevations, the leaf temperature excess of grasses and shrubs is often of the same magnitude as what we measured (−5 to 15°C; Blonder et al., 2020; Scherrer & Korner, 2010). Aside from mean leaf temperatures, within-leaf heterogeneity in surface temperature can strongly affect insects living on leaves but is rarely considered (Caillon et al., 2014; Pincebourde & Woods, 2012; Saudreau et al., 2017). The within-leaf thermal heterogeneity in *B. sagittata* (range ~10°C when in full sun) is comparable to ranges observed for apple leaves in temperate/low altitude regions (Saudreau et al., 2017), for leaves of *Clusia* shrubs in tropical forests (Pincebourde & Suppo, 2016), and for leaves of various temperate forest trees including oak (Leigh et al., 2017). The within-leaf heterogeneity is due to several mechanisms, most importantly the interaction between leaf microtopography and the position of the sun (Saudreau et al., 2017). High within-leaf thermal heterogeneity is apparently a general rule.

More than 30 years ago, Robert D. Stevenson used biophysical theory to conclude that body temperatures of small ectotherms are dominated by the temperature of the air layers around them (Stevenson, 1985a). This conclusion is correct but has generated confusion—because some authors have interpreted his results erroneously to mean that small insects are unable to elevate their body temperatures above *ambient* air temperature (i.e. the temperature of the air outside the surface boundary layers where insects live). For most small insects most of the time, however, the relevant air temperature is that of the air within the boundary layer of their substrate. Boundary layer temperatures can differ markedly from ambient air temperatures even a few centimetres away, and they are controlled by the biophysical properties of the larger object (size, emissivity, orientation to the sun, thermal capacity, rate of transpiration, etc.) and local characteristics of air flow (wind speed and turbulence). Warmer leaf surfaces heat up the air within their boundary layer, thus contributing to warming of tiny insects both by conduction of heat directly to the insect body and by convection of heat to the air bathing the insect. We acknowledge however that other factors can eliminate this biophysical process; increasing wind speed, for instance, likely decreases all temperature deviations and homogenizes surfaces and body temperatures (Pincebourde & Woods, 2012; Vogel, 2009). Consequently, there is no simple, single relationship between size and body temperature. Instead, the diversity of substrates in natural environments generates many possible relationships. This property was nicely illustrated in a community of tropical ants, with different species living in boundary layers with different thermal properties depending on the identity of the surface (leaf surface vs. ground surface) and the body size of ants (Kaspari et al., 2015).

Because small arthropods effectively assume the thermal characteristics of much larger objects, the thermal diversity available to tiny ectotherms can be estimated relatively straightforwardly by imaging the thermal landscapes of these large objects (Woods et al., 2015). This effect is crucial for tiny insects living on plant surfaces, which provide a large temperature range across which they can behaviourally thermoregulate. Some species exploit this thermal diversity across leaf surfaces (Caillon et al., 2014; Woods, 2013), while others, like aphids, may be constrained by their feeding needs (e.g. resting near veins to reach the phloem) from exploiting this heterogeneity (Cahon et al., 2018). Based on the thermal dynamics of sphere models, we estimate that small insects could alter their body temperatures by up to 10°C simply by moving across a single leaf (<20 cm) or across a single host plant (<1 m; Figure 5). By contrast, large insects may adjust their body temperature by up to 10–20°C (Figure 3a; Figure S5) by shuttling between shade and sun within the host plant, especially if we assume that their body temperature is close to air temperature when in the shade, or by changing posture. We suggest that there is a size dependence of the different strategies (i.e. shuttling distance) likely employed by insects to take advantage of ubiquitous thermal heterogeneity in their environments. Similar rules certainly apply for small organisms living on other kinds of surfaces, including the rocky intertidal (Gedan et al., 2011) and rocks in the desert (Pike et al., 2012).

All else being equal, body size relative to boundary layer thickness sets the thermal habitat diversity available to insects. Large insects may however have different body temperatures depending on their body coloration (Clusella-Trullas & Nielsen, 2020; Kingsolver, 1983; Nielsen & Kingsolver, 2020), reflectance of near-infrared radiation (Munro et al., 2019; Tsai et al., 2020), rate of evaporation (Toolson, 1987) and body posture in relation to the sun (Kingsolver, 1985). Larger arthropods thus probably have a larger menu of ecological and evolutionary 'choices' for adjusting realized body temperatures to their thermal performance curves and physiological limits. Body size therefore appears as an important component of (thermal) niche construction wherein organisms modify their microhabitat (Laland et al., 1999) and, potentially, their microclimate to ultimately increase their fitness. As a consequence, it is not obvious whether we should expect to see a correlation between body size and thermal limits generated by differential coupling between body and leaf surface temperature. Here we report similar thermal limit (~46°C) for two species of similar body height (yet different body lengths). Shield bugs (Pentatomidae) in other thermally challenging regions share similar CTmax (e.g. Australia; Chanthy et al., 2012). Studies reporting thermal limits for species in an entire community are rare (Kaspari et al., 2015; Pincebourde & Casas, 2019; Scheffers et al., 2013; Stillman & Somero, 2000), but such approaches are promising for better determining links between fine-scale microclimate and thermal limits (Pincebourde & Woods, 2020).

High temperatures (sub-lethal) generally lead to smaller body sizes in insects and other groups via plasticity, development (Dillon & Frazier, 2013) and evolution (Ma et al., 2021; Stillwell, 2010). For example, yellow dung flies and fruit flies develop fewer, smaller cells when exposed to higher temperatures (Adrian et al., 2016; Blanckenhorn & Llaurens, 2005; Czarnoleski et al., 2013). This warming-induced reduction in body size could feedback on their

thermal budget by decreasing the importance of radiation and increasing the importance of conduction and convection within the boundary layer. In other words, those species may switch to a different thermal regime as they become immersed more fully in boundary layers. The consequences may be favourable if the surface offers cooler microsites—but disastrous if it is superheated (Kaspari et al., 2015). From our results, we estimate that a reduction of 50% in body size (e.g. from 4 to 2 mm in body height) should lead to a decrease in the insect body temperature excess relative to the leaf surface of about 3°C, which largely encompasses the magnitude of warming projected by most climate scenarios for 2050 at temperate latitudes in North America (IPCC, 2014). This should be especially true for organisms living at the surface of near-inert objects such as the ground or wood. For leaf-dwelling ectotherms, however, uncertainty remains as to how the plant surface temperature itself will respond to environmental changes (Pincebourde & Woods, 2012).

Our results have unexpected implications for predicting the effects of climate change on different size classes of terrestrial arthropods. For large arthropods, the importance of managing radiative loads will be magnified; the success of individuals will depend on how well they behaviourally thermoregulate and the availability of suitable patches for shuttling (Sears et al., 2016). For small arthropods, the outcome is more difficult to predict. It is possible that high levels of microclimatic diversity on, for example, leaf surfaces will provide cool refuges even as mean surface temperatures rise. It is also possible, however, that mean temperatures will rise enough that microsite choice is no longer sufficient, at which point small arthropods may hit a thermal wall. In conclusion, better predictions about the impacts of warming on small-bodied biodiversity—which includes most terrestrial biodiversity—will depend on identifying and incorporating the fine-scale mechanisms driving the heat budgets of these ectotherms. 'The life of a leaf' (Vogel, 2012) clearly matters for 'the little things that run the world' (Wilson, 1987) in the context of their evolutionary ecology and fate in a changing climate.

AUTHORS' CONTRIBUTIONS

S.P., M.E.D. and H.A.W. conceived the ideas and designed the methodology; S.P., M.E.D. and H.A.W. collected the data; S.P., M.E.D. and H.A.W. analysed collectively the data; S.P., M.E.D. and H.A.W. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.4qrfj6q9c (Pincebourde et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.