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RESEARCH ARTICLE

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A hierarchical approach to understanding physiological associations with climate

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Abstract

Aim: Our understanding of species' responses to climate depends on choosing the scale for the analysis. Processes driving physiological adaptation that occur at the small spatial scales most relevant to animals may be masked in correlations between organismal traits and broad-scale climatologies, but the extent to which this undermines our understanding of the macroevolution of physiological traits is unknown.

Location: Global.

Time period: Current.

Major taxa studied: Lizards.

Methods: We investigated relationships between physiological traits (water loss rate, standard and field metabolic rates, thermal preferences and critical thermal limits) and environmental conditions in 369 lizard species across sets of environmental predictors representing different processes across hierarchically nested spatial scales: macroclimate, microclimate and biophysical.

Results: We found that microclimatic and biophysical predictors had greater explanatory power than macroclimatic predictors for all traits except standard and field metabolic rates. Across spatial scales, standard metabolic rate was negatively related to maximum temperatures whereas field metabolic rate was positively related to minimum temperatures. Thermal preference and critical limits showed expected relationships with environmental temperature, but preferred temperature and critical thermal maxima were most strongly associated with soil water potential, as was evaporative water loss.

Main conclusions: The use of proximal environmental predictors, via the principles of microclimatic and biophysical modelling, can be more informative in comparative physiological analyses than the more traditional application of macroclimatic data. In our study it led us to new, testable hypotheses about the role of habitat structure mediated by soil moisture. New datasets and computational methods mean that proximal environmental predictors can be readily computed for any kind of organism and their application to comparative studies should improve our understanding of physiological evolution.

KEYWORDS
biophysical ecology, comparative physiology, ecophysiology, environment, lizards, microclimate

1 | INTRODUCTION

Macrophysiology seeks to understand the mechanisms underlying broad-scale variation in the physiology of organisms (Gaston et al., 2009). Macrophysiology has its roots in the early 20th century, but has only recently been established as a scientific discipline (Chown et al., 2004; Gaston et al., 2009). Despite the challenges that still need to be overcome (Chown & Gaston, 2016), macrophysiological approaches have provided significant contributions to the understanding of the ecology and distribution of species, as well as their responses to climate change (Chown & Gaston, 2008; Deutsch et al., 2020; Lancaster & Humphreys, 2020; Sunday et al., 2012, 2014).

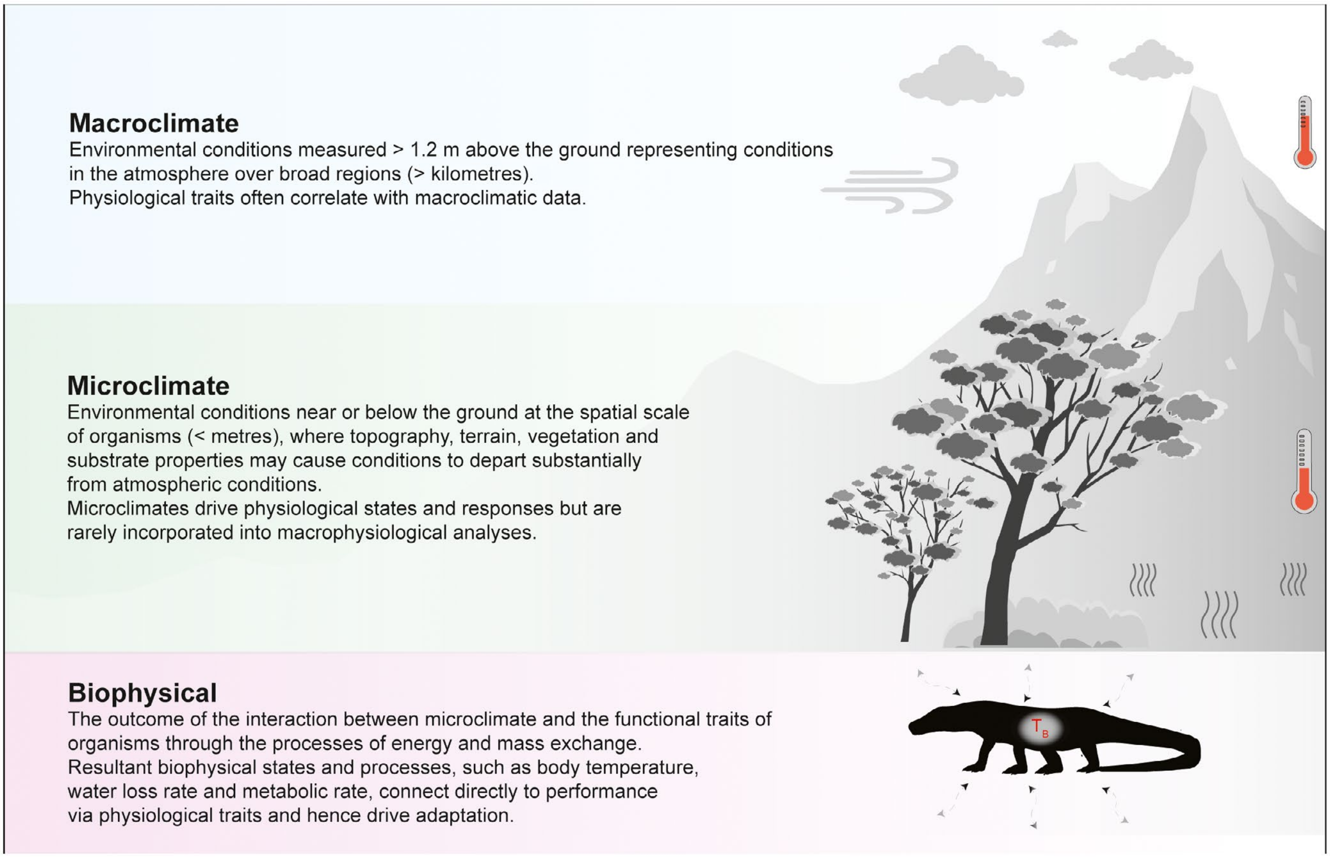
To date, most macrophysiological studies have been based on macroclimate data, that is, point or gridded data derived from weather stations representing general atmospheric conditions (e.g., Fick & Hijmans, 2017). These include studies of variation in water balance (Addo-Bediako et al., 2001; Cox & Cox, 2015; Kellermann, Loeschcke, et al., 2012; Titon & Gomes, 2015; Williams et al., 2012), metabolism (Deutsch et al., 2020; Dillon et al., 2010; Rezende et al., 2004; White et al., 2007; Withers et al., 2006), and thermal physiology (Addo-Bediako et al., 2000; Clusella-Trullas et al., 2011; Diamond et al., 2012; Lancaster & Humphreys, 2020). However, correlations between physiology and macroclimatic variables ultimately reflect the outcome of interactions between organisms and their microenvironments and biotic communities (Warne et al., 2019). Thus, the integration of interactions between physiology and environment at more proximal, organismal scales can greatly contribute to macrophysiology (Baudier et al., 2018; Chown & Gaston, 2016; Gouveia et al., 2013; Hodkinson, 2003).

Microclimates are environmental conditions at the spatial and temporal scale of organisms (usually < 1 m and < 1 hr) and can differ substantially from macroclimate (Klinges & Scheffers, 2020). At the microclimatic scale, conditions can be more extreme but organisms have access to an increased environmental heterogeneity (e.g., vegetation cover, shelter), which aids them to reduce exposure to environmental stresses (e.g., heat load and dehydration; Potter et al., 2013; Scheffers et al., 2014; Woods et al., 2015). Microclimate directly affects the ecological performance and survival of organisms, driving adaptive responses (Farallo et al., 2020; Kearney et al., 2018; Porter & Gates, 1969; Tracy, 1976). Ultimately, interactions between microclimates and organisms affect physiological responses such as body temperature, water loss and metabolic rates that in turn impact performance (Kearney et al., 2021). These consequences can be computed with the principles of biophysical ecology (Campbell & Norman, 1998; Gates, 1980; Kearney & Porter, 2020; Porter & Gates, 1969; Tracy, 1976).

Previous studies have provided evidence of microclimatic and organismal factors influencing physiological variation. For example, although in some cases thermal physiology correlates with precipitation (e.g., Clusella-Trullas et al., 2011), shade availability and microclimatic temperatures can also explain variation in thermal traits at local scales (Farallo et al., 2020; Huey et al., 2009; Kellermann, Overgaard, et al., 2012; Pintanel et al., 2019). Additionally, shelter availability (Kearney et al., 2018; Schwarzkopf & Alford, 1996), and organismal aspects such as body size and behaviour affect the water balance of ectotherms (Farallo et al., 2020; Gouveia et al., 2019; Pirtle et al., 2019), which is known to evolve in response to aridity (Cox & Cox, 2015). Finally, metabolic rates of ectotherms are not only related to air temperature, but also to microclimatic temperatures and food availability (Angilletta, 2001; Dupoué et al., 2017; Shah et al., 2021). Thus, a global analysis investigating these interactions of organisms with their environment at improved resolutions could lead to new, testable hypotheses for physiological variation.

The hierarchy from macroclimate to microclimate, to the biophysical effects on the organism, relates to physiology in complex ways (Figure 1). Quantifying this hierarchy for hundreds of species represents a sizeable task. But now, new analytical tools allow users to accurately estimate microclimatic and biophysical variables for ectotherms on a global scale at high spatial and temporal resolutions (Kearney et al., 2019; Kearney & Porter, 2020). Such approaches have previously uncovered novel patterns regarding species distributions and vulnerability to climate change (Nowakowski et al., 2018; Pinsky et al., 2019; Sunday et al., 2014). These approaches can now be applied to examine whether microclimatic and biophysical predictors can better explain macrophysiological variation than traditional methods that apply solely coarse climatic data.

Here we used a mechanistic modelling approach to understand whether the physiological variation of lizards can be better explained by proximal (i.e., microclimatic and biophysical) than distal (i.e., macroclimate) spatial scales. We derived a suite of relevant environmental variables at macroclimatic (gridded hourly reanalysis weather data) and microclimatic scales (macroclimatic data downscaled to a set of equivalent microclimatic conditions at high resolution) (Kearney et al., 2019). Moreover, using biophysical modelling (Kearney & Porter, 2020), we converted the microclimatic conditions into operative temperatures, metabolic rates, water loss rates and the potential for plant growth. Thus, we obtained a hierarchical set of covariates representing different scales: macroclimate (hourly gridded climatic data), to microclimate (downscaled climate data at 30-m resolution, 1 cm above the ground), to biophysical (actual responses of organisms). With a phylogenetically informed approach, we compared the strength and direction correlations of physiological traits and environmental/biophysical predictors across spatial scales. We hypothesized that proximal predictors can explain better



Macroclimate

Environmental conditions measured > 1.2 m above the ground representing conditions in the atmosphere over broad regions (> kilometres).

Physiological traits often correlate with macroclimatic data.

Microclimate

Environmental conditions near or below the ground at the spatial scale of organisms (< metres), where topography, terrain, vegetation and substrate properties may cause conditions to depart substantially from atmospheric conditions.

Microclimates drive physiological states and responses but are rarely incorporated into macrophysiological analyses.

Biophysical

The outcome of the interaction between microclimate and the functional traits of organisms through the processes of energy and mass exchange.

Resultant biophysical states and processes, such as body temperature, water loss rate and metabolic rate, connect directly to performance via physiological traits and hence drive adaptation.

FIGURE 1 Hierarchical relationship between climate and the physiology of organisms

the physiological variations of lizards than distal predictors. Hence, we predicted that variables extracted from microclimatic and biophysical scales would explain more physiological variation than those extracted from macroclimatic data. From this, we were able to consider the potential direct and indirect effects of climate on macrophysiological patterns, and ultimately, we proposed hypothesis to be tested through more focal studies.

2 | MATERIALS AND METHODS

2.1 | Physiological traits

We analysed six physiological traits related to water balance, metabolism and thermal physiology. For water balance, we considered the rate of evaporative water loss, which is the rate at which the animals lose water through the integument and respiration (Mautz, 1982). For metabolism, we considered standard/resting metabolic rate (SMR) as the metabolic rate under resting and fasting conditions. SMR is usually measured by indirect calorimetry (Lighton, 2008). In contrast, field metabolic rate (FMR) is the metabolic rate estimated in free-ranging animals, measured using doubly labelled water (Speakman, 1997). For thermal physiology, we chose the preferred temperature (T_{pref}), defined as the mean body temperature selected by ectotherms in thermal gradients in the laboratory, in the absence of biotic and abiotic constraints. T_{pref} has been associated with the optimum for whole physiological performance (Angilletta, 2009). We also considered the critical thermal limits, minimum (CT_{min}) and critical thermal maximum (CT_{max}), which indicate the body temperatures at which the animal loses its capacity for movement.

2.2 | Data collection

We gathered data from the literature, starting where possible from previously published compilations of evaporative water loss (EWL) (Cox & Cox, 2015; Mautz, 1982), T_{pref} (Clusella-Trullas et al., 2011) and CT limits (minimum and maximum; Bennett et al., 2018; Diele-Viegas et al., 2018), to which we applied our additional criteria for data selection (see below). We only considered data from studies of wild-caught animals that provided precise locality data (coordinates, location's name).

2.3 | General criteria for data selection

We selected data using the following criteria: (a) data were from adults, to eliminate ontogenetic effects on physiological measurements; (b) individuals were not subjected to acclimation treatments that lasted more than 3 weeks; (c) animals were wild-caught; (d) animals were not starved or exposed to chemical compounds; and (e) animals were fasted before the experiments.

Additionally, if more than one study reported data for the same species, we selected the one with a higher sample size (*n*). If a study reported data separately for males and females, we used the arithmetic mean of the two sexes. If a study reported data for different seasons we selected the data that matched the species' activity period. If a study reported the data graphically, or the location as a map image, we used a web-based tool to extract the data from those figures (WebPlotDigitizer 4.1; https://automeris.io/WebPlotDigitizer).

For all selected studies, we gathered the locality from which the animals were collected and the lizards' body masses. However, if the study did not report the latter information, we estimated body mass based on the snout–vent length as provided elsewhere (see Meiri, 2010; Meiri et al., 2013; for all the species returned in our search *c*. 35% had their body mass estimated). Finally, we included the species' taxonomy as reported by the primary literature, and afterwards we adjusted for the more recent synonyms following an online source, the Reptile Database (Uetz et al., 2018).

Although we considered only animals that were not acclimated, short-term thermal conditions may affect physiological traits (e.g., Andrews & Pough, 1985). Hence, we also recorded the thermal conditions under which the animals were maintained before the experiments (e.g., room temperature, basking opportunities). In most of the studies, the animals were maintained under variable thermal conditions or with basking opportunities, which likely minimizes acclimatory effects (e.g., for SMR, 74% of the species were maintained with variable thermal conditions and with basking opportunities). Additionally, many studies did not report detailed conditions under which the animals were kept (e.g., 63% of the species for T_{pref}). Hence, we were not able to determine the magnitude of acclimation effects and we did not include them as a factor in our analyses.

2.4 | Evaporative water loss

We used the dataset provided by Cox and Cox (2015) to select studies that measured evaporative water loss of lizards. In addition to our general criteria for data selection, we considered studies that quantified EWL following typical standard protocols (described in Cox & Cox, 2015). For each of the studies, we recorded the mass specific EWL (mg/g/hr) and the temperature at which the experiments were conducted. We then transformed these data to 'skin' resistance (hereafter resistance; s/cm) following Withers et al. (2000). We calculated the surface area of the animals using an empirical allometric function (Withers et al., 2000). The vapour density gradient was calculated from the reported relative humidity and temperature using the WETAIR function of NicheMapR (Kearney & Porter, 2020), assuming saturated air at the skin surface.

2.5 | Metabolic rate

When surveying the literature for metabolic rates, we started from prior compilations by Bennett and Dawson (1975) and Andrews and Pough (1985). Next, we searched online sources (Web of Science and Google Scholar) for studies published after 1985 using the words: "metabolism", "metabolic rate", "oxygen consumption", "energetics", "lizards", "reptiles", or "squamate". From the studies returned, we selected those that measured standard and resting mass-specific metabolic rates of oxygen consumption (μl O_2/g/hr). As in Andrews and Pough (1985), standard conditions were defined when metabolism was quantified for fasting animals during periods of inactivity (e.g., nighttime for diurnal species). Resting was defined when the metabolic rate was measured during periods of activity (e.g., daytime for diurnal species). We recorded the reported values for metabolic rate and the body mass of the animals.

Finally, we also recorded the temperatures at which the metabolic rates were measured. Importantly, we chose the mean metabolic rate at the test-temperature closest to the mean body temperature on the animals in the field (Meiri et al., 2013) or the preferred body temperature. In cases where we were not able to find any of this information (e.g., *Oligosoma macgregori*; 11 species in total) we chose the test-temperature used for the closest relative.

2.6 | Field metabolic rate

We searched in the literature for studies that evaluated the energetic expenditure of free-living lizards, using the following keywords in the same online sources listed above: "field metabolic rate", "lizards", "reptiles", "energetic expenditure", "activity metabolism", "free-range metabolism", "field metabolism" and extracted FMR data as rates of CO_2 production measured by the doubly labelled water technique (ml/g/day). For those studies considering more than one season, we selected the one corresponding to the species' most active season (Meiri et al., 2013) or, for those species active year-round, we selected the season with the highest sample size.

2.7 | Thermal preference

We collected thermal preference data starting from the dataset compiled by Clusella-Trullas et al. (2011), which we updated through a literature search for studies published after 2011. We searched online sources for the following words: "thermal preference", "preferred temperature", "thermoregulatory behavior", "selected temperature", "thermal choice", "lizards", "reptiles", "squamate". We selected studies that followed standard protocols for T_{pref} determination (Clusella-Trullas et al., 2011); studies in which data were collected during times of activity (daytime for diurnal and nighttime for nocturnal); studies that used the thermal gradient relevant for the thermal ecology of the species (i.e., photothermal for heliothermic and thigmothermal for thigmothermic species); and, we selected the arithmetic mean over median T_{pref}. In one study, individuals were short-term acclimated (fewer than 14 days) before the experiments, we then selected the treatments with highest sample sizes (Corn, 1971).

2.8 | Critical thermal limits

We collected the critical thermal maximum and minimum from the datasets published by Bennett et al. (2018) and Diele-Viegas et al. (2018). From these datasets, we selected studies following standard protocols (Lutterschimdt & Hutchinson, 1997) and that quantified either the loss of righting responses or the onset of spasms as the endpoint. We then recorded the critical thermal limits (maximum or minimum), and the body mass of the species. In three studies, species were short-term acclimated (fewer than 14 days) before the experiments, we then selected the treatments with highest sample sizes (Corn, 1971; Huang et al., 2006; Huang & Tu, 2008). We also recorded the ramping rate (cooling or heating rate the animals were exposed during the experiments) and the temperatures at which the experiments started. However, for the great majority of the studies, neither starting temperature (20% and 23% of the species for CT_{min} and CT_{max}, respectively) nor the ramping rates (28% and 32% of the species for CT_{min} and CT_{max}, respectively) were commonly reported. Hence, we did not incorporate these effects into our analyses.

2.9 | Microclimatic and biophysical modelling

For each species and site, we used the NicheMapR package (Kearney & Porter, 2017, 2020) to transform macroclimatic data into microclimatic and 'biophysical' variables. (NicheMapR R package, Kearney & Porter, 2020). First, we extracted macroclimate data from the National Centers for Environmental Predictions (NCEP) dataset of 6-hourly meteorological variables at 200 × 200 km resolution using the RNCEP package for the R environment (Kemp et al., 2012). Second, to compute microclimate, we used the function *micro_ncep* of NicheMapR that integrates NCEP data and terrain/shade adjustments. The function *micro_ncep* is integrated with the package microclima (Maclean et al., 2019), which models the mesoclimatic processes that govern fine-scale variation in temperature, arising from variation in radiation, wind speed, altitude, surface albedo, cold air drainage, as well topographic and vegetation effects on wind speed and radiation. As a result, the *micro_ncep* function generates time series of microclimatic air temperature, humidity, wind speed, soil temperature and soil water potential, as well as solar and infrared radiation conditions. The function accounts for topographic effects (hill shade via horizon angles as well as slope and aspect) in association with the package elevatr, which is connected to the Amazon Web Services Open Data. We set a 30-m resolution for the terrain corrections extracted from the digital elevation data. We simulated unshaded microclimatic conditions at 1 cm above the ground with locally estimated slope and aspect, with the soil moisture routine turned on (Kearney & Maino, 2018) and with soil properties drawn from the SoilGrids dataset (Hengl et al., 2017). Simulations were run for 5 years (2014 to 2018) to allow sufficient spin-up time for soil moisture calculations (predictions from 2014 were excluded). Finally, we computed the heat and water budget of a dry-skinned ectotherm at 1 cm above the ground using the microclimatic predictions as input from which we obtained 'biophysical' predictors as described below.

In addition, we applied two more approaches using different forcing data to consider whether the results are sensitive to the dataset used as input. The first also uses the NCEP data, but with a coarser resolution for the digital elevation map (500 m). The function *micro_ncep* was also used as described above, but in this case, we set the parameters of the microclimatic modelling to not include high resolution terrain data (*slope* = 0, *aspect* = 0, *soilgrids* = 0, *dem.res* = 0). The second approach (function *micro_global* in NicheMapR) is an implementation of the long-term average monthly climatology of New et al. (2002). We used all default settings to downscale the climatologies, simulating unshaded conditions on flat ground, with the soil moisture routine (Kearney & Maino, 2018) turned on. Next, we describe the variables computed through the approach using the function *micro_ncep* with high resolution terrain corrections, but the same procedures can be used to extract the data using the two other approaches.

2.10 | Macroclimatic data

The *micro_ncep* function extracts the NCEP macroclimatic data via functions from the microclima package, which disaggregates the raw NCEP output to hourly estimates (Kearney et al., 2019). Specifically, we obtained the mean, minimum and maximum values for 1.2 m ('surface') air temperature (°C). In order to avoid extremes of temperatures, minimum and maximum were extracted respectively as the 5th and 95th quantiles of the data. We computed the mean of vapour pressure deficit (Pa) as the difference between the saturated 1.2 m air water vapour pressure, calculated using the VAPPRS function, and the vapour pressure, calculated using the WETAIR function of NicheMapR based on the air temperature and relative humidity extracted from the NCEP datasets. Finally, we obtained the mean monthly rainfall (mm) as an index of water availability.

2.11 | Microclimatic data

From the 'metout' output table of *micro_ncep* we also extracted the air temperature and humidity conditions experienced by the lizards in the open at 1 cm above the ground (the microclimate model downscales the 1.2 m values to a user-specified height). Then, we computed the mean, minimum and maximum 1 cm air temperature (°C) and we used the 1 cm relative humidity to compute the air water vapour pressure deficit (Pa). In order to avoid extremes of temperatures, minimum and maximum were extracted respectively as the

5th and 95th quantiles of the data. As an indicator of water availability at microclimatic scales, and to account of the effects of water on plant growth, we calculated the mean of the soil water potential at 2.5 cm depth. The soil water potential generated by our simulations integrates aspects of rainfall, humidity, radiation and temperature (Kearney & Maino, 2018) that can be related to moisture requirements for plant growth and biomass (Boyer, 1968).

2.12 | Biophysical modelling

We modelled the heat and water exchange of a lizard at steady-state, without thermoregulatory behaviour, using the *ectotherm* function in NicheMapR (Kearney & Porter, 2020). All organismal parameters were set to default values, other than body mass. In the absence of detailed data on body temperature thresholds for thermoregulatory behaviour (e.g., shade seeking, burrowing, climbing) and on levels of shade and heights of perches available to and used by the lizards, we simulated them to remain in the open in full sun at a height of 1 cm. Some species (< 10%) in our dataset are arboreal and they may experience different conditions on trees than on the ground (Algar et al., 2018; Barlett & Gates, 1967). If the lizard is high in shaded vegetation, these conditions may approach those of our macroclimatic variables, which represent free atmosphere (> 1.2 m) conditions in the shade. However, they may also approach conditions near the ground if they are basking on sun-exposed trunks (Barlett & Gates, 1967). Our analysis implicitly assumes that arboreal species are basking on sunlit trunks.

We then computed the mean, minimum and maximum predicted body temperatures (i.e., operative temperatures, T_e; °C) of the ectotherm as an indicator of the thermal variation experienced by the animal, the total evaporative water loss as an indicator of hydric stress, and their metabolic rate. To avoid extremes, minimum and maximum were extracted respectively as the 5th and 95th quantiles of the data. In addition, as a biophysical proxy for plant growth we computed the number of days unsuitable for vegetation growth (days with soil water potential below the threshold at which the vegetation wilts) using the function *plantgro*. This function computed the plant water content given threshold values of soil water potential at which the permanent wilting point occurs (assumed here to be −1,500 kpa, a generic agricultural threshold; Wiecheteck et al., 2020), using the soil properties from the microclimatic modelling as input.

2.13 | Phylogenetic analyses

We applied phylogenetic procedures by pruning the most complete phylogenetic tree available for squamate reptiles (Tonini et al., 2016) using the package geiger, which matched the species both in the tree and in our datasets (function *treedata*). Even though this phylogeny contains information for more than 9,000 species, some of the species in our datasets had no phylogenetic estimation and were thus dropped from the pruned tree (Supporting Information Table S7).

We performed phylogenetic comparative methods using the packages nmle, phytools and caper. We applied phylogenetic general least squares (PGLS), which fit a generalized least squares model adjusting the phylogenetic dependence by incorporating the expected variance. We set the models using a maximum likelihood approach, which provides the Pagel's λ as an estimate of phylogenetic signal (Mundry, 2014). We verified each model by applying graphic diagnosis (Q-Q plot, normality and distribution of residuals; Mundry, 2014).

At each of the scales, we first considered multi-predictor models on each physiological trait. At macroclimate scales (i.e., variables measured at a reference height of 1.2 m), our initial model included as predictors mean, minimum and maximum air temperatures, mean vapour pressure deficit, and rainfall as predictors, and the phycological traits (Resistance, SMR, FMR, T_{pref}, CT_{min}, or CT_{max}) as responses. At microclimate scales (i.e., variables measured at a height of 1 cm), the initial models included mean, minimum, and maximum air temperatures, mean vapour pressure deficit, mean soil water potential (2.5 cm depth; note that for this variable we used the absolute values, so a negative slope with water soil potential means the dependent variable is decreasing as the soil environment becomes more desiccating) as predictors, and the physiological traits as responses. Finally, at the biophysical scale, the predictors were mean, minimum and maximum operative temperatures, metabolic rate, water loss, and wilting point, and the physiological traits were used as responses. Hence, for each scale, we had six models (one for each physiological trait) incorporating initially the predictors listed above. In all the models, mean air temperatures (and operative temperatures at biophysical scales) showed high collinearity and thus this variable was excluded from the analyses. We also tested for interactions between the variables in the models. Next, we used the Akaike information criterion (AIC) values to select the models with the highest explanatory power (Quinn & Keough, 2002). We then selected the best model following the AIC with small sample bias, AICc, using the package MuMIn. We ranked the models with the Akaike weight (w), the probability that a model has the best fit among those tested, that is, a model with w closer to 1 is the best model (Johnson & Omland, 2004). Finally, we used R^2 and F statistics to compare the models with better fit among the spatial scales (Johnson & Omland, 2004). We considered that the higher the R^2 (> 5%) the better the fit.

All the analyses were performed in the R environment (v. 3.3.4, R Core Team, 2017) and we accept significant effects at an alpha level of 5%.

3 | RESULTS

3.1 | Species and phylogenetic signal

In our final models, we considered 69 species for Resistance (Supporting Information Figure S1), 72 species for SMR (Supporting Information Figure S2), 53 species for FMR (Supporting Information Figure S4), 210 species for T_{pref} (Supporting Information Figure S6), 115 species for CT_{min} (Supporting Information Figure S7), and 136 species for CT_{max} (Supporting Information Figure S9). The strongest phylogenetic signal was found for FMR, T_{pref} and CT_{max} ($\lambda > .9$). Resistance showed the least phylogenetic signal (confidence limits on λ overlapping with zero) and SMR and CT_{min} showed moderate phylogenetic signal (see Supporting Information).

3.2 | Forcing datasets

We applied three different forcing datasets to compute macro, microclimate, and biophysical variables. We found that the relationships between physiological traits and climatic/biophysical variables are sensitive to the forcing data applied (Figure 2). When using datasets with higher temporal resolution (i.e., with NCEP dataset), we found that biophysical variables better fitted resistance, and that microclimatic variables better fitted T_{pref} and CT_{max}, than macroclimatic variables. However, if we consider the results yielded from datasets with average monthly climatologies, biophysical variables fit better FMR and CT_{min} than macroclimatic conditions.

3.3 | Water loss

Resistance was affected by climatic and biophysical variables, but biophysical predictors had the strongest explanatory power (Figure 3 and Supporting Information Table S1; see also Supporting Information Tables S2 and S3). At the macroclimate scale ($F_{1,67} = 7.909$, $R^2 = .267$, $p < .001$), resistance was negatively correlated with minimum air temperatures (PGLS intercept $\beta = -0.059 \pm 0.016$, $p < .001$) and with rainfall ($\beta = -0.0009 \pm 0.0002$, $p = .001$). The interaction between minimum air temperatures and rainfall was also significant ($\beta = 0.00003 \pm 0.00001$, $p = .008$). At microclimate scales ($F_{2,67} = 11.42$, $R^2 = .257$, $p < .001$), resistance was positively correlated with soil water potential ($\beta = 0.141 \pm 0.0464$, $p = .003$), and negatively with minimum air temperatures ($\beta = -0.0238 \pm 0.0105$, $p = .027$). At biophysical scales ($F_{2,67} = 14.52$, $R^2 = .305$, $p < .001$), the best model for resistance included minimum operative temperatures as predictors ($\beta = -0.0185 \pm 0.0104$, $p = .08$) and wilting point ($\beta = 0.00003 \pm 0.00009$, $p < .001$), being negatively associated with the former, and positively with the latter.

3.4 | Metabolism

The SMR of the lizards was not correlated with climatic or biophysical predictors (Supporting Information Figure S3 and Table S4). At the macroclimate scale ($F_{3,68} = 4.46$, $R^2 = .113$, $p = .014$), the best-scoring model included the test temperature (PGLS intercept $\beta = 0.0510 \pm 0.0171$, $p = .003$) and maximum air temperature ($\beta = -0.0216 \pm 0.0168$, $p = .204$). At the microclimate scale ($F_{2,69} = 4.94$, $R^2 = .123$, $p = .009$), the best-fitting model for SMR included again test temperature ($\beta = 0.0549 \pm 0.0174$, $p = .002$) and maximum air temperature ($\beta = -0.0223 \pm 0.0140$, $p = .116$). For

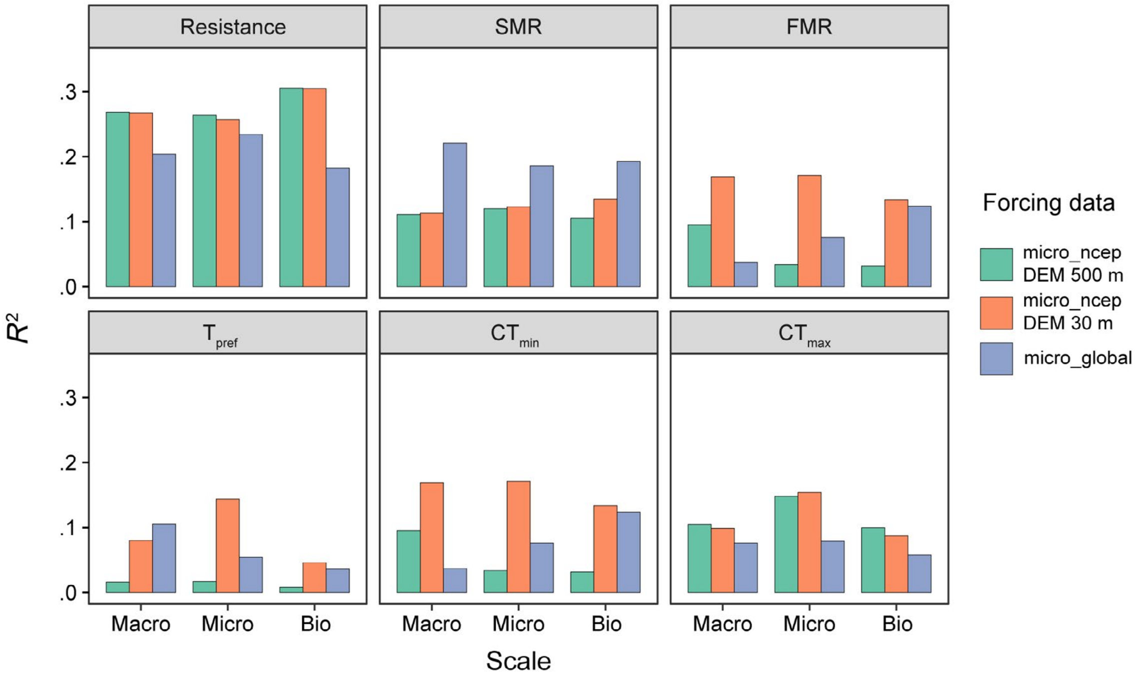


FIGURE 2 Coefficients of determination of the best fitted model using a phylogenetic least squares analysis of the relationship between physiological traits and climatic variables estimated at different spatial scales. Three different climatic modelling approaches, using different climate forcing data as input, were applied. Resistance = skink resistance; SMR = standard metabolic rate; FMR = field metabolic rate; T_{pref} = thermal preference; CT_{min} = critical thermal minimum; CT_{max} = critical thermal maximum

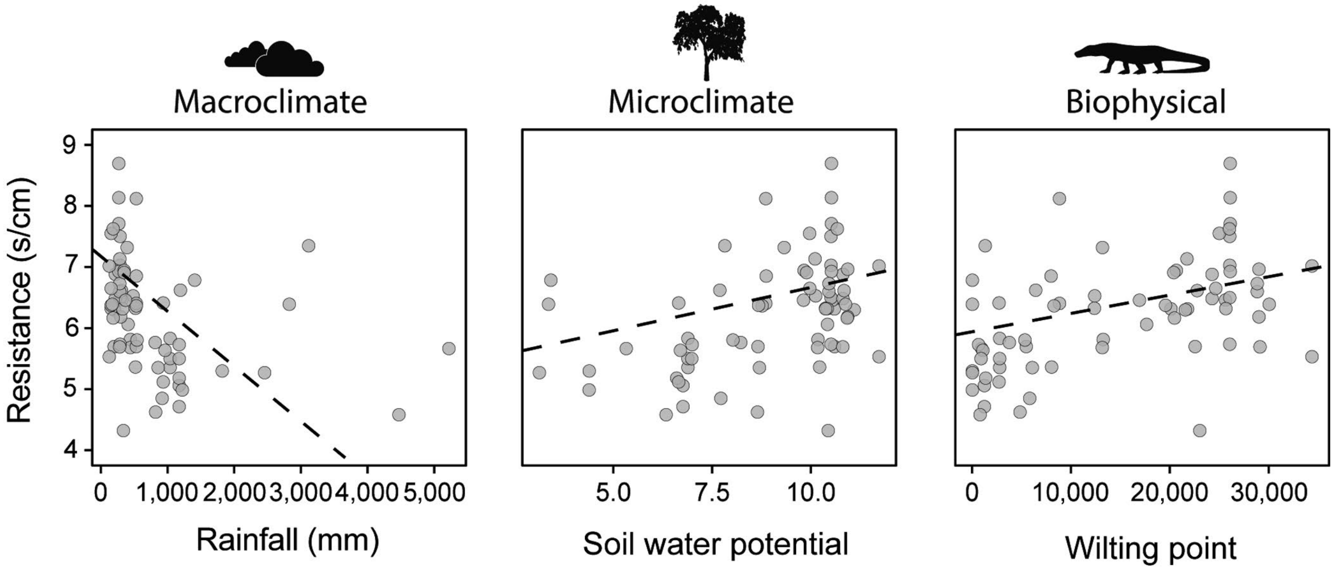


FIGURE 3 Resistance to water loss of lizards is affected by environmental and biophysical variables. Variables derived from biophysical models have a stronger explanatory power ($R^2 = .305$) than those derived from macroclimate ($R^2 = .267$) and microclimate ($R^2 = .257$) . Soil water potential is negative logarithm-transformed and wilting point represents the number of days unsuitable for vegetation growth. The black dashed line indicates the phylogenetic general least squares fit

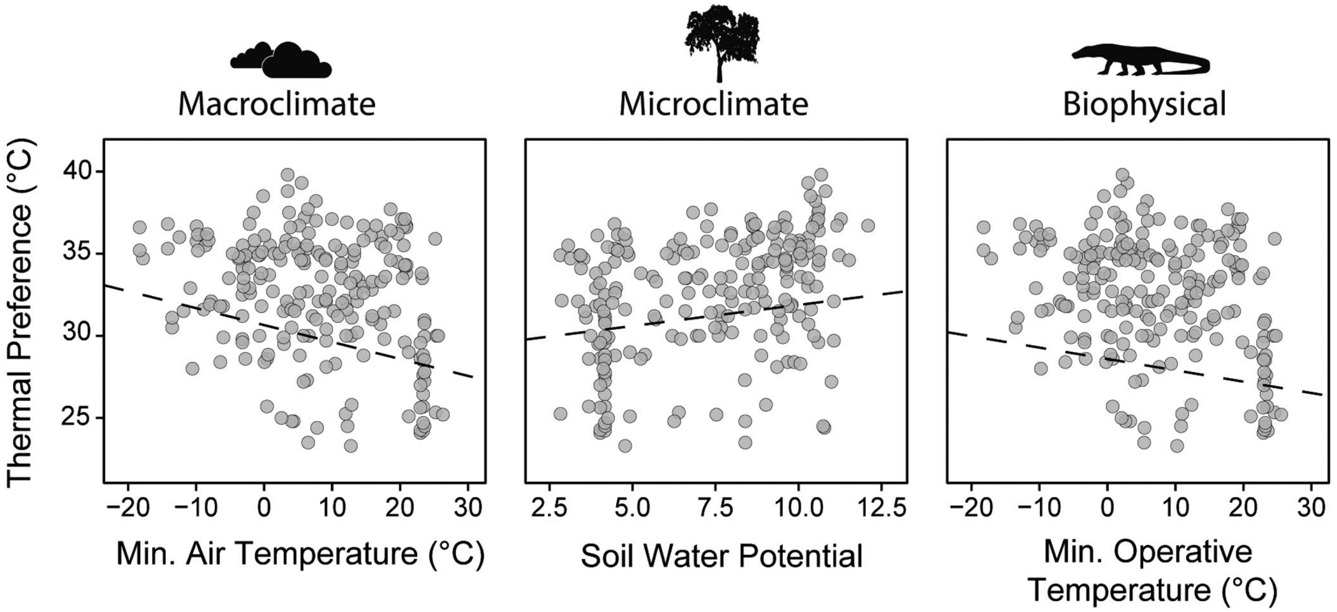


FIGURE 4 Thermal preferences of lizards are explained by environmental variables estimated at different scales. Microclimate ($R^2 = .144$) can explain a higher amount of variability than macroclimate ($R^2 = .08$) and biophysical scales ($R^2 = .046$). Soil water potential is negative logarithm-transformed. The black dashed line indicates the phylogenetic general least squares fit

the biophysical models ($F_{2,69} = 5.45$, $R^2 = .134$, $p = .006$), SMR was affected by test temperature ($\beta = 0.0575 \pm 0.0174$, $p = .001$), but minimum operative temperatures were also present in this model ($\beta = -0.0257 \pm 0.0137$, $p = .06$).

FMR was not correlated with climatic variables (Supporting Information Figure S5 and Table S7). At macroclimates, the best-fitting model for FMR ($F_{1,51} = 2.82$, $R^2 = .052$, $p = .098$) included minimum air temperatures ($\beta = 0.0155 \pm 0.0092$, $p = .098$). As well for the microclimate scale, the best model for FMR ($F_{1,51} = 2.89$, $R^2 = .053$, $p = .094$) included minimum air temperature ($\beta = 0.0151 \pm 0.0088$, $p = .094$). Moreover, FMR was not affected by biophysical variables ($F_{1,51} = 2.95$, $R^2 = .054$, $p = .091$), but the best model included minimum operative temperatures ($\beta = 0.0154 \pm 0.0089$, $p = .091$).

Using a global dataset with lower temporal resolution, we observed an effect of rainfall on the SMR of lizards, with a consistent effect of temperature across the spatial scales (Supporting Information Tables S5 and S6). As well, temperature and water-related metrics affected FMR (Supporting Information Tables S8 and S9).

3.5 | Thermal physiology

We found that T_{pref} was affected by climatic and biophysical variables across spatial scales, but microclimatic conditions had the strongest explanatory power (Figure 4). At macroclimate scales, T_{pref} was affected by minimum air temperature, and by the interaction of vapour pressure deficti (VPD) and minimum air temperature ($F_{3,205} = 6.01$, $R^2 = .08$, $p < .001$; Figure 4 and Supporting Information Table S10). In this model, T_{pref} correlated negatively with air temperature ($\beta = -0.103 \pm 0.032$, $p = .001$), VPD was also present but not significant ($\beta = 0.0008 \pm 0.0004$, $p = .102$). At microclimate scales, T_{pref} was affected by minimum air temperature, soil water potential, and their interaction ($F_{3,207} = 11.55$, $R^2 = .144$, $p < .001$; Supporting Information Table S4). In this model, T_{pref} was correlated negatively with minimum air temperatures ($\beta = -0.248 \pm 0.058$, $p < .001$), and positively with soil water potential ($\beta = 0.256 \pm 0.08$, $p = .004$). The interaction showed a positive effect ($\beta = 0.024 \pm 0.007$, $p = .001$). For the biophysical scale, T_{pref} was affected by minimum and maximum T_e ($F_{3,207} = 5.065$, $R^2 = .046$, $p = .007$; Supporting Information Table S4). T_{pref} showed a negative correlation with the minimum T_e ($\beta = -0.248 \pm 0.166$, $p = .001$) and positive with maximum T_e ($\beta = 0.064 \pm 0.0.261$, $p = .013$).

The CT_{min} was predicted by variables estimated at different spatial scales, with similar amounts of variation explained across spatial scales (Supporting Information Figure S8 and Table S13). At the macroclimate scales ($F_{3,112} = 6.509$, $R^2 = .169$, $p < .001$), CT_{min} was positively correlated with minimum air temperatures ($\beta = 0.1882 \pm 0.0472$, $p < .001$) and rainfall ($\beta = 0.0018 \pm 0.0008$, $p = .046$), with the interaction of these two predictors having a negative effect ($\beta = -0.0001 \pm 0.00004$, $p = .022$). At the microclimate scales ($F_{3,112} = 6.636$, $R^2 = .171$, $p < .001$), CT_{min} was correlated positively with minimum air temperature ($\beta = 0.1214 \pm 0.0351$, $p < .001$) and vapour pressure deficit ($\beta = 0.0024 \pm 0.001$, $p = .016$), but negatively correlated with maximum air temperatures ($\beta = -0.2886 \pm 0.0984$, $p = .004$). At the biophysical scale ($F_{2,111} = 7.509$, $R^2 = .134$, $p < .001$), CT_{min} was positively correlated with minimum operative temperatures ($\beta = 0.1275 \pm 0.0343$, $p < .001$), but negatively correlated with maximum operative temperatures ($\beta = -0.0805 \pm 0.0383$, $p = .038$).

Finally, CT_{max} was also correlated with predictors estimated at different spatial scales, with microclimate explaining greater amounts of variation (Figure 5 and Supporting Information Table S16). At macroclimate scales ($F_{2,133} = 7.388$, $R^2 = .099$, $p < .001$), CT_{max} was negatively correlated with rainfall ($\beta = -0.0006 \pm 0.0003$, $p = .039$). At the microclimate scale ($F_{2,133} = 12.18$, $R^2 = .154$, $p < .001$), CT_{max} was correlated negatively with minimum air temperatures ($\beta = -0.057 \pm 0.027$, $p = .036$), but positively correlated with soil water potential ($\beta = 0.479 \pm 0.101$, $p < .0001$). At the biophysical scale ($F_{2,133} = 6.495$, $R^2 = .087$, $p = .002$), CT_{max} was correlated negatively with minimum operative temperatures ($\beta = -0.0541 \pm 0.029$, $p = .006$), but positively with wilting point ($\beta = 0.00008 \pm 0.00008$, $p = .005$).

In general, the 6-hourly global dataset correction for terrain slopes had the best performance for the thermal physiological traits (Supporting Information).

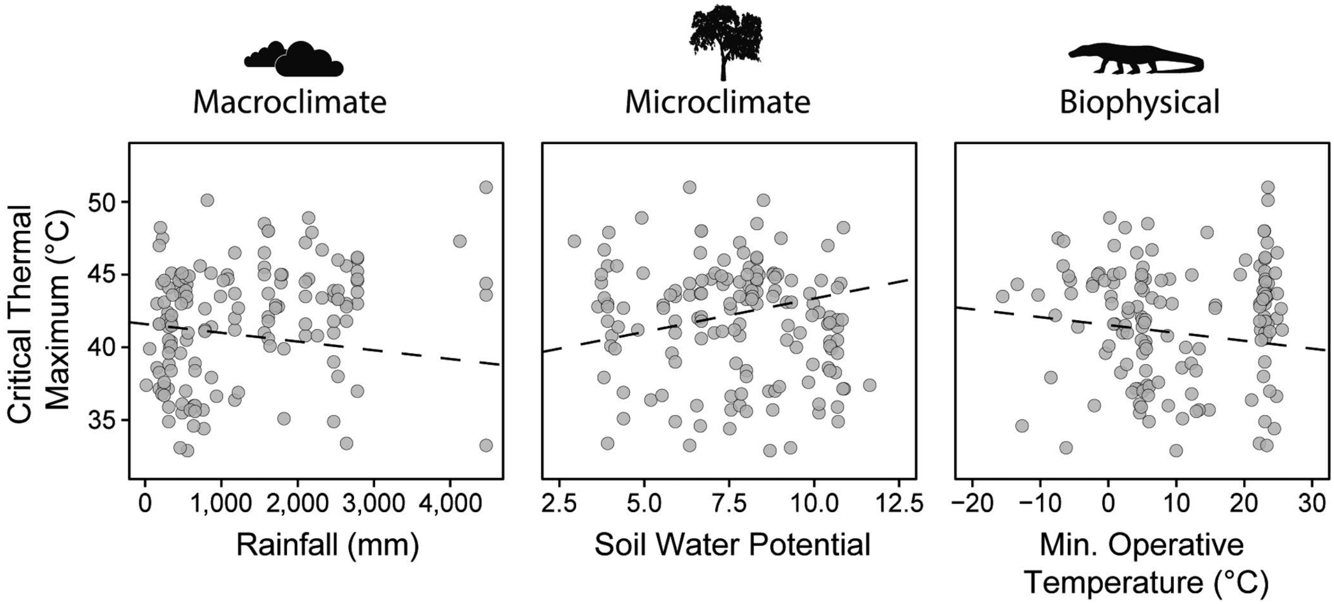


FIGURE 5 Critical thermal maximum of lizards is affected by variables estimated at different spatial scales. Microclimate can explain higher amounts of variation ($R^2 = .154$) than macroclimate ($R^2 = .093$) and biophysical variables ($R^2 = .087$). Soil water potential is negative logarithm-transformed. The black dashed line indicates the phylogenetic general least squares fit

4 | DISCUSSION

Our hierarchical approach revealed that microclimatic and biophysical variables can explain a greater amount of physiological variation than macroclimatic variables, especially regarding aspects of water balance and thermal physiology. The nature of the correlations we found suggest that some causal pathways may be indirect via the effects of vegetation and led us to new testable hypotheses about the nature of climatic adaptation.

Resistance to water loss in lizards is known to be associated with habitat aridity (Cox & Cox, 2015; Duvdevani & Borut, 1974; Mautz, 1980; Thompson & Withers, 1997; Warburg, 1966) and previous comparative analyses have found this to be generally true (Cox & Cox, 2015; Mautz, 1982; Withers et al., 2000). Our results confirmed that species inhabiting regions with higher minimum air temperatures and higher soil moisture exhibited lower water resistance. The strongest effects of soil dryness, quantified as water potential, suggested that microclimatic components (e.g., soil properties) provide a more nuanced perspective on desiccation potential than macroclimatic variables like rainfall and humidity. This supports our prediction that proximal factors are powerful in explaining variation in water balance. Yet we did not observe evaporative water loss at the biophysical scale as a strong predictor, which would be most correlated with resistance to water loss if the selective force was simply environmental ‘dryness’. However, it is increasingly recognized that lizards can behaviourally regulate their water loss rates (hydroregulation) through microhabitat selection (Huang et al., 2020; Kearney et al., 2018; Pirtle et al., 2019; Rozen-Rechels et al., 2021; Ryan et al., 2016; Sannolo & Carretero, 2019). The overall water balance depends on both gains (e.g., from food) and losses and it may be that soil dryness is capturing both water availability and water loss in the one metric. The general correspondence with minimum temperature was unexpected and may combine with the soil dryness metric to represent tropical and/or islands/coastal areas with additional buffering due to the presence of forest or moderating oceanic effects.

The SMR of lizards was predicted equally well by temperature at all the hierarchical levels. It has generally been found that ectotherms (fish and especially insects) from cold climates have elevated metabolic rates – the metabolic cold adaptation hypothesis (Addo-Bediako et al., 2002; Gaston et al., 2009; Holeton, 1974; White et al., 2012; Wohlschlag, 1960). This pattern has also been reported in lizards (Al-Sadoon, 1986; Angilletta, 2001; Christian et al., 1998; Hare et al., 2010; Patterson & Davies, 1989; Plasman et al., 2020) and our data indicate it is a widespread phenomenon (see also Žagar et al., 2018). The correlation with maximum temperatures rather than minimum temperatures is consistent with the original idea of metabolic cold adaptation whereby the overall physiological processes are adjusted upwards as species invade colder environments (Kawall et al., 2002).

We also found that the strength of the relationships between temperature and FMR were similar across the hierarchical spatial levels. This can be interpreted as a purely plastic response because of the way body temperature drives metabolic rate (Christian et al., 1996, 2003; Mautz & Nagy, 2000; Murray et al., 2015). FMR is measured for free-living animals that have the potential for active thermoregulation. One might expect a stronger correlation with the biophysical predictor – operative body temperature – for FMR. However, we did not include thermoregulatory behaviours in our predictions of operative temperature (due to a lack of species-specific knowledge about thermoregulatory thresholds). Also, ectotherms spend a large amount of time inactive in retreats (Huey et al., 1989) and the integrated active and inactive body temperatures are equally well represented by proximal and distal variables (see also Dillon et al., 2010; Huey & Kingsolver, 2019).

Previous work found T_{pref} to be negatively associated with rainfall at the macroclimatic scale, which was interpreted to reflect limited opportunities for basking due to high cloud and vegetation cover (Clusella-Trullas et al., 2011). However, we found that T_{pref} increased as minimum air temperature and operative temperature declined. Yet the strongest predictor overall was soil dryness – a microclimatic predictor. This is consistent with Clusella-Trullas et al. (2011), who found rainfall of the driest month was the best macroclimatic predictor. Soil dryness integrates multiple atmospheric factors as well as soil properties and may be acting as a proxy for vegetation density, which can powerfully constrain thermoregulatory opportunities for ectotherms (Basson et al., 2017; Pike et al., 2011; Rozen-Rechels et al., 2021; Ryan et al., 2016). Likewise, we found stronger correlations of CT_{max} with microclimatic and biophysical predictors, especially soil dryness. As with T_{pref}, our study suggests that climate drives the evolution of CT_{max} indirectly through its effects on vegetation cover and hence shading and other buffering effects (Kellerman, Overgaard et al., 2012). Indeed, it has been demonstrated that lizard species from forested habitats have lower CT_{max} (Huey et al., 2009, 2021).

The CT_{min} was strongly predicted by temperature metrics, consistent with previous intra- and interspecific associations between CT_{min} and temperature (Garcia-Porta et al., 2019; Labra et al., 2009; Sunday et al., 2019). Across all spatial scales, minimum air temperatures were negatively associated with CT_{min}, and at micro and biophysical scales CT_{min} was also positively related to maximum air/body temperatures. Ectotherms frequently experience body temperatures below the CT_{min} in nature, mostly when they are inactive (Huey et al., 2021), and therefore unable to thermoregulate. Thus, the very general relationship we observed between CT_{min} and our temperature metrics at all hierarchical scales is not unexpected.

4.1 | Conclusions and future directions

A hierarchical assessment of the correlation of physiological traits with environmental variables allowed us to develop more specific hypotheses for how climate drives trait evolution. We acknowledge that our study was limited in some respects. First, we did not apply species-specific parameters for the biophysical predictions that would allow specific details of thermoregulatory behaviour (e.g., thresholds for activity, behavioural repertoire). This was simply due to a lack of data and future studies could improve this part of our analyses as functional trait databases with the requisite parameters grow. Data limitations also prevented us from modelling species according to ecological habits (arboreal, semi-aquatic, terrestrial, saxicolous) but this could further refine the modelling of microclimate experienced by the lizards (Algar et al., 2018) and would be aided by recent developments in under-canopy microclimate modelling (Maclean & Klinges, 2021). Second, our approach is based on traits estimated for a single population, assuming no intraspecific variation (Hernando-Pérez et al., 2019, 2020), a factor that may affect the results. Third, we used a relatively short time window to model the climatic and biophysical conditions (4 years), given that long-term environmental conditions (e.g., long droughts) may impact physiological responses.

We must also highlight that different climatic data sources may yield different results, given distinct spatial and temporal resolutions (see Figure 2). By applying three different types of forcing data, we showed that the relationships between physiology and environment can be sensitive to the type of climatic data used (e.g., trade-off between temporal and spatial resolutions). This could make comparisons between studies difficult given that the correlations yielded are dependent upon the climatic datasets used.

Despite these caveats, our analyses represent a proof of concept that greater insight into the evolution of ecophysiological traits can be gained by taking a hierarchical approach to developing predictor variables. Overall, we found that macroclimatic predictors were less informative than microclimatic or biophysical predictors. Moreover, the nature of the associations we detected reinforces previous work suggesting that climate can often act indirectly via microclimatic influences on habitat structure (Clusella-Trullas et al., 2011; Kellermann, Overgaard, et al., 2012).

To test these ideas, we suggest the following hypotheses:

1. Given the potential effects of habitat structure on physiology, future studies could evaluate if environmental history at a site (e.g., drought, fire and associated effects on vegetation) is related to geographic variation in physiological traits within species.
2. Metabolic cold adaptation should be prevalent in lizards occurring in places where, even during the active season, it is difficult for them to achieve their ancestrally preferred body temperatures, even when thermoregulatory behaviour is allowed for. This could be tested through a combination of field body temperature measurements and biophysical modelling, the latter enabling predictions to be made across entire seasons or generations (e.g., Maeno et al., 2021).
3. Our results strongly agree with a growing body of literature indicating the effects of shade on the evolution of the thermal physiology of ectotherms (reviewed in Bodensteiner et al., 2021). There is a solid indication that across geographic and phylogenetic scales (Gunderson et al., 2018; Hertz, 1979; Huey et al., 2009; Kellermann, Overgaard, et al., 2012; Muñoz & Losos, 2018) thermal traits (T_{pref} and CT_{max}) evolve more strongly in response to vegetation cover and the availability of shade than to general atmospheric conditions. This could be tested with gridded products of leaf area index (LAI) or plant area index (PAI) (Tang et al., 2012, 2014).

Overall, macro and microclimatic conditions, habitat structure and behaviour might influence ectotherm physiological evolution. Major ecological processes, and the consequences of environmental changes, should be considered in light of distinct spatial levels. Broader evaluations of the interaction between physiology and environment, incorporating multiple scales and characteristics of organisms, will improve our understanding of the physiological evolution of ectotherms and their responses to climatic changes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

R.O.A., M.R.K., D.G.C. and C.R.W. designed the study. R.O.A. and C.R.W. collected the data. R.O.A., M.R.K. and C.R.W. analysed the data. R.O.A., M.R.K., D.G.C. and C.R.W. wrote the first version of the manuscript. All authors contributed to and approved the final version.

DATA AVAILABILITY STATEMENT

The data and the R script supporting the results of this study are archived in the Bridges data repository of Monash University (https://doi.org/10.26180/16892503) – https://bridges.monash.edu/articles/dataset/_/16892503.

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BIOSKETCH

Rodolfo O. Anderson is interested in understanding the mechanisms that underlie species distribution using comparative physiology and biophysical ecology.

SUPPORTING INFORMATION

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