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The world still isn't flat: Lessons learned from organismal interactions with environmental heterogeneity in terrestrial environments

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Abstract. Over the past decade, ecologists and physiologists alike have acknowledged the importance of environmental heterogeneity. Meaningful predictions of the responses of organisms to climate will require an explicit understanding of how organismal behavior and physiology are affected by such heterogeneity. Further, the responses of organisms themselves are quite heterogeneous: physiology and behavior vary over different time scales and across different life stages, and because physiological systems do not operate in isolation of one another, they need to be considered in a more integrated fashion. Here, we review case studies from our laboratories to highlight progress that has been made along these fronts and generalizations that might be made to other systems, particularly in the context of predicting responses to climate change.

Running title: interactions with environmental heterogeneity

Introduction

Much of our work over the past decade has considered how the world is not flat from an environmental perspective and what that might mean for predicting species range dynamics (e.g., (Sears et al. 2011, Sears and Angilletta 2015, Sears et al. 2016a). This work was prompted by a failure to accurately predict geographic ranges for broadly ranging species when implementing well established behavioral and physiological mechanisms (Buckley et al. 2010). Though we could predict northerly movement of widespread species in response to warming climates, our models struggled to predict the actual geographic extent of extant ranges very well.

Consequently, we became interested in how spatial and temporal heterogeneity of thermal and hydric resources impact the biology of animals and their interactions with each other. Two general results arose from this work: 1) given a statistical distribution of environmental conditions, spatial arrangement can influence organismal performance as much as the mean environment (and its variance), and 2) physiological rates depend on previous exposure to environmental conditions (e.g., physiological rates measured at constant environmental conditions typically cannot predict animal performance over cycling conditions). Despite their importance, we have quite a way to go before these insights can be dealt with in the context of predicting species range dynamics.

But there is another problem: organisms themselves are not flat. Animals can buffer themselves from environmental variation using behavior (Huey et al. 2003, Huey and Tewksbury 2009) or physiological plasticity (Chevin et al. 2010, Huey et al. 2012, Seebacher et al. 2015),

meaning that two animals are likely to experience the same environment differently. Behavior is often less costly (say, the energetic costs of moving amongst micro-environments to avoid lethal temperatures) than having to make physiological adjustments to maintain physiological homeostasis. This strategy works especially well for animals where the encounter rates of favorable patches is predictable and/or probable over short time frames. When behavior is too costly, or environmental variation is minimal for behavior to be effective, physiological acclimation can be a useful means to maintain homeostasis. Such a strategy is favored when within generation environmental variation is more variable than among generation variation. Either strategy can be problematic in the long term because both behavior and plasticity are buffers to the environment, and as such prevent selection from acting on underlying genetic variation for both physiology and behavior (Huey et al. 2003).

To make matters even worse, the dynamic between behavior and environmental heterogeneity might be inherently unpredictable (Killen et al. 2013). Sometimes, the choice of habitat depends on the physiological status of the individual (fed versus fasted, hydrated versus dehydrated, gravid versus non-gravid, young versus old, etc). For instance, dehydrated animals might choose sites that favor cooler body temperatures to minimize further dehydration at the expense of optimal physiological performance (similar to {Lorenzon:vw}). Also, animals might choose micro-habitats due to potential interactions with other animals, e.g., individuals might avoid optimal micro habitats if occupying that habitat exposes the individual to competition or predation ({Mitchell:tg}). Thus, it should be no surprise that empirical data often

mismatches our ‘theoretical’ expectations because we only consider optimal performance along one (or a few) ecological axes.

Here, we overview some of our work that addresses how animals deal with environmental variation through space and times. Through a set of case studies, we illustrate pitfalls that need to be addressed with future research, with some potential solutions. Further, we suggest future avenues of work that highlight the incorporation of physiological and behavioral mechanisms into models of species range dynamics, particularly with regard to climate change.

Animals don’t live in constant environments

Although, the environmental mean of abiotic factors such as temperature and humidity are clearly important for animal performance, few if any organisms experience mean conditions. Through time, animals often experience daily, thermal or hydric cycles, and these cycles are often correlated (Campbell and Norman 1998). Animals largely use physiological plasticity (e.g., reaction norms) to deal with temporal variation that cannot be modified through behaviors such as thermo- or hydro-regulation. Over space, similar variation of abiotic factors can occur at any given time. Both temporal and spatial variation create problems for prediction (see Table 1 in (Sinclair et al. 2016)). First, sequences of temperatures might be relatively unpredictable without a sufficient model of behavior (Sears and Angilletta 2015, Sears et al. 2016b). Second, physiology acclimates at different temporal scales (Schulte et al. n.d.), from seconds to months; so, the sequence of temperatures experienced will also make prediction difficult without an adequate model of acclimation/acclimatization. Third, environmental variables co-vary in ways

that might limit or prevent physiological acclimation for any one system (Riddell et al. 2018a).

Below we show several examples to make these points.

Temporal variation of environments

Ideally, in many terrestrial systems, we would like to be able to predict animal performance over daily thermal or hydric cycles. Both temperature and vapor pressure deficit (the environmental driver of evaporation rates) vary in a predictable pattern with cooler temperatures (and more humid conditions) occurring during morning hours and warmer temperatures (and drier conditions) occurring later in the day. Typically, researchers have measured some aspect of animal performance at different points along a reaction norm (often with respect to temperature) to define functions that predict the thermal sensitivity (Huey et al. 1979). From a technical standpoint, each point along the reaction norm is measured under constant conditions (for some amount of time) in a randomized order about the reaction norm (Angilletta et al. 2002). The explicit assumption is that randomized conditions prevent any sort of predictable acclimatory response. An additional assumption is that the response to environmental conditions is similar whether measured over constant or variable conditions (i.e., previous exposure to environmental conditions does not affect performance). Unfortunately, this second assumption seems to be false. For instance, (Niehaus et al. 2012) were not able to predict the growth and development of striped marsh frogs over cycling thermal environments from functions fitted from exposure to constant environmental conditions. In fact, their predicted estimates of development erred from -43.8 to +44.8%, and growth erred from -35.6% to +24.1%. Others have found similar results

(reviewed in (Sinclair et al. 2016)). In most all cases, errors of prediction did not appear to be systematic; thus, better analytical or simulation methods need to be developed if we hope to predict performance over temporally variable conditions (e.g. (Kingsolver et al. 2015, Kingsolver and Woods 2016)).

Another issue, outside the responses of the animal per se, is the unpredictability of rare events (Kearney et al. 2012). In some sense, this is more an issue of availability than an issue of our understanding of how animals interact their environments. Solutions to this problem will likely be found through modeling techniques that simulate environments with different levels of stochasticity. More than anything, this issue emphasizes the necessity of collecting data and modeling organism-environment interactions over ecologically relevant timescales.

Spatial variation of environments

The spatial variation and distribution of environmental resources imparts other problems for organisms. Take any statistical distribution of an environmental factor that dictates whether an animal can be active. Ignoring space, the organism can be active as long as some part of the range of this factor encompasses its preferred range (Buckley et al. 2010). For instance, *Sceloporus* lizards typically are active within a small range of body temperatures (approximately 32°C-36°C). As long as operative temperatures in the environment enable an individual to achieve a body temperature within that range, typical models will assume that the animal remains active. But this assertion is likely wrong, or at least misleading (Sears and Angilletta 2015). Just because an operative temperature occurs in the environment doesn't mean that the

animal can locate it. Thus, the spatial distribution or arrangement will dictate a temperature's availability, the movement paths necessary to locate those temperatures, and the energetic costs associated with that movement (Sears and Angilletta 2015, Sears et al. 2016b). In this sense, behavior determines the sequence of physiological states experienced by the animal. These physiological states determine when and where activity can occur in the environment. And once space is considered explicitly, each individual will have its own idiosyncratic activity patterns along with the associated energetics required to achieve that activity level.

But how can we model potential activity or performance under different arrangements of thermal resources? How can we infer an individual's physiological state given some set of past body temperatures? We would argue that more sophisticated modeling approaches will solve this problem. Until recently, the state of the art for predicting thermoregulatory performance was encapsulated by Huey and Slatkin's classic cost-benefit model (Huey and Slatkin 1976). This model makes a simple prediction: animals should thermoregulate more when the cost is low. From that prediction, many studies measured the body temperatures of organisms in the context of the availability of preferred temperatures in the environment (e.g., (Blouin-Demers and Nadeau 2005). Unfortunately, these studies were merely descriptors whose generality is limited to the place and time over which they were collected. Further, from Huey and Slatkin's theoretical treatment, it was unclear as to what a low versus high cost environment might be. The most likely explanations were likely related to the variance and/or accessibility of temperatures in a specific environment; e.g., in low cost environments, favorable temperatures are easier to access and incur lower energetic costs due to locomotion.

To explore this idea, we developed an individual based model of animal movement that was constrained by thermoregulatory decisions (Sears and Angilletta 2015). We simulated the activity of ‘virtual lizards’ in spatially explicit thermal landscapes. During the simulations, we kept track of body temperatures, movement distances, and energetic costs of movement. The take-home message from the simulations was that the availability and arrangement of operative temperatures influenced the thermoregulatory accuracy and energetic cost of activity as much as the magnitude of environmental temperature itself (Figure 1). To test this idea, we performed a set of mesocosm experiments at the Sevilleta LTER site in NM (Sears et al. 2016b). By manipulating patterns of shade in our arenas, we were able to set up a similar set of thermal conditions that were used during our simulations. We then implanted lizards with data loggers (that could keep track of body temperatures) and allowed the animals to thermoregulate within these arenas. Simultaneously, we modeled the thermal conditions within the arenas and used our individual based simulations to predict the regulatory performance of our experimental animals. Interestingly, our model predicted the thermoregulatory performance of our experimental animals quite well (Figure 2). What these results then suggest is that, in nature, the energetic costs of activity in different habitats under similar climatic conditions might differ by two- to three-fold. To date, models that predict species range dynamics do not consider spatially-explicit, small-scale variation in abiotic factors and their potential effects on energetics. Indeed, this will be a fruitful area for research in the future.

Further, the arrangement of thermal resources has other physiological and ecological effects. For instance, we have conducted experiments where the behavior of individuals was

monitored in our experimental enclosures while alone versus while paired with a conspecific (Rusch et al. 2018). Interestingly, when alone, individuals elicit a stress response with respect to the spatial distributions of temperatures. Individuals in environments where favorable temperatures were clumped together showed higher levels of circulating corticosterone than individuals in environments where favorable temperatures were dispersed throughout the environment. These stress responses were magnified when individuals were paired with another individual, and the total distances moved by individuals were longer when housed with another individual than when alone. Both the stress response and increased movement would likely result in even higher energetic expenditures. These results suggest that we have much to learn regarding how individuals interact with others both within and among species. Within species, interactions among individuals through behaviors such as territoriality and mating will likely be affected by the thermal structure of habitats; among species competition and predator-prey dynamics will also be affected by the thermal environment.

Behavior is not an option for some life cycles

Consequences of the environment on different life stages

When behavior isn't an option, physiological performance will determine how, or if, an individual can tolerate environmental variation. For instance, distinct life stages within a species can experience abiotic environments differently (Crozier et al. 2008, Kingsolver et al. 2011). These experiences result from differences in size, morphology, or even mobility. For instance, developing lizard embryos depend on the choices that mothers have made when choosing a nest

because developing embryos have no meaningful opportunity to thermoregulate. If the mother's choice of nests is too warm or too cool, then embryos might not survive to hatching (Angilletta et al. 2000). Furthermore, if a female chooses a nest that is not quite optimal, embryos might experience sublethal effects that have implications post-hatching. Recent work on Eastern fence lizards (*Sceloporus undulatus*) illustrates how the lethal and sublethal effects of temperature on embryos might affect species range dynamics (Michael J Angilletta et al. 2013, Levy et al. 2015, Carlo et al. n.d.). First, the acute effects of high lethal temperatures on developing embryos was incorporated into a species range model to predict the effects of climate warming. Across the range, fitness was reduced from 2%-35% over models based solely on adult physiology when forecasting the range by 2100 (Levy et al. 2015). Next, the chronic effects of projected elevated nest temperatures reduced annual survivorship by up to an additional 24% compared to models that did not include the chronic effects of temperature (Carlo et al. n.d.)). This result itself might be optimistic given further phenotypic effects of elevated temperatures on embryos: embryos that experienced elevated nesting temperatures developed faster, hatched to a relatively smaller body size, and grew more slowly for the first three weeks post hatching. At the southern edge of the species range, slower growth and smaller body size might mean not reaching the age of first reproduction in time for lizards' first clutch of eggs. The demographic effects of a delay in reproduction might further accelerate population losses.

Consequences of physiological plasticity and trade-offs

When behavioral responses to the environment are limited, an additional consideration for understanding organisms' tolerance to changing environments rests on their capacity to acclimatize to local abiotic conditions. Lungless salamanders provide an example where range dynamics cannot be understood without incorporating physiological plasticity into our models (Riddell et al. 2018b). Being lungless, plethodontid salamanders require wet skin to facilitate gas exchange, restricting individuals to moist environments. The reliance on wet skin for cutaneous gas exchange increases vulnerability to rapid dehydration, making salamanders particularly sensitive to variation in their hydric (humidity) environment. In fact, activity on the forest floor is limited by how much water is lost by an individual while active. It would seem that an easy way around this problem would be to become more water tight. The problem with this solution is that reducing water loss rates also inhibits oxygen from diffusing across the skin and into the circulatory system. Thus, a simple trade off exists to balance water loss and oxygen consumption (Riddell et al. 2018a).

We have found that Southern gray-cheeked salamanders (*Plethodon metcalfi*) are able to modify skin resistance to water loss in a manner that would seem to offset environmental constraints on activity: in drier environments, salamanders are water tight, in wetter environments, salamanders are leaky (Riddell and Sears 2015). We can observe seasonal changes in water loss in nature in response to vapor pressure deficits, and we can induce similar plasticity in the laboratory (Riddell et al. 2018b). Without incorporating plasticity into our projections of the species range, we are not able to predict the extant range very well; yet once plasticity is incorporated, we can predict the the limits of their range and the uneven distribution of individuals within their range (Figure 3). Further, we are able to pinpoint that younger, smaller salamanders

are at a particular risk to changing climates (which would also create a demographic bottleneck in many populations). Thus, understanding these dynamics is the difference between predicting a high degree of extinction across the range in response to warming climate versus only modest predicted losses.

If we simply modeled potential activity across a range of environmental humidity, this plasticity would suggest that activity levels would be similar across elevations and that animals are always in positive energetic balance (Riddell et al. 2018a)(Figure 4). The problem is that water loss is correlated with metabolic rates. For any given body size, leaky individuals expend more energy than do water tight individuals. When we added this covariation to models of surface activity, there is a minimum skin resistance (>5 s/cm) over which animals can be in positive energy balance. Further, simulations demonstrate diminishing returns for activity as salamanders become more water tight with a threshold (~ 7 cm/s) in skin resistance over which further gains in activity cannot be attained. It shouldn't be surprising that we only have measured skin resistance in field-fresh animals that fall within this range of skin resistances. The importance of this example is that if we only study physiological plasticity along one physiological axis, we will potentially be misled as to an organism's ability to tolerate changing environments. Other studies are

Unexpected outcomes of the interaction between physiology and behavior

One final insight that merits particular attention when studying responses to environmental heterogeneity: we cannot merely assume that organismal responses to changing environments is

the passive response of physiological performance to environmental conditions. That is, we cannot ignore the interplay between physiology and behavioral responses to environmental change. It should be noted that ignoring behavior has provided some potentially important insights regarding the responses of ectotherms to climate (e.g., (Ghalambor et al. 2008, Deutsch et al. 2008). In fact, projections that ignore behavior might represent a null expectation to change. But, adding thermoregulation to such projections is not so simple. Organisms thermoregulate to different degrees, and operative temperatures in an environment differ for organisms with different coloration and morphology (Pincebourde et al. 2016).

To illustrate our point, we return to the *Sceloporus* system (Figure 5). One of the big questions that remains to understand future responses to climate change is whether females have the capacity to modify nesting behavior in response to warming environments. In the southern portion of the range, females nest in the forest understory and would need to dig deeper nests to offset warming at the soil surface. In the northern portion of the range, females nest in the open, outside of the forest canopy because nests would likely not develop in the cooler understory conditions (Angilletta et al. 2009). Consequently, due to nest site selection, nests in the north experience warmer maximal temperatures (by up to 5°C). Under warming conditions, these females could either nest deeper into the soil or nest in the forest understory to cool temperatures. If females choose to move into the forest, their maximal temperatures will actually cool with climatic warming! Thus, warmer conditions might enhance activity for adults and allow nests to develop under more optimal conditions, resulting in higher fitness in northern populations. In the south, however, warmer temperatures might limit adult activity and subject

embryos to the negative consequences of chronic exposure to warmer temperatures. Thus, southern populations of fence lizards might see accelerations of population losses.

Genomic basis for adaptive evolution

For this review, we have focused on phenotypic evolution while ignoring its genomic basis. That said, we would like to take an opportunity to point out that relatively few studies have explored the genomic basis of variation in environmentally-sensitive traits (especially in vertebrate species) in the context of species ranges and climate change. To understand whether physiological adaptation can keep pace with climatic change, we will need to understand the genetic underpinnings of environmentally-sensitive traits (Diamond 2017). The problem here is twofold: 1) is there sufficient genetic variation (heritability) that might allow animals to respond to selection and 2) what are the specific pathways under selection (and how might adaptation in these pathways interact with other physiological processes)? With respect to the first question, there is some evidence that thermally sensitive traits can evolve rapidly in natural and seminatural environments. For example, populations of brown anoles (*Anolis sagrei*) that were transplanted to warmer and more variable thermal conditions rapidly evolved higher thermal tolerances and wider thermal breadths when compared to source populations {Logan:uu}. With respect to the second question, green anoles (*Anolis carolinensis*) evolved increased cold tolerances in response to an extreme cold event (Campbell-Staton et al. 2017), and genomic analyses revealed genes associated with nervous system function were under selection for southern populations of green anoles. It is unclear how general such responses might be at the

genomic level and whether such responses limit the responses of other physiological pathways. That said, with the increased availability of genomic tools for non-model organisms, it is now possible to estimate the evolutionary potential in response to climatic change across a species range (Gienapp et al. 2017). We might expect that additive genetic variances for thermally-sensitive traits might be higher at the core (or ancestral parts) of the range, while additive genetic variances might be lower at the leading edge of a range expansion. Such an understanding of the genetic diversity across the range, coupled with an understanding of processes that impede or facilitate gene flow will be extremely important to predict the evolutionary potential of species under climate change (Bontrager and Angert 2019).

Implications for the predicting niche and responses to climate change

Throughout this review of our recent work, we have illustrated how the world isn't flat whether thinking about environmental conditions or the organisms that occupy them. As a result, generalizations that apply across all species might be hard to come by despite their intellectual appeal (Judson 1994). A lack of generality of specific mechanisms means that predictions of species ranges will likely be idiosyncratic to some focal species. That said, those examples might provide insights for particular groups of animals that function similarly in their environments. With that in mind, we do have several suggestions for future work:

1. *We need to integrate heterogeneity explicitly in our modeling approaches.* Decades of collecting physiological data at constant temperatures have been both enlightening and

limiting. Though the variation in physiological performance itself has been enlightening, we are still not able to reliably predict physiological performance under fluctuating conditions, nonetheless predict how acclimation/acclimatization across timescales will affect physiological performance under novel conditions.

2. *We need to integrate life cycles into our models.* In fact, this problem affects prediction of species distribution whether using mechanistic approaches (that we endorse) or statistical models (such as those using MAXENT). Eggs and adults are fundamentally different organisms and have their own sets of requirements that might be unique to that particular life stage, and this is the simplest case. Recent work has begun to make progress in this area, though more work is necessary.
3. *We need better understandings of how behavior affects potential responses.* In some sense, we need to know the “unknown unknowns”. Some behavior, such as habitat selection under thermoregulatory behavior is not horribly difficult (though technically tedious). But interactions between individuals might create novel circumstances that we would not expect. To that end, we would encourage more work in the context of abiotic factors be performed explicitly with intra- and inter-specific interactions in mind.
4. *We need to better understand behavioral flexibility.* We have been acutely aware that reaction norms for physiological performance is fundamental to understanding responses to changing environments, but outside of thermoregulatory studies, we know relatively little how plastic behavior might be to similar changing conditions.

5. *We need to understand the genomic basis for organismal trait variation to be able to predict evolutionary responses.* One of the big questions ahead of us is whether adaptation can keep pace with the rate of climate change. Before we can really answer this question, we need to understand the genetic architecture of environmentally sensitive traits, and how selection might act on standing genetic variation in populations across the range. With the rapid development of next generation sequencing methods and bioinformatic tools, the time is ripe for making progress in this area.

Figure Legends

Figure 1. Effect sizes for a set of individual based simulations of thermoregulation for varying sized lizards. A) The spatial configuration of temperature is as important as temperature itself for thermoregulatory performance (accuracy). B) The spatial arrangement of temperature drives patterns of movement. C) As animals increase in size, the spatial arrangement of temperatures becomes more important.

Figure 2. Predicted (A) and actual (B) body temperatures of lizards from a mesocosm experiment of thermoregulation. C) Variances in body temperature were similar between modeled and actual lizards, with the relative magnitudes correctly predicted by our individual based simulation.

Figure 3. Species range projections without and with acclimatization for *Plethodon metcalfi* under current conditions, conditions in 2050, and conditions in 2100. Yellow to green areas are predicted suitable habitat. Solid lines show the current range.

Figure 4. A) Salamanders that are water tight have lower rates of oxygen consumption. B) Energy balance for a salamander increases with increasing skin resistance when tradeoffs between skin resistance and oxygen consumption are considered. C) Increasing skin resistance increases the potential for activity up to a threshold, beyond which longer durations of activity are not achieved.

Figure 5. Predicted shifts in nest temperatures for fence lizards in NJ (the northern range) and SC (the southern range). Nests become cooler under climate change in the north and warmer under climate change in the south.

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Figure 1

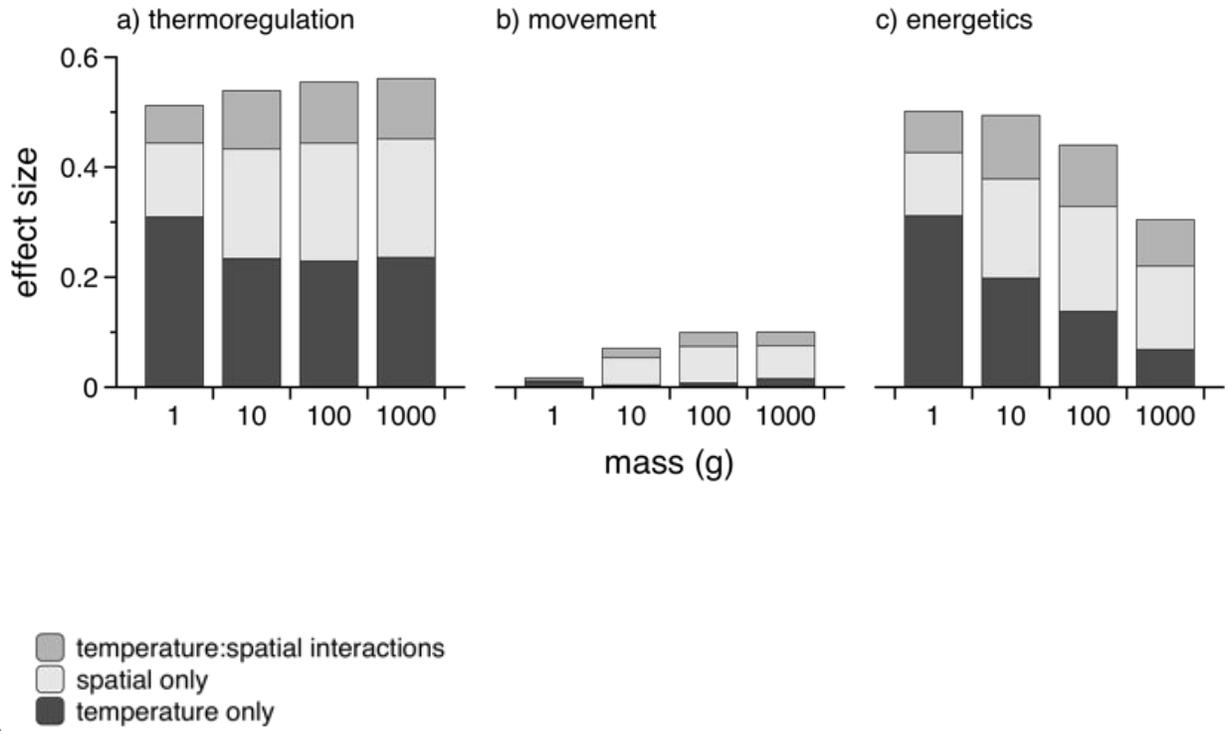


Figure 2

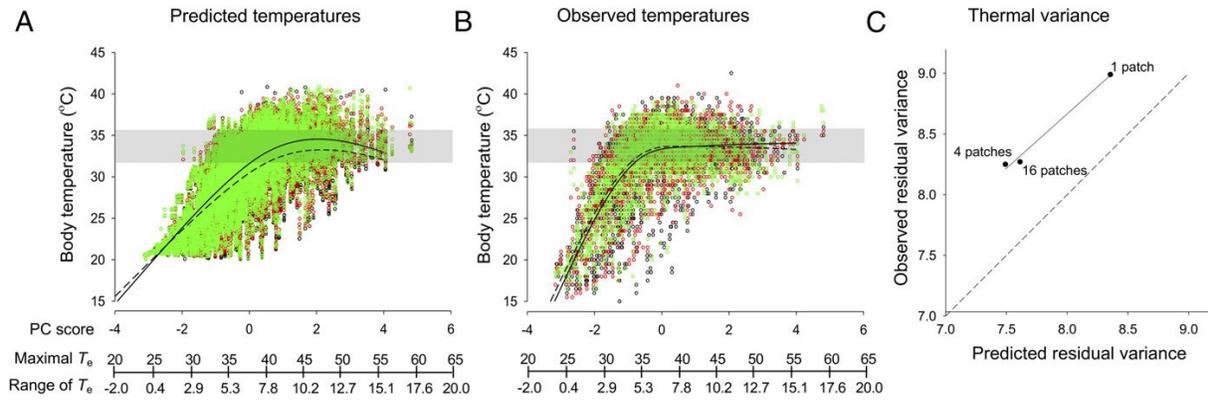


Figure 3

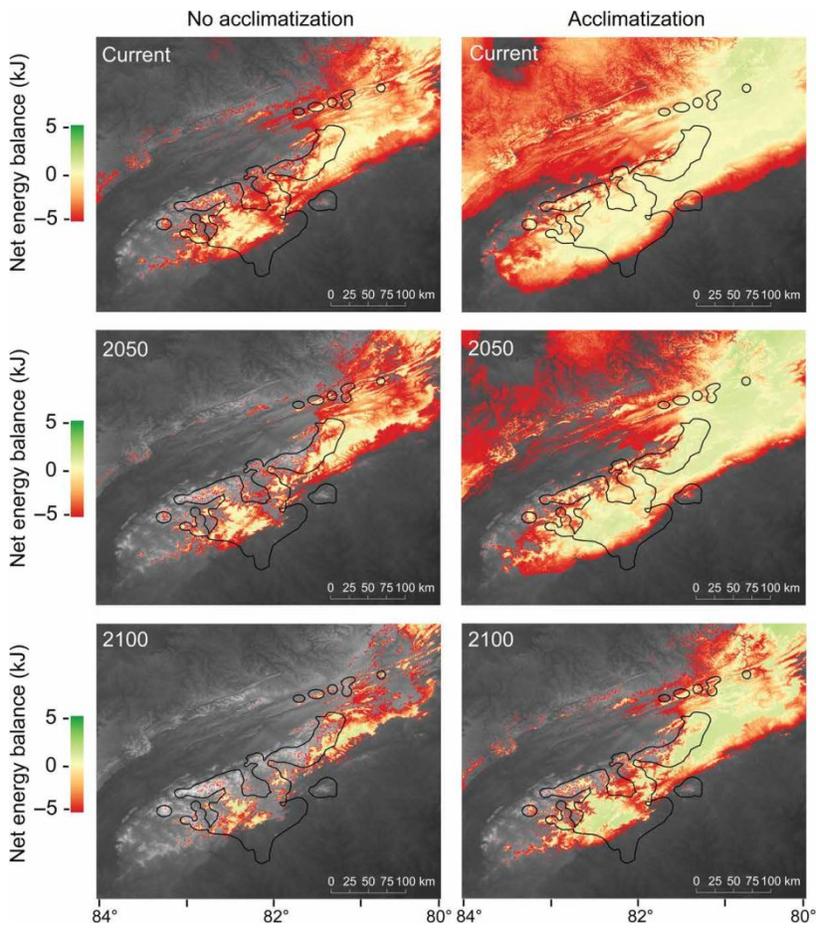


Figure 4

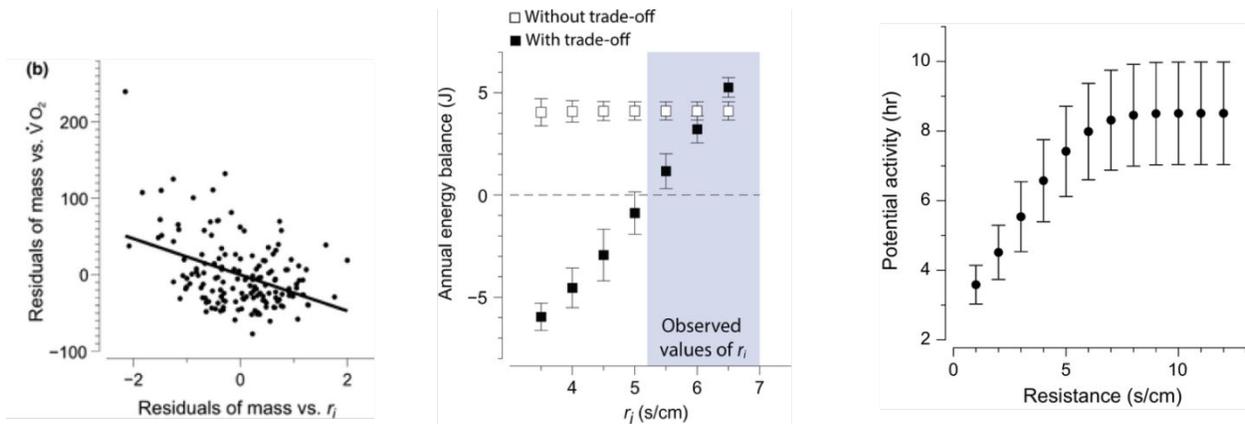
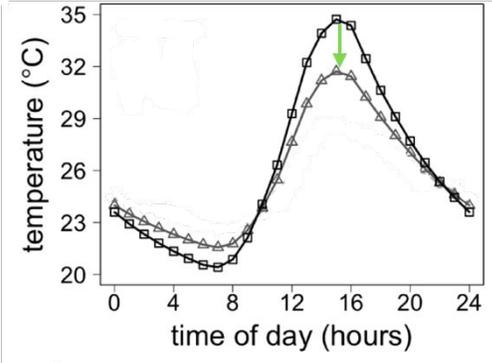


Figure 5

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