

COMMENTARY

In a globally warming world, insects act locally to manipulate their own microclimate

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A key challenge, as CO₂ accumulates and Earth warms, is to predict the responses of ecological systems—the suite of interacting populations embedded in the abiotic arena of temperature, moisture, and biogeochemistry. Thermal performance theory (1–3) has come to the fore as a powerful approach toward understanding such biotic change. Thermal performance theory posits that a suite of organismal traits like thermal minima, maxima, and optima—all underlain by physiology—translate gradients of an organism's thermal environment into gradients of its performance. “Performance” in this case is an evolutionary catchall that ultimately translates into reproduction, growth, and, at bare minimum, survival. Thermal performance theory's underlying logic—one used by global change scientists—is that temperature constrains the abundance and distribution of populations and communities: The abiotic predicts the biotic. Toward developing that understanding, students of thermal performance theory have been keenly aware of the importance of natural history, the diversity of ways that organisms experience temperature. In PNAS, Pincebourde and Casas (4) report how seven arthropod species that feed on leaves in the same French apple orchard engineer widely different microclimates for themselves in the process. By flipping the arrow between abiotic and biotic, the authors show how species do not just occupy their thermal niches, they create them.

It is relatively straightforward to measure the thermal environment of large organisms like lizards, birds, and tortoises (2). In the shade, one measures air temperature; in the sun, one adds the effect of radiant heat. For the first generation of biotic change models, climatologists provided the necessary data on mean air temperature and number of hours of sun from the world's weather stations. Thus began the early marriage of thermal performance theory and climatology (5).

At the same time, microclimatologists (often agronomists interested in the temperature and humidity experienced by leaves) were documenting fine-scale differences

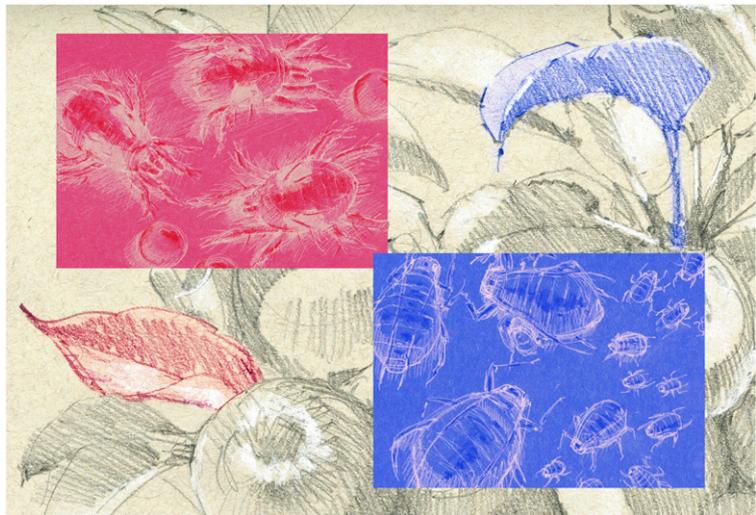


Fig. 1. In an apple orchard, leaf parasites engineer their thermal environments. Aphids (blue) cool their occupied leaves to make them conform to their thermal tolerances; spider mites (red) heat their leaves to the same end. Artwork by Deborah Kaspari.

between the temperatures of surfaces and the well-mixed air just millimeters above them (6, 7). These boundary-layer environments existed as a thin film of air, a few millimeters thick, which on windless days could superheat in the sun and supercool in the shade relative to the surrounding air. Boundary-layer environments would exist as an interesting side note save for the fact that a large fraction of Earth's terrestrial life, including its plants, frequently experience boundary-layer temperatures.

Global change biology has retained a reliance on the well-mixed atmosphere measured by your generic weather station.* Still, much of the thermal ecology of insects makes little sense when weather station temperatures are used as inputs. For example, in a tropical forest, the ants that travel through the boundary layer have upper thermal tolerances of 40 to 57 °C, far in excess of the ecosystem's warmest

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*This has led to the well-traveled joke among a certain class of thermal ecologist: Q: What organism's thermal ecology is best modeled with weather station data? A: The spider that lives inside the weather station.

air temperatures but approached with regularity on a sunny, still day on forest surfaces (8). Large portions of the tropical canopy occasionally superheat, causing ants to retreat to the shade.

Pincebourde and Casas (4) introduce us to an even more complex challenge for thermal performance theory and, hence, global change biology: the phyllosphere—the sum total of the leaf surfaces found in a given ecosystem. The phyllosphere is unique and deserving of attention. First, it is very big, far exceeding the surface of terrestrial Earth in most ecosystems: There may be 4 ha of corn phyllosphere for every hectare of cornfield, and double that for a managed tree plantation (9). Which is also to say that the phyllosphere is edible and supports the largest group of terrestrial animals, the herbivores. Moreover, unlike the relatively inert branch that an ant traverses, leaves actively thermoregulate (10). A key way is via transpiration, when leaf hydraulics open stomata, releasing water and promoting evaporative cooling. As a thermal environment, the phyllosphere is very much alive.

Pincebourde and Casas (4) explore the thermal ecology of some of the most abundant animals of the phyllosphere—the small herds of aphids and spider mites that colonize and exploit the leaves of apple trees. These arthropods are functional parasites, obtaining food and shelter from their host without typically killing it. They are also relatively immobile, affixing themselves to leaves by plunging into leaves, digging into the epidermis, or tunneling through the mesophyll. These parasites thus experience, over hours and days, their host's range of temperatures from their particular spot on the leaf. This sets up the potential conflict between a leaf's chosen temperature and that of their parasites. And as parasites so often do (11), some of these arthropods manipulate their host.

The authors begin with quantifying upper thermal limits. Each species is run through a course of temperatures in a controlled laboratory setting (sitting on a plucked leaf at 100% humidity). After an hour, the moribund are tallied and, for each species, an LD₅₀ is calculated. The seven arthropods reveal an 8 °C range in upper thermal limit, remarkable given that they appear to occupy the same macroenvironment: apple tree leaves. For perspective, this range for arthropods from a single orchard is close to the range of thermal maxima recorded globally for all of *Drosophila*, a model taxa in thermal ecology. However, this result is consistent with a growing number of studies that show a large fraction of the global diversity in thermal traits can be found in any given community (8). What generates this diversity?

This is where microclimatology meets parasitology. Pincebourde and Casas (4) demonstrate that the different feeding methods of the apple tree's parasites have direct consequences for the host plant's hydraulics. Rosy apple aphids, for example, tend to colonize new succulent leaves, slip a stylet into a phloem vessel, and drink the solution, extracting compounds and secreting sugary honeydew. Aphids actually enhance the photosynthesis rate of leaves beyond that of control leaves—in a similar way, perhaps, to the manner in which anticoagulants in mosquito saliva force its host to part with its blood supply. And all that excreted excess water enhances transpiration by nearly 200% over controls, significantly cooling the leaves to temperatures below those of uninfested leaves. It should come as no surprise that this aphid has the lowest thermal tolerance (around 37 °C). The aphid modifies its host environment to better suit its own upper thermal limit.

In contrast, the two-spotted spider mite, with an upper thermal limit of around 46 °C, has a different feeding tactic with different effects on leaves. It punctures plant cells, disrupts leaf tissue, and decreases transpiration by 75% (somehow without affecting its host's rate of photosynthesis). As a result, leaves infested by mites

heat to about 8 °C above that of the surrounding air, while leaves infested with aphids cool the leaves down close to air temperature (Fig. 1). Interestingly, the pear lace bug, the only parasite that significantly reduces leaf performance (i.e., photosynthesis), did not manipulate leaf temperature.

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The authors next use a biophysical model of leaf temperature to explore the implications of these results in a warming world. They find that, like the ants of the Panama rainforest, the distribution of thermal tolerances among the seven herbivore/parasites only makes sense in the context of the boundary-layer temperatures they help engineer. That said, when their orchard's 2017 temperature extremes (i.e., the 99th percentile of air temperature) are plugged into the model, the resulting leaf temperatures when infested by each arthropod put a number of the parasites at risk. Even the most robust arthropod, the hot-blooded spider mite, is only 2 °C away from a hot death.

This work highlights a number of research opportunities. First and foremost is predicting biotic change in the highly interactive and ubiquitous phyllosphere. Pincebourde and Casas (4) provide a strong conceptual framework for understanding the 8 °C range in upper thermal limits of apple tree parasites: Aphids accelerate transpiration; mites inhibit it; and leaf miners, trapped within the moist confines of the leaf, have few opportunities for evaporative cooling. Thermal performance theory suggests that the magnitude, duration, and frequency distribution of temperature all shape thermal traits and, hence, biotic outcomes (2, 12). Predicting those variables across all 8 ha of leaves in 1 ha of apple orchard will be a challenge. Moreover, a thermal-limit protocol that places subjects on inert leaves for 1 h at 100% relative humidity likely underestimates, for example, the capacities of aphids to regulate the rate they tap into phloem. In that vein, Bujan and Kaspari (13) have shown that plant fluids rich in sugar can enhance a canopy ant's critical thermal maximum by up to 5 °C. Thermoregulation uses a lot of carbohydrates.

Likewise, the natural history underlying the thermal trait diversity in this orchard is a playground for community ecologists seeking to answer the question, How many parasite/herbivores can an apple orchard maintain? Pincebourde and Casas (4) already hint at vertical differences in where the populations live, as well as differences in ages of leaves they inhabit. And the authors make the intriguing prediction of priority effects (i.e., whoever arrives first, wins) for the mites, given their ability to raise leaf temperatures above the lethal limits of their competitors. Finally, given the short generation times of many of the participants, seasonal variation in temperature and humidity could serve—via its effects on transpiration—to favor different populations in the cool wet spring and hot dry summers.

In the end, the authors make a convincing case that the front lines of climate change run through the diversity of plants, animals, and microbes that make up ecological communities. Communities of species that maintain a diversity of thermal tactics should be more resistant and resilient in a warming world.

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