Broad-scale ecological implications of ectothermy and endothermy in changing environments

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ABSTRACT

Aim Physiology is emerging as a basis for understanding the distribution and diversity of organisms, and ultimately for predicting their responses to climate change. Here we review how the difference in physiology of terrestrial vertebrate ectotherms (amphibians and reptiles) and endotherms (birds and mammals) is expected to influence broad-scale ecological patterns.

Location Global terrestrial ecosystems.

Methods We use data from the literature and modelling to analyse geographic gradients in energy use and thermal limits. We then compare broad-scale ecological patterns for both groups with expectations stemming from these geographic gradients.

Results The differences in thermal physiology between ectotherms and endotherms result in geographically disparate macrophysiological constraints. Field metabolic rate (FMR) is stable or decreases slightly with temperature for endotherms, while it generally increases for ectotherms, leading to opposing latitudinal gradients of expected FMR. Potential activity time is a greater constraint on the distributions of ectotherms than endotherms, particularly at high latitudes. Differences in the primary correlates of abundance and species richness for two representative taxonomic groups are consistent with the consequences of these basic physiological differences. Ectotherm richness is better predicted by temperature, whereas endotherm richness is more strongly associated with primary productivity. Finally, in contrast to endotherms, ectotherm richness is not strongly related to abundance.

Main conclusions Differences in thermal physiology affect how organisms interact with and are constrained by their environment, and may ultimately explain differences in the geographic pattern of biodiversity for endotherms and ectotherms. Linking the fields of physiological and broad-scale ecology should yield a more mechanistic understanding of how biodiversity will respond to environmental change.

Keywords

Abundance, climate change, distribution, diversity, physiology, temperature.

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INTRODUCTION

Endotherms such as birds and mammals have been the focus of many broad-scale ecological analyses. Ectotherms have been a central group in physiological ecology (Pough, 1980), but data on their broad-scale ecology have only recently been compiled and analysed (Clarke & Gaston, 2006). Here we review analyses of these newly available data to compare the physiological, ener-

getic and ecological constraints on abundance, distribution and diversity for terrestrial vertebrate ectotherms and endotherms. This focus on broad-scale ecology complements previous comparisons of ectotherm and endotherm physiology, life history, ecology and evolution (e.g. Pough, 1980; Ricklefs & Wikelski, 2002; Shine, 2005) and follows upon recent syntheses highlighting the potential of linking physiology with ecology and evolution (Gaston *et al.*, 2009; Kingsolver, 2009). The study of

variation in physiological traits over large scales (termed macrophysiology by Chown *et al.*, 2004) has deep historical roots and is rapidly developing given the increasing imperative for accurate predictions of how species will respond to climate change (Chown & Gaston, 2008).

The different energetic and performance implications of body temperature regulation for ectotherms and endotherms are central to understanding broad-scale ecological patterns, which typically span substantial gradients in temperature and other environmental variables. Endotherms maintain relatively constant body temperatures, although their degree of homeothermy varies (reviewed by Angilletta *et al.*, 2010). Ectotherm body temperatures tend to follow environmental temperatures more closely (i.e. poikilothermy), but many ectotherms effectively thermoregulate behaviourally (Huey, 1982). At cooler body temperatures, many biochemical processes slow, including the metabolism and assimilation of energy (Hemmingsen, 1960). Endothermy is energetically costly – endothermic vertebrates tend to require at least an order of magnitude more energy than ectotherms of the same size (Pough, 1980; Nagy, 2005). However, the high metabolic rates of endotherms enable rapid regeneration of energy supplies and thus greater endurance (Wieser, 1985), and their higher body temperature can confer additional performance advantages (Angilletta *et al.*, 2010).

Here we first review how differences in the physiology of vertebrate endotherms and ectotherms govern their responses to environmental temperature, energy availability and water availability. Subsequently, we illustrate how these responses result in differential geographic patterns of energy use, thermal limits and seasonal activity. Finally, we evaluate the consequences for the distribution, abundance and diversity of the groups in the face of global change. We focus on terrestrial vertebrates for which the most accurate global distributional data exist. We intend our assessment of ectothermy and endothermy to provide a starting place for considering how physiological complexities influence organisms' differential broad-scale response to environmental gradients and their potential perturbations under global change. Thorough physiological reviews (McNab, 2002; Angilletta, 2009) and more detailed analyses (e.g. Kearney *et al.*, 2009) available elsewhere address how additional physiological details may be crucial to determining the exact environmental responses of particular organisms.

PHYSIOLOGY OF ECTOTHERMY AND ENDOTHERMY

Temperature

The influence of air temperature on ectotherm body temperatures (depending on the degree of behavioural thermoregulation) renders them particularly sensitive to their environment (Huey, 1982). Performance curves depict hump-shaped relationships describing the performance (e.g. locomotion) of an organism as a function of an abiotic variable, most often body temperature (Angilletta, 2009; Kingsolver, 2009). Performance curves illustrate how environmental temperature strongly con-

strains an ectotherm's performance and activity time according to both diurnal and seasonal temperature variation (Porter *et al.*, 1973). Activity time is a key predictor of ectotherm population dynamics (Adolph & Porter, 1993; Sinervo *et al.*, 2010). Environmental temperature also modifies growth rates and time to maturation (Angilletta *et al.*, 2004). Endotherm performance also varies as a function of body temperature, but body temperature variation tends to be much smaller, and effects on performance have been scarcely documented (Angilletta *et al.*, 2010).

Temperature also affects rates of energy use and assimilation. For endotherms within their thermoneutral zone, metabolic rates vary little with ambient temperature. However, metabolic rates increase rapidly outside the thermoneutral zones, which can vary appreciably by species and latitude (Scholander *et al.*, 1953; Canterbury, 2002). In ectotherms, body temperature exerts an exponential effect on metabolic rates, with individuals with warmer body temperatures requiring disproportionately more energy per unit time (Bennett, 1982; Gillooly *et al.*, 2001; Dillon *et al.*, 2010). Although the rate of energy assimilation varies little for endotherms due to their constant body temperatures, the rate at which ectotherms can assimilate energy forms a hump-shaped relationship with temperature (i.e. the performance curve) (Huey, 1991). The performance breadth for assimilation tends to be narrower than that for locomotion because energy assimilation relies on the sequential execution of multiple behavioural and physiological processes (Angilletta, 2001). Behavioural thermoregulation buffers changes in environmental temperature and subsequently energy use and assimilation (Kearney *et al.*, 2009), but its extent and effectiveness varies taxonomically and geographically (Huey *et al.*, 2003).

Energy availability

Although temperature affects rates of assimilation, metabolism and activity, organisms may also be constrained by the availability of resources to metabolise and assimilate. For broad-scale analyses, net primary productivity (NPP) is often used as a coarse proxy for biological energy available to consumers, although the extent to which it reflects the actual pool of resources used by any given group will vary (see Clarke & Gaston, 2006, for a discussion of energy forms and their relevance to organisms). Regardless of energy availability, ectotherms may be unable to acquire energy in cold environments where their activity is limited. In contrast, endotherms can maintain high levels of activity in cold environments if sufficient energy exists to meet their elevated metabolic needs (Porter & Gates, 1969). Experimental manipulations of feeding rates suggest that endotherms thermoregulate more precisely when food is abundant (Angilletta *et al.*, 2010). The energetic maintenance costs of ectotherms are more than 10 times lower than those of endotherms (Bennett & Nagy, 1977; Pough, 1980). Ectotherms may thus survive without feeding for extended periods, buffering periods of low resource availability in contrast to the much more continuous feeding requirements of most endotherms (Shine, 2005). In summary, although energy

availability is expected to be a primary constraint on the abundance and distribution of endotherms, it is expected to be insufficient for explaining abundance and distribution in ectotherms as they tend to be limited by rates of energy assimilation rather than availability.

Water

In any particular environment, endotherms tend to require much more water than do ectotherms of a similar size due to their higher metabolic rates (Schmidt-Nielsen, 1964). However, endotherms have acquired adaptations that increase water-use efficiency in water-limited environments (Schmidt-Nielsen, 1964). For example, desert species use hyperthermia to limit water needs (Tieleman *et al.*, 2003). Regardless, the need to evaporate water to maintain body temperatures below lethal limits can constrain activity in hot, water-limited environments (Wolf & Walsberg, 1996). Water loss poses a greater challenge for small organisms with higher surface area to volume ratios, and has been observed to dramatically reduce the survival of small desert birds (McKechnie & Wolf, 2009).

Metabolism has less influence on the water balance of ectotherms (McNab, 2002). However, the capacity for behavioural thermoregulation in amphibians is limited because the cooling effect of evaporative water loss through their water-permeable skin counteracts heat gain from basking (Tracy, 1976). Although water balance can be a critical constraint for both endotherms and ectotherms, we do not address water balance further as general methods for quantifying water balance are not yet available.

GEOGRAPHIC GRADIENTS MEDIATED BY PHYSIOLOGY

Energy use

How do energy requirements interact with geographic gradients of energy availability? Energy use over time has frequently been measured as field metabolic rate (FMR, kJ day^{-1}) using doubly labelled water (Nagy *et al.*, 1999; Nagy, 2005). We extend an existing analysis for mammals and birds (Anderson & Jetz, 2005) to include reptiles to examine the correlation between environmental temperatures, net primary productivity (NPP) and FMR. For reptiles, we estimated annual temperature (°C, 10′ spatial resolution) (New *et al.*, 2002) and NPP [tonnes of carbon (tC) ha^{-1} year^{-1}, 18-year average of annual values from the DOLY global model, 0.5° spatial resolution] (Woodward *et al.*, 1995) corresponding to the locations of reptile FMR measurements (Nagy *et al.*, 1999). We mass-corrected FMR using empirical scaling exponents (birds 0.644, mammals 0.678, reptiles 0.768) from White *et al.* (2006) (see Appendices S1 and S2 in Supporting Information for additional methods and references). We assume strict thermoconformity and thus use air temperature as a proxy for operative environmental temperatures (reviewed in Angilletta, 2009) in our analyses, but note that
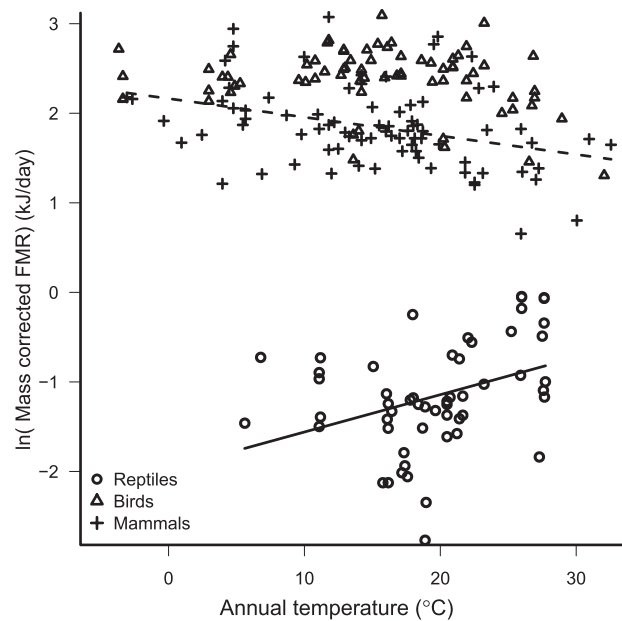

Figure 1 The log of mass corrected (grams) field metabolic rate decreases with annual temperature (°C) for mammals (+, dashed line) increases for lizards (o, solid line) and shows no trend for birds (Δ). Data are from Anderson & Jetz (2005) and Nagy (2005).

this proxy can be particularly problematic due to radiation and heat exchange with the ground.

Despite suggestions that FMR increases with increasing resource availability (Mueller & Diamond, 2001), we find that NPP is generally a poor predictor, explaining at most 8% of the variation in FMR for any group (Fig. S1). The effect of temperature on FMR was more pronounced (Fig. 1). We found that FMR decreased with increasing environmental temperatures for mammals (slope ± 95% CI = −0.021 ± 0.012, $F_{[1,79]}$ = 11.58, r^2 = 0.13, $P < 0.01$) and more weakly for birds (−0.006 ± 0.008, $F_{[1,73]}$ = 1.90, r^2 = 0.03, $P = 0.17$), consistent with increased thermoregulatory costs beyond the low end of their thermoneutral zones (see the detailed analysis in Anderson & Jetz, 2005). Conversely, FMR increased with increasing environmental temperatures for reptiles (0.042 ± 0.027, $F_{[1,53]}$ = 8.52, r^2 = 0.14, $P < 0.01$). This finding is consistent with an increase in metabolic rates with increasing temperatures for ectothermic organisms due to biochemical kinetics (Gillooly *et al.*, 2001). However, FMR probably also increased due to increased activity (see below) and increased assimilation rates in warmer environments.

Thermal limits

Tropical organisms tend to have narrower thermal tolerance, presumably due to less seasonal temperature variation at low latitudes (Janzen, 1967; Ghalambor *et al.*, 2004; Deutsch *et al.*, 2008; Sunday *et al.*, 2010; Clusella-Trullas *et al.*, 2011). Lizards have broader thermal tolerances (thermal maxima – minima) at higher latitudes (slope ± 95% CI = 0.18 ± 0.06, $F_{[1,126]}$ = 32.1,
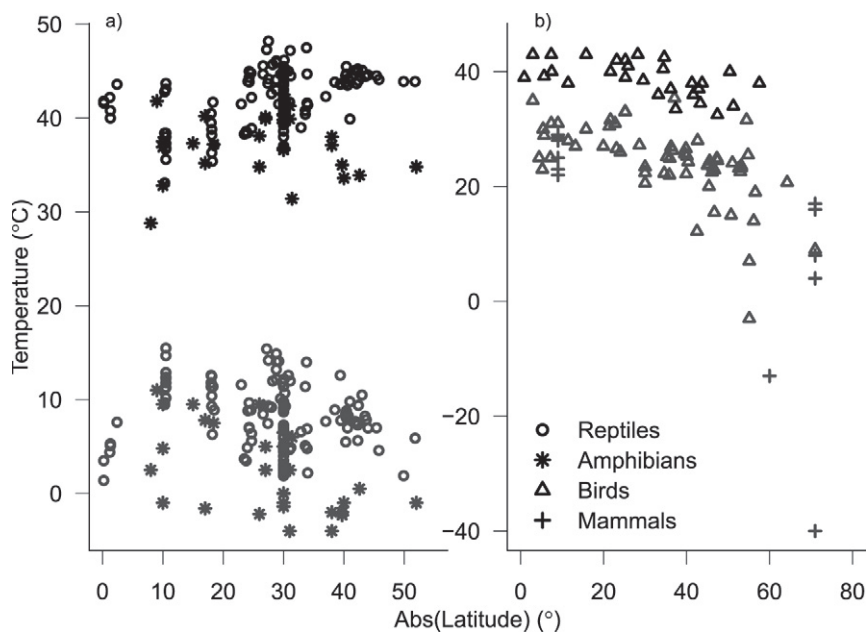
Figure 2 Latitudinal patterns in thermal minima (dark gray) and thermal maxima (black) for (a) lizards (o) and amphibians (*) and (b) birds (Δ) and mammals (+). The temperatures are critical thermal or lethal limits for ectotherms and the limits of the thermoneutral zone for endotherms. Data are from (a) Sunday *et al.* (2010) and (b) a variety of sources (see Appendix S1). Latitudes reflect (a) location of measurement and (b) geographic range centroids. Only terrestrial species are included.

$r^2 = 0.20$, $P < 10^{-7}$) (Fig. 2; see Huey *et al.*, 2009). Reptile lower thermal limits exhibit a weak decline across all latitudes ($P = 0.06$), but the decline is much more pronounced beyond 10° latitude (slope ± 95% CI = -0.14 ± 0.07, $F_{[1,120]} = 16.4$, $r^2 = 0.12$, $P < 10^{-4}$). All data equatorward of 10° are for chameleons, which have the capacity for activity at low temperatures (Bennett, 2004). In contrast, upper thermal limits for reptiles counterintuitively increase with latitude (slope ± 95% CI = 0.12 ± 0.04, $F_{[1,126]} = 35.3$, $r^2 = 0.22$, $P < 10^{-7}$) as temperate lizards tend to occur in warm deserts whereas many tropical lizards live in forests (Huey *et al.*, 2009). A similar shift in thermal breadth is observed for amphibians (slope ± 95% CI = 0.21 ± 0.14, $F_{[1,28]} = 8.1$, $r^2 = 0.22$, $P < 0.01$). Although amphibian's upper thermal limits do not vary strongly with latitude ($P = 0.9$), their lower thermal limits exhibit a strong decrease (slope ± 95% CI = -0.22 ± 0.11, $F_{[1,28]} = 11.7$, $r^2 = 0.29$, $P < 0.01$). The stronger latitudinal variation in lower thermal limits for amphibians may be due to their thermal physiology tending to be more evolutionarily labile than that of lizards (Navas, 2002).

The thermal tolerance of endothermic organisms has received less attention, as distributions may be constrained by the energetic requirements of thermoregulation more severely than by thermal tolerance, but limited evidence for inter- and intra-specific geographic gradients in thermal tolerances exists (reviewed in Garland & Adolph, 1991). Most thermal tolerance data for endotherms represent the limits of the thermoneutral zone rather than lethal limits (Monahan, 2009) and data on both lower and upper limits are available for very few species. Although we did not find a straightforward shift in the breadth of the thermoneutral zone for select birds and mammals, the zone can extend to very cold temperatures at high latitudes (Fig. 2). We note that across species, temperate endotherms tend to have a broader thermoneutral zone than those in the tropics (Scholander *et al.*, 1950). Predictable geographic gradients in

thermal tolerance, which have been well-documented for ectotherms but less so for endotherms, provide insight into thermal niche breadth and sensitivity to climate change (Deutsch *et al.*, 2008).

Seasonal patterns of energy use and activity time

We calculate potential activity times and metabolic rates for an idealized thermoconforming ectothermic lizard and endothermic non-migratory bird, both diurnal and of size 10 g, to explore the influences of temperature and seasonality across latitude and subsequently across global geographic space using gridded temperature data at 3-h intervals (Appendix S1; Déqué *et al.*, 1994). We repeat the analysis for 50-g organisms (Fig. S2).

For activity time calculations, we assume that an endotherm can only be active during daylight hours when environmental temperatures fall within the mean minimum ($T_L = -18.0$ °C) and maximum ($T_{UL} = 42.8$ °C) lethal limits of the 12 birds compiled in Monahan (2009). The minimum corresponds to the non-breeding season, while the maximum corresponds to the breeding season. We do not account for latitudinal variation in thermal tolerance due to our limited data. We assume that the ectotherm can only be active during daylight hours when environmental temperatures (thus assuming no behavioural thermoregulation) fall within their critical thermal limits. We estimate the critical thermal minima ($CT_{min} = 9.6$, 4.7 °C) and maxima ($CT_{max} = 40.8$, 45.0 °C) for the low- and high-latitude sites, respectively, using the latitudinal data from Fig. 2. These thermal constraints on activity are broader than those characteristic for lizard species (lizards are generally not active over their entire thermal tolerance range), but this should not bias our latitudinal comparison because activity limits are a relatively constant distance from critical thermal limits across lizards (Huey, 1982).

Figure 3 A comparison of the proportional time available for activity (top) and metabolic rate (W, bottom) for idealized endothermic (circles) and ectothermic (triangles) vertebrates across seasons. The metrics are calculated using hourly temperature data from weather stations located in Chilpancingo, Guerrero, Mexico (17.55° N, left) and Grand Rapids, Manitoba, Canada (53.18° N, right). Metabolic rate calculations account for environmental temperature dependence; activity time calculations additionally account for variation in usable daylight. Metabolic rate calculations reflect basal metabolic rate and account for environmental temperature dependence; activity time calculations additionally account for variation in usable daylight.
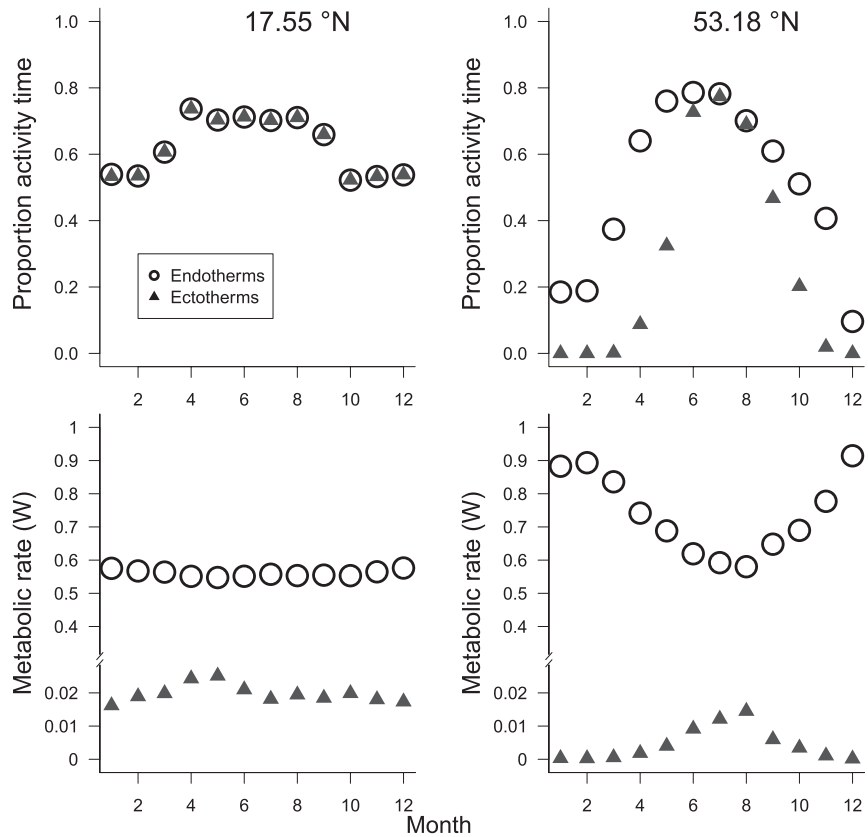
We model a thermoconforming ectotherm to highlight the distinction between ectotherms and endotherms. Many ectotherms effectively behaviourally thermoregulate, which would reduce the activity time differences between the two groups. We do not model the array of different, intermediate thermoregulatory strategies to avoid the need for species-specific assumptions (such as reflectivity and basking behaviour) and unavailable radiation data for implementing biophysical models. Our analysis provides a baseline against which to evaluate the effects of processes like behavioural thermoregulation. We acknowledge that variation between species and individuals as well as latitudinal and seasonal gradients in solar radiation may modify our results. Although biophysical models accounting for the variation in radiation (Kearney *et al.*, 2009) suggest the importance of the availability of shade for preventing overheating and enabling activity, these models rely on coarse calculations of radiation across latitude and estimates of shade based on remotely sensed vegetation indices. Such generalizations are not appropriate for particular weather stations, so we chose to model a thermoconforming ectotherm. We acknowledge this limitation and highlight the need for more detailed work on well-studied species to critically complement the broad overview attempted here.

For basal and resting metabolic rate (*MR*, W) for our idealized bird and lizard, respectively, we used the following equations for body temperature (*T*, °C) and body mass (*M*, g) dependence from Gillooly *et al.* (2001):

$$MR_{endotherm} = \exp[-9100/(T+273)+29.49]M^{0.75}/60$$

and

$$MR_{ectotherm} = \exp[-8700/(T+273)+26.85]M^{0.75}/60.$$

We use data compiled in Root (1988) to estimate the metabolic cost of thermoregulation according to the Scholander–Irving model: $COND(T_{crit} - T)$, where *COND* is the thermal conductance (the metabolic cost for raising the temperature when below T_{crit} by 1 °C; $COND = 2.3 \times 10^{-3}$ W °C^{-1}). We assume T_{crit} = 24.6 °C (mean of endotherm CT_{min} data in Fig. 2) and calculate the basal metabolic rate assuming body temperature equals the thermal optimum of 40.3 °C (mean across North American bird species from Root 1988). We note that basal metabolic rates tend to be strongly positively associated with field metabolic rates and show highly similar body size dependence (Koteja, 1991; Degen & Kam, 1995; Nagy, 2005). Thus the patterns explored here should represent a good first-order approximation of basic variation in energy use. We find that at the lower-latitude site, both the diurnal ectotherm and endotherm are able to be active throughout the day (Fig. 3). At the higher-latitude site, both organisms exhibit seasonal variation in activity time and the ectotherm's activity is largely restricted to the warm summer months (Fig. 3). We note that few vertebrate ectotherms and no lizards occur at such high latitudes and those that do are able to persist through dormancy. Neither organism
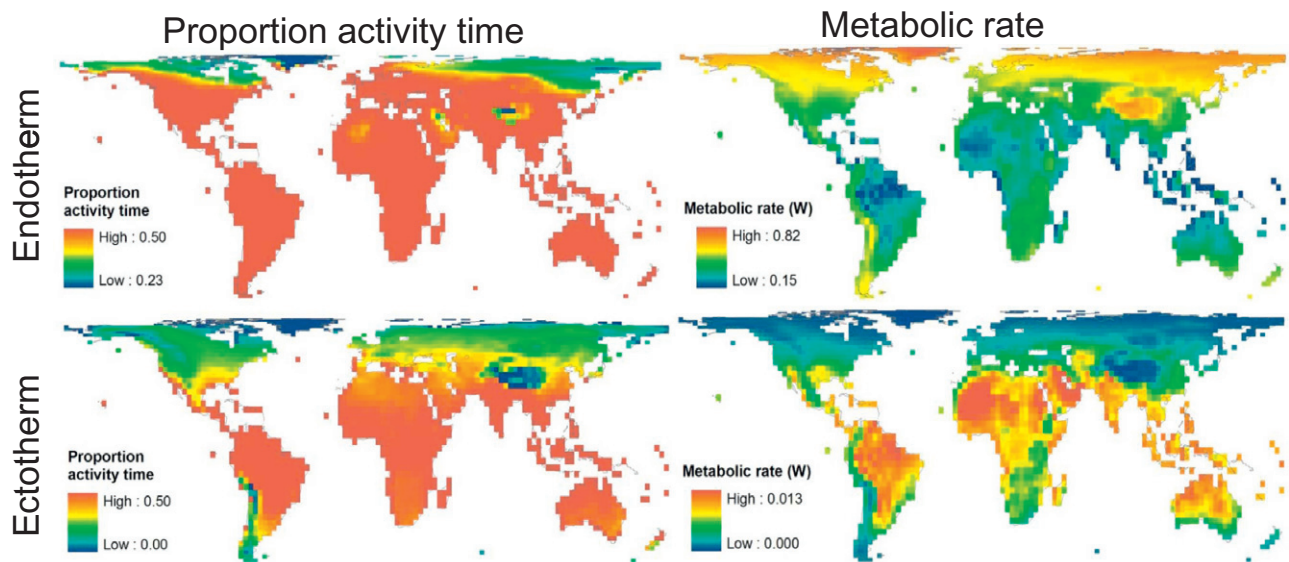
Proportion activity time

Metabolic rate

Figure 4 Annual average daily activity time (proportion) and daily metabolic rate for an idealized endotherm and ectotherm, calculated using 3-h interval temperature and local daylight estimates. Patterns in metabolic rate (or energy needs) are a function of spatial gradients in temperature through the year. Patterns in activity times reflect gradients in day length and suitable temperatures for activity. Note different colour scales.

exhibits much seasonal variation in metabolic rate at the lower-latitude sites. However, the endotherm exhibits substantial metabolic costs for thermoregulation in the winter at the higher-latitude site. The annual metabolic rate for the endotherm thus increases with increasing latitude. The ectotherm's metabolic rate increases slightly in the warm summer months and at low latitudes, but this seasonal trend is small compared with the seasonal trends in activity time for the ectotherm and metabolic rates for the endotherm.

This simple analysis illustrates how temperature may differentially constrain the latitudinal distributions of endotherms and ectotherms via energetics (Fig. 4; see Kearney *et al.*, 2009, for a more detailed analysis for ectotherms). At high latitudes, ectotherms tend to be limited by activity time as several months of intense activity in the summer are generally insufficient for persistence throughout the year despite low metabolic demands. In contrast, the geographic patterns of activity of endotherms show only slight geographic variation. Endotherms instead tend to be limited by the high metabolic demands of thermoregulation at mid to high latitudes which can be difficult to offset despite continuous potential activity. Some endotherms have evolved hibernation and migration to avoid these high metabolic expenditures. However, some endotherms have likewise done so to avoid periods with low potential activity times or resources (McNab, 2002).

ECOLOGICAL CONSEQUENCES OF PHYSIOLOGY

Distributions

Research examining the mechanistic basis of species distributions is accelerating (Angilletta, 2009; Kingsolver, 2009). Mecha-nistic range models (which describe physiological, energetic and demographic constraints on species ranges) can be informative in inferring how the environment sets range limits (Kearney & Porter, 2009; Buckley *et al.*, 2010). Biophysical models compute the energy budget of an organism to estimate metrics such as activity time or discretionary energy and can thus be used to assess how environmental conditions differentially influence ectotherms and endotherms. While low temperatures sharply reduce the activity times and thus the distributions of vertebrate ectotherms (Kearney & Porter, 2009; Buckley *et al.*, 2010), they increase the energetic expenditures of vertebrate endotherms (Porter *et al.*, 2002). In a classic demonstration of energetic constraints on distributions, Root (1988) found that the northern range limits of numerous bird species corresponded to an isotherm where the metabolic rate required was *c.* 2.5 times the basal metabolic rate (Repasky, 1991; but see Canterbury, 2002). For ectotherms, comparing estimates of potential activity time from biophysical models with observed distributions suggests that the thermal dependence of activity is a strong constraint on distributions (Kearney & Porter, 2009; Buckley *et al.*, 2010).

Mountains, with their drastic climatic changes over small distances, also highlight the implications of ectotherm versus endotherm physiology for distributions. Janzen (1967) proposed that the more constant environmental conditions in the tropics would lead to the evolution of greater thermal specialization of tropical organisms. Mountain passes would thus be physiologically 'higher' in the tropics (Janzen, 1967; Ghalambor *et al.*, 2004). This thermal specialization is expected to be more pronounced for ectotherms due to the thermal dependence of their activity. McCain (2009) used data from elevation gradients to test Janzen's key prediction: that the elevational range sizes of organisms on mountains increase with increasing latitude.

Although elevational range size increased with increasing latitudes for all ectothermic taxa examined, the only endothermic group to show a strong increase in range size was bats (potentially due to thermoregulatory tradeoffs to enable flight). Overall, there is strong evidence that ectotherm distributions tend to be strongly constrained by activity time. For endotherm distributions in cold environments, metabolic costs may play an important role (Figs 3 & 4).

Abundance

As ectotherms have low energy requirements (Bennett & Nagy, 1977; Pough, 1980), we expect that coarse estimates of overall energy availability (e.g. NPP) may have a limited influence on ectotherm abundance relative to that of temperature. Specifically, we expect that the total amount of energy utilized by ectotherms will be more strongly influenced by thermal constraints on resource acquisition and assimilation than by resource availability (Diaz, 1997). However, where the environment is sufficiently warm for activity, thermoregulation toward preferred temperatures reduces the influence of environmental temperatures on metabolic rates and performance (Huey et al., 2003). The cost of behavioural thermoregulation can be substantial, but these costs are scarcely quantified despite a long-standing cost–benefit model of thermoregulation (Huey & Slatkin, 1976; see also Angilletta, 2009). In contrast, energy availability is likely to have a greater influence on endotherms, which are able to maintain optimal body temperatures if sufficient resources exist to meet their high metabolic demands in cold environments (Wieser, 1985).

To the extent that abundance mirrors patterns in energy availability, the pattern should be stronger at the community level, summing over all of the species that collectively face that constraint, than at the population level. Nevertheless, population-level patterns have been more thoroughly examined due to the types of data most commonly available. Energetic constraints on both endotherm and ectotherm abundance are evidenced by the decrease in population density with increasing body mass, since larger organisms have greater energetic needs (reviewed by Blackburn & Gaston, 1999). Populations have been termed energy equivalent because density decreases at approximately the same rate as metabolic rates increase, resulting in equal energy use among populations. Energetic equivalence has been documented for groups including mammals (Damuth, 1987), birds (Meehan et al., 2004) and lizards (Buckley et al., 2008). Energetic use in ectotherms is expected to increase with environmental temperature in the absence of major behavioural thermoregulation, while energetic use for endotherms is expected to be independent of temperature within their thermoneutral zone. Allen et al. (2002) found that mass-corrected population densities were inversely related to temperature for ectotherms but not endotherms as predicted. However, using a larger dataset of lizard population densities, Buckley et al. (2008) showed that population energetic equivalence did not extend to temperature. Meehan et al. (2004) demonstrated that total bird community abundance decreases in low-temperature environments where the birds must expend more energy to raise body temperatures into their thermoneutral zone. The influence of temperature on abundance may be buffered in ectotherms by thermoregulation but is acute in endotherms due to their energetic costs for thermoregulation.

In a comparison of density–body size relationships across taxa, Currie & Fritz (1993) found that the relationships for vertebrate ectotherms and endotherms had similar slopes but that ectotherms were nearly three orders of magnitude more abundant than endotherms. They observed little influence of productivity on population densities for either group. Community bird abundance has been found to increase with increasing energy availability in several studies (Hurlbert, 2004; Meehan et al., 2004). Buckley et al. (2008) observed a relatively weak increase in lizard population density with increasing productivity. Obtaining relevant measures of energy availability over geographic scales is notoriously difficult (reviewed by Evans et al., 2005), and may contribute to the heterogeneity of results. Yet, overall, observations support the prediction that the abundance of endotherms is jointly limited by temperature and energy availability whereas thermal constraints tend to dominate for ectotherms.

Diversity: species richness and turnover

Many hypotheses have been put forward to explain geographic patterns of species richness (Rohde, 1992; reviewed in Mittelbach et al., 2007), and although they invoke a variety of mechanisms, all mechanisms ultimately must explain differential rates of origination, extinction or immigration over geographical gradients. Some of these hypotheses, particularly those based on temperature averages or variability, are expected to operate differently on endothermic versus ectothermic groups. As mentioned above, Janzen (1967) thought that climatic variability might explain latitudinal variation in thermal niche breadths, and others (Stevens, 1989) have subsequently argued that such variation could ultimately explain latitudinal richness gradients. In addition, some researchers have proposed that rates of molecular evolution, microevolution and even speciation increase with increasing environmental temperature in ectothermic groups (Rohde, 1992) and could drive latitudinal gradients. This may be due to the greater levels of mutagenesis ectotherms are exposed to in warmer conditions, but ecological and co-evolutionary processes may play an additional role (Gillman et al., 2009). Wiens (2007) identified an increase in diversification rates with decreasing latitude in some amphibians. One analysis suggests faster speciation rates at high latitudes in mammals and birds but no latitudinal trend in diversification rates (Weir & Schluter, 2007). Separate evidence points to increased rates of mammalian microevolution in warmer climates (Gillman et al., 2009).

A third richness hypothesis that might lead to stronger latitudinal gradients for ectotherms than endotherms is phylogenetic niche conservatism (Wiens et al., 2010). For ectotherms in particular, molecular and biochemical constraints on the evolution of thermal performance curves coupled with the geo-

graphic origin of clades may influence patterns of richness and species turnover. For example, the latitudinal richness gradient for several major frog clades has been attributed to their tropical origin and conservatism of physiological constraints (Wiens *et al.*, 2009). Endotherms may be better able to escape thermal limits on distributions if sufficient energetic resources exist for thermoregulation.

All four classes of terrestrial vertebrates show broadly similar global patterns of species richness (Grenyer *et al.*, 2006; Lamoreux *et al.*, 2006), with values greatest in tropical areas and decreasing toward the poles. In a large meta-analysis of pre-existing studies, Hillebrand (2004) found no difference in the slope of the latitudinal gradient between endotherms and ectotherms. More detailed examinations of these richness patterns do identify important differences among these vertebrate groups, however. Reptile and amphibian richness appears to be more strongly related to temperature and temperature-related variables (e.g. potential evapotranspiration) compared with mammal and bird richness (Pianka, 1966; Schall & Pianka, 1978; Currie 1991; Fig. 5). Grenyer *et al.* (2006) found greater congruence in bird and mammal global richness patterns than between amphibians and either endothermic group. Belmaker & Jetz (2011) confirmed substantial differences between amphibians and birds or mammals in the strengths and slopes of environment–richness associations. We conclude that despite fairly high congruence at the global scale, the richness of vertebrate ectotherm communities appears to be more strongly related to temperature than endotherm richness.

One hypothesized mechanism to account for the link between energy availability and species richness is species–energy theory, which contends that energy availability constrains population size and that more species can persist in a community with more individuals as larger population sizes lead to reduced extinction risk (Wright, 1983). Datasets that span broad spatial gradients and that include information on community-level abundance are uncommon, making tests of these relationships rare over large scales. Buckley & Jetz (2010) found that neither lizard abundance nor species richness vary predictably with a coarse estimate of resource availability (NPP) (Fig. 5). In birds, total abundance increases with NPP or surrogates thereof, and species richness tends to increase with abundance (Fig. 5; Hurlbert, 2004; Pautasso & Gaston, 2005). However, as with lizards, bird communities with more species tend to have abundances distributed more evenly, as evidenced by the divergent rarefaction curves in Fig. 5. Thus, even in birds, a purely individuals-based explanation of species richness remains inadequate (Currie *et al.*, 2004; Hurlbert, 2004; Hurlbert & Jetz, 2010).

Of course, important biological differences exist among birds, mammals, reptiles and amphibians besides thermoregulatory behaviour, and consequently it is difficult to attribute differences in richness patterns to any particular cause with certainty. For example, amphibians clearly differ from the other groups in their water requirements, and are consequently most diverse in places that are wet as well as warm (Buckley & Jetz, 2007). In contrast, some of the most species-rich regions for reptiles occur in areas that are warm and dry (Schall & Pianka, 1978; Currie,

1991). Indeed, reptiles appear to have the strongest relationship with temperature or solar radiation among the vertebrate and invertebrate groups that have been examined thus far (Whittaker *et al.*, 2007), and they exhibit the most spatially disparate richness pattern of the four terrestrial vertebrate classes (Lamoreux *et al.*, 2006). Birds, on the other hand, are able to escape seasonally harsh environments and take advantage of seasonal resource pulses via migration (Hurlbert & Haskell, 2003).

Ectotherms are expected to have a higher rate of spatial turnover in species composition compared with endotherms due to their smaller range sizes (Soininen *et al.*, 2007), which are generally thought to result from their smaller body sizes and their being sharply constrained by thermal tolerances. Broad-scale analyses of species turnover have been much less common than broad-scale analyses of species richness (but see Gaston *et al.*, 2007). The first such study to compare turnover between vertebrate endotherms (birds and mammals) and ectotherms (amphibians) found that although areas of high turnover are congruent in the New World, areas of low turnover are not (McKnight *et al.*, 2007). Congruence was highest between birds and amphibians, with each group exhibiting similar congruence with mammals. Species turnover across space does generally occur faster for ectotherms than endotherms (Buckley & Jetz, 2008; Qian, 2009).

IMPLICATIONS OF ECTOTHERMY AND ENDOTHERMY IN THE FACE OF CLIMATE CHANGE

Interfacing our knowledge of thermal physiology with current and projected future climates enables us to address the potential impacts of climate change, and increased temperatures in particular, on organisms. We have highlighted the contrasting effects of increased temperatures on the potential activity times and energy needs of ectotherms and endotherms, two direct outcomes of their different physiology that critically affect their broad-scale ecology. Climate change may increase the potential activity time of temperate ectotherm species; in the tropics it may reduce potential activity time during the reproductive season while also increasing maintenance costs (Huey *et al.*, 2009; Kearney *et al.*, 2009; Dillon *et al.*, 2010). The most severe consequences for ectotherms may arise from high temperatures causing overheating or unsustainably short potential activity times due to heat avoidance (Kearney *et al.*, 2009; Sinervo *et al.*, 2010). Latitudinal gradients in thermal breadth suggest greater biological impacts in the tropics than in temperate zones (Deutsch *et al.*, 2008; Huey *et al.*, 2009).

A recent model of thermal limits on activity time, which was validated for Mexican lizards and applied globally, suggests that reduced activity time due to climate change may result in substantial extinctions (Sinervo *et al.*, 2010). As yet, similar field demonstrations of increased heat *per se* causing widespread die-offs or fatally limiting foraging activity of populations are not available for endotherms. Low-latitude endotherms tend to have higher body and critical temperatures than ectotherms and may thus be more buffered in their activity and energy requirements.
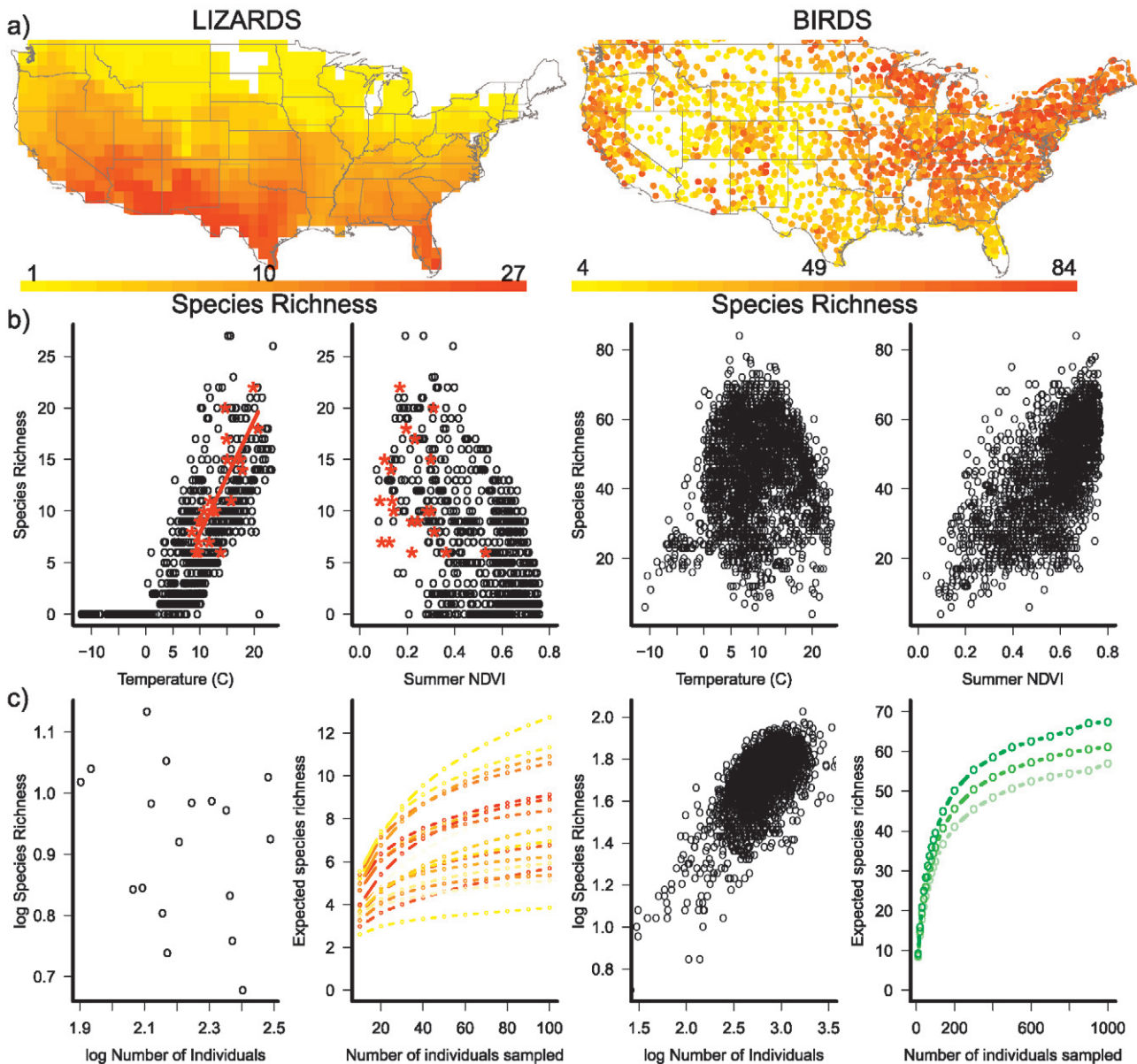
Figure 5 A comparison of broad-scale ecological patterns for lizards (left) and birds (right). We depict (a) spatial patterns of species richness and (b) correlate species richness to temperature and summer NDVI (normalized difference vegetation index). In (c), we present the relationship between the number of individuals and the number of species and rarefaction curves (warmer red colours indicate higher temperatures and darker green colours depict higher NDVI). All bird data are from analyses of the North American Breeding Bird Survey by Hurlbert (2004). The lizard data are from species range maps (a, and circles in b) and from the National Park Service Inventory and Monitoring initiative (red stars in b and all data in c) (Buckley & Jetz, 2010). See Appendix S1 for additional methods.

Nevertheless, short-term population declines in response to extreme heat events have been demonstrated (e.g. in European birds) and have been linked to indirect estimates of thermal tolerance (Jiguet *et al.*, 2006).

A particular concern in endotherm arid specialists, which lack easy access to water, is increasing evaporative water loss in the face of increased intensity and frequency of heat events. Projections for hot days in example desert locations suggest that water needs by 2080 could increase by 95% for small-bodied (5 g) and 65% for medium-bodied (50 g) birds, leading to dramatically

reduced survival times (McKechnie & Wolf, 2009). At least in arid environments, water loss rather than overheating is likely to be the main constraint on endotherm activity and survival in a future warmer world.

There is a growing focus on using organismal physiology to predict the responses of vertebrate ectotherms to climate change, ranging from approaches that are specific and complex (Kearney & Porter, 2009; Buckley *et al.*, 2010) to those that generalize physiological constraints (Deutsch *et al.*, 2008; Kearney *et al.*, 2009; Sinervo *et al.*, 2010). For endotherms, biophysical

models for a few species (Porter *et al.*, 2002) and some broader generalizations in the context of climate change (McKechnie & Wolf, 2009; Monahan, 2009) have been developed, but predictive models have lagged due to the more complex link between environmental temperatures and fitness in endotherms (La Sorte & Jetz, 2010). Yet the stark ecophysiological contrast between ectotherms and endotherms already points to the importance of considering physiology in predicting species responses to climate change.

CONCLUSIONS

New information on species physiological traits and their geographic distribution, increasingly detailed global environmental data layers, and obvious research challenges in the face of rapid climate change have reinvigorated a broad-scale perspective on physiological ecology (Chown *et al.*, 2004; Gaston *et al.*, 2009). Here we have highlighted how the key physiological differences between ectotherms and endotherms result in highly disparate geographic gradients of constraints on behaviour and ecology. The dichotomy offers simple, yet powerful, first-order expectations and predictions about the distribution, abundance and diversity of the two groups. In particular, the differential effects of temperature on activity times and energy needs as well as the different latitudinal patterns of thermal niche breadth lead to distinct geographic gradients of environmental suitability. Although much remains to be learned about the historical biogeographic and evolutionary context of physiological constraints on the diversification of ectotherms and endotherms (but see Wiens *et al.*, 2007), the environmental constraints evaluated here offer a clear indication of what ultimately are macrophysiological, regional constraints on community structure (Ricklefs, 2007).

Extended knowledge about the broad-scale geography and ecology of species ecophysiological traits thus offers exciting new opportunities for scientific inference. To date, the limited availability of physiological data presents a surprisingly hard constraint. Even fundamental information such as critical temperatures has only been measured for a tiny proportion of vertebrate species yet is vital for parameterizing basic or applied macrophysiological models. As such, there is a dire need to measure and assemble additional physiological and trait data within and between species across broad spatial and temporal gradients. There is an additional need to investigate vital rates in the field and how they vary with temperature and resource availability. An understanding of how the differential physiology of ectotherms and endotherms leads to differential broad-scale patterns of distribution, abundance, diversity and community structure will be an important means of understanding and predicting the implications of global change for biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods (with additional details in Tables S1 and S2).
Appendix S2 Supplementary references.
Figure S1 Field metabolic rate as a function of net primary productivity.
Figure S2 Proportion activity time and metabolic rate for 50 g organisms.
Table S1 Georeferenced reptile field metabolic rate data.
Table S2 Endotherm thermal tolerance data.

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BIOSKETCHS

Lauren Buckley focuses on how an organism's biology influences its response to environmental change.

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