

RESEARCH ARTICLE

Linking physiology and climate to infer species distributions in Australian skinks

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Abstract

1. Climate has a key impact on animal physiology, which in turn can have a profound influence on geographic distributions. Yet, the mechanisms linking climate, physiology and distribution are not fully resolved.
2. Using an integrative framework, we tested the predictions of the climatic variability hypothesis (CVH), which states that species with broader distributions have broader physiological tolerance than range-restricted species, in a group of *Lampropholis* skinks (8 species, 196 individuals) along a latitudinal gradient in eastern Australia. We investigated several physiological aspects including metabolism, water balance, thermal physiology, thermoregulatory behaviour and ecological performance.
3. Additionally, to test whether organismal information (e.g. behaviour and physiology) can enhance distribution models, hence providing evidence that physiology and climate interact to shape range sizes, we tested whether species distribution models incorporating physiology better predict the range sizes than models using solely climatic layers.
4. In agreement with the CVH, our results confirm that widespread species can tolerate and perform better at broader temperature ranges than range-restricted species. We also found differences in field body temperatures, but not thermal preference, between widespread and range-restricted species. However, metabolism and water balance did not correlate with range size.
5. Biophysical modelling revealed that the incorporation of physiological and behavioural data improves predictions of *Lampropholis* distributions compared with models based solely on macroclimatic inputs, but mainly for range-restricted species.
6. By integrating several aspects of the physiology and niche modelling of a group of ectothermic animals, our study provides evidence that physiology correlates with species distributions. Physiological responses to climate are central in establishing geographic ranges of skinks, and the incorporation of processes occurring at local scales (e.g. behaviour) can improve species distribution models.

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KEYWORDS

ectotherms, lizards, metabolism, thermal physiology, water loss

1 | INTRODUCTION

The distribution of species varies remarkably, with some species restricted to a specific area, while others exhibit distributions that span continents. The reasons behind this variation in species distribution have been studied by ecologists and evolutionary biologists for many years, with climate being considered as a major factor affecting range size (Kearney & Porter, 2009). The way species respond to climatic conditions is due, in part, to the alignment of physiology with climatic variation, with important outcomes for species ecology and distribution (Calosi et al., 2010). The idea of climate and physiology shaping species distribution is known as the climatic variability hypothesis (CVH; Janzen, 1967; Stevens, 1989).

The CVH posits that species with a wider range of physiological tolerance to climatic conditions can persist across a wider geographical area (Stevens, 1989). This is because individuals exposed to wide climatic variability needs broad physiological tolerance ranges to survive and, consequently, expanding their distributional range (Bozinovic et al., 2011). In other words, species with broad distributions are able to occupy a wide range of climates due to their broad physiological tolerance, while range-restricted species may be physiologically adapted to specific, narrow climatic conditions (Sheldon et al., 2018). Indeed, several studies have shown that physiological adaptations to climatic variability are associated with range sizes. For example, arthropods and tadpoles that occur at high latitudes, where climatic variation is greater, exhibit broader thermal physiological tolerances than their tropical counterparts (Calosi et al., 2008, 2010; Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022; Shah et al., 2017). Similarly, species living across altitudinal gradients show broader thermal physiological tolerances compared to species restricted to narrow altitudinal ranges (Pintanel et al., 2019; Shah et al., 2017); and the thermal tolerance of cave-dwelling invertebrates is related to the thermal variation they are exposed and to subterranean depth they occupy (Mammola et al., 2019; Raschmanová et al., 2018).

Although the CVH has received support from many studies, its validity is sometimes questioned or remains inconclusive (Sheldon et al., 2018). For instance, in a coastal-inland gradient, thermal breadths of plants did not correlate with climatic conditions and to their ranges (Chiono & Paul, 2023). Moreover, metabolism correlates with range sizes of temperate and tropical mayflies, but not for stoneflies (Shah et al., 2021). Likewise, different species of underground invertebrates exhibit contrasting physiological responses to similar thermal gradients (Mermillod-Blondin et al., 2013; Rizzo et al., 2015). In other words, mechanisms driving species distributions are complex and may not be fully captured by CVH studies focusing on single physiological aspects. Specially for ectotherms, most studies investigating CVH have focussed on thermal physiology, but

other factors, such as water balance, energy inputs and thermoregulatory behaviour, also play a role in responding to climate and, consequently, on their distributions (Kearney et al., 2013; Kellermann et al., 2009). Thermoregulatory behaviour, for instance, can slow down the evolution of physiological traits, by reducing exposure to environmental stresses (Buckley et al., 2015). That is, processes occurring at local scales (e.g. behaviour) can have a greater impact on physiological traits than climate (Anderson, White, et al., 2022), but this is not always considered in studies investigating the CVH. To fully understand the mechanisms shaping physiological responses to climate and ultimately geographic distributions, integrative approaches that capture several organisms' aspects (e.g. physiology and behaviour) are needed (Muñoz & Bodensteiner, 2019).

To examine the CVH in detail, temperature can be used as a unifying key factor, as it impacts virtually all physiological processes of organisms (Angilletta, 2009). Environmental temperature determines the range of thermal conditions in which organisms can function (i.e. thermal limits), and changes in temperature can prompt changes in their ability to regulate body temperatures in the field and in the laboratory (Huey et al., 2003). Furthermore, the relationships between metabolism and geographical distribution of organisms are influenced by temperature (Munch & Salinas, 2009), and temperature plays a significant role in water balance as it can increase evaporation rates (Kellermann et al., 2009; Porter & Gates, 1969; Rozen-Rechels et al., 2019). Therefore, thermal sensitivity of physiological responses to changes in environmental temperatures can indicate how changes in climatic conditions are related to distributional ranges (Louthan et al., 2021). As predicted by CVH, species with widespread distribution may then exhibit low physiological sensitivity and high tolerance to changes in temperature, as they have to cope with a broad range of environmental temperatures, while range-restricted species may have evolved higher sensitivities and low tolerances due to the limited range of temperatures they experience (Huey & Kingsolver, 1989). This might ultimately be reflected in ecologically relevant performance measures (e.g., locomotion), which can be assessed through thermal performance curves (Huey & Kingsolver, 1989; Sinclair et al., 2016).

The understanding of the mechanisms shaping species distributions can be enhanced by expanding the CVH to encompass multiple physiological traits, behaviour and performance measures (Muñoz & Bodensteiner, 2019). The *Lampropholis* skinks are small ectotherms (~1.2 and 2.4 g) that form a monophyletic group and exhibit a strong phylogeographic structure across dry habitat barriers along the east coast of Australia, with widespread and range-restricted species (Chapple, Chapple, et al., 2011; Chapple, Hoskin, et al., 2011; Singhal et al., 2018). Some *Lampropholis* species, such as *L. delicata*, can be found across almost the entire latitudinal gradient of the Australian east coast, while others have limited ranges from the tropics to the

subtropics (Wilson & Swan, 2021). As range-restricted species are found along the latitudinal gradient of Eastern Australia, range sizes could be independent of thermal fluctuations (i.e. latitudinal position), making *Lampropholis* skinks a good system to study the effects of climate and physiology on their distribution.

In our study, we had a twofold aim. First, we tested the CVH predictions by investigating whether physiological traits correlated with the distribution of *Lampropholis* skinks across a latitudinal gradient. We collected data on metabolism (metabolic rate), water balance (evaporative water loss) and thermal physiology (field body temperatures, thermal preference and critical limits). We also quantified the thermal dependence of ecological performance (i.e. locomotion) to compute thermal performance curves, which can indicate the optimum conditions for ecological activities (Huey & Kingsolver, 1989). Then, we compared sensitivity with thermal changes in metabolism and water loss, critical limits, thermal preferences and thermal performance curves between range-restricted and widespread species. In accordance with the CVH, we expected widespread species to exhibit broader thermal tolerances, lower thermal sensitivity of physiological traits and broader thermal performance curves. Divergences in thermoregulatory behaviour can also be anticipated, with range-restricted species—especially from tropical regions—showing higher field body temperatures and thermal preferences as an indicative of some degree of specialisation to narrow range of hot temperatures (Angilletta et al., 2010; Chiono & Paul, 2023).

Second, we aimed to determine the significance of physiology and behaviour in shaping the distribution of *Lampropholis* skinks. We used the data collected on their physiological traits and applied mechanistic niche modelling to map the skinks ranges. This type of modelling considers the effects of microenvironments, physiology and behaviour that are not included in correlative models using coarse climatic layers (Kearney & Porter, 2020). We compared the results from our mechanistic models with models based solely on climatic information to assess the role of organismal information in limiting species distribution. As the CVH hypothesises that physiology and climatic factors have a greater effect on range size (Stevens, 1989), we expected the mechanistic models to provide a more accurate representation of the skinks' distributions.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted three fieldwork trips to collect range-restricted and widespread species across a latitudinal gradient in eastern Australia. The trips were split in three distinct years (2018–2020), encompassing the same seasons (late Spring–Summer: November–December) in order to avoid seasonal effects. The fieldwork sites included north Queensland, southeast Queensland and central-eastern New South Wales (NSW), Australia (Table S1). In each trip, we collected *Lampropholis* species co-occurring at that latitude. In north Queensland, near Townsville, we collected the widespread *L. delicata*, and two

range-restricted species (*L. mirabilis*, *L. similis*). In southeast Queensland, near Brisbane, we collected the widespread *L. delicata*, and three range-restricted species (*L. adonis*, *L. amacula*, *L. couperi*). Finally, in central-eastern NSW, we collected two widespread species (*L. delicata*, *L. guichenoti*), and the range-restricted *L. caligula*. This approach allows us to compare the physiological traits of widespread species (*L. delicata* and *L. guichenoti*) and range-restricted species (all others) both within, and among, latitudes. For more details about collection sites and species, see Table S1. All procedures involving animals described in this study were approved by the School of Biological Sciences Animal Ethics Committee—Monash University (Project ID: 2018-16711).

2.2 | Field collection and laboratory housing

In the field, we actively searched for skinks during their active time (8:00–16:00). Once spotted, we collected skinks by hand or by mealworm fishing. We then immediately (<15s) recorded the body temperature of the skink with a cloacal thermometer (EcoScan Temp JKT Temperature Meter; EuTech Instruments). The sex of skinks was determined in the field, and only adult males were collected to avoid effects of sex in our analyses. These were transported to Monash University (Clayton, Victoria, Australia). Upon arrival, the skinks were individually marked with a unique identification using nontoxic paint on their dorsal surface. The skinks were held in groups of four to six animals and maintained at 22°C, with a 12-h light:12-h dark photoperiod. Lamps for basking and shelters for refuge were provided. Skinks were fed crickets (*Acheta domesticus*, on average 5 per skink), dusted in calcium and vitamins, three times weekly. Water was ad libitum. Importantly, before each experiment, skinks were not fed for at least 48h to avoid absorptive effects on physiological measurements. Between experiments, skinks recovered in their respective cages for at least 24h, before being used in another experiment. All individuals had the same housing conditions and body mass of skink did not change over the experiments.

The experiments commenced 3 days after the skinks had arrived in the laboratory. We started with the metabolism and evaporative water loss experiments. Two days after finishing these experiments, we conducted the T_{pref} measurements. Next, we conducted the measurements of sprint speed, and finally, we quantified the lower critical thermal limits, followed by the upper thermal limits.

2.3 | Metabolism and water loss

Rates of carbon dioxide production and water loss were measured using positive pressure open-flow respirometry, according to standard techniques (Lighton, 2008). We first weighed the skinks (Sciencetech ZSA210, ± 0.0001 g), which were placed in small insulated glass chambers (25 mL) that were subsequently put in a controlled-temperature chamber (Dometic Cool Ice 22L) that maintained temperature within $\pm 1.5^\circ\text{C}$. All individuals had their metabolic rates and

evaporative water loss measured at five temperatures (15, 20, 25, 30 and 35°C) that they might encounter in the field (experiment took place from 08:00 to 18:00). The respirometry system was supplied with room air that was pushed through a column of soda lime (Labchem, Ajax Finechem Pty Ltd) and Drierite (W. A. Hammond Drierite Company Ltd) to remove CO₂ and water vapour, respectively. The flow rate of air through each of the eight channels of the system was regulated nominally to 60 mL min⁻¹ by a mass flow controller (Aalborg, Model GFC17; Orangeburg), as is appropriate for these skinks (Merritt et al., 2013). Animals were allowed a 15-min settling period at the beginning of measurements. Following this settling period, mean rates of CO₂ production and H₂O loss were calculated for a minimum period of 60-min. Following standard procedures for respirometry (Lighton, 2008) and methods utilised for a congeneric species (Merritt et al., 2013), we calculated the CO₂ and H₂O production for the most stable and constant 5-min period of CO₂ production and H₂O loss. Individuals were tested at only one temperature per day. All experiments were conducted in a random order (e.g. population of origin, individual skink, test-temperature).

2.4 | Locomotor performance and thermal performance curve

All individuals ran along a 1-m race track set to eight temperatures (15, 20, 23, 25, 27, 30, 33 and 35°C) in a random order. Each individual ran twice at each test temperature. Skinks were acclimatised to the race temperature within a thermal chamber (10×10 cm) for 30 mins prior to each trial, and rested 30 mins between trials. We measured the cloacal temperature of the skinks at the onset of the running to ensure they were at the desirable test temperature. A paintbrush tapped behind the individual provided motivation to sprint. A high-speed camera (Casio Exilim EX-ZR50) positioned 1 m above the race track was used to record each run. The fastest run at each temperature was considered the maximum velocity (cm/s).

Thermal performance curves (TPCs) of maximum velocity were estimated using the package *rTPC* (Padfield et al., 2021) in the R environment (R Core Team, 2021). We followed Angilletta (2006) and first we fitted multiple models applied to describe the thermal performance curves of ectotherms (Gaussian, Weibull, Quadratic). Then, we selected the model with the lowest Akaike Information Criteria (Angilletta, 2006). We found that the Weibull model had the best fit for all species, except for *L. couperi* (quadratic) and *L. delicata* from North Queensland (Gaussian). For comparative purposes, as different fits can completely alter parameters estimations (Angilletta, 2006), we used Weibull distribution to fit thermal performance curves for all species. For each individual, we bound the curves with the critical thermal limits (minimum and maximum). Optimal performance temperatures (T_{opt} ; the temperature at which an individual performs its maximum speed); the maximum speed (maximum speed predicted by the thermal performance curve) and the thermal performance breadth (B80; the range at which an individual performs at 80% its maximum) were extracted from each individual curve.

2.5 | Thermal preference

T_{pref} was determined by placing lizards in a four-lane aluminium runway (40×100 cm) with a thermal gradient ranging from 15 to 35°C. The thermal gradient was produced by resting one end of the runway on a cold plate and the other under two 250-W infrared lamps, which produce heat but not the potential confounding factor of light. A row of numbered iButton dataloggers (model DS 1921CVF50; Maxim Integrated) ran the length of the runway to track surface temperature for each minute of the trial. Four video cameras (Panasonic HC-V160) were suspended above the gradient to record thermoregulatory behaviour. Skinks were placed individually into a randomly assigned lane and given 15 mins to acclimatise under a plastic cup in the runway's centre (this time of acclimatisation was not included in the analysis). The order and time of the day the skinks were tested was randomly selected. At the onset of each trial, the plastic cup was removed and each skink's positioning along the gradient was recorded for 4 h. No food or water were provided during the test to avoid influencing behaviour. Videos were analysed to determine time spent at each iButton location along the temperature gradient. Temperatures were only recorded if the skink was stationary for at least two mins, as that allowed body temperature (T_b) to be inferred as the skink equilibrated to its immediate surroundings, given the 1.3 ± 0.3 min time constant for the heating and cooling rates of *Lampropholis* species (Fraser & Grigg, 1984). The average of all selected body temperatures was recorded as T_{pref} .

2.6 | Critical temperatures

We determined CT_{max} and CT_{min} by placing skinks individually inside Falcon tubes in a water bath (Labec DCW-1015). Temperature either increased or decreased at a rate of 1°C/min. For both traits, start temperature was 18°C, and we monitored in real time the temperature inside an empty falcon tube also placed in the water bath throughout the experiments. The tubes were turned every 30 s. The CT endpoints were measured as the temperature the skinks lost their ability to right themselves within 15 s, when manually turned upside down inside the tube. Immediately after the loss of the righting reflex, we measured the body temperature of the skinks by recording their cloacal body temperature using a calibrated hand thermometer (EcoScan Temp JKT Temperature Meter; EuTech Instruments). Immediately after, we removed the skinks from their tubes and placed them in a shallow dish with water at ambient temperature until they recover.

2.7 | Biophysical modelling

We used the R package *NicheMapR* to model the physiological rates of the skinks (Kearney & Porter, 2020). *NicheMapR* includes a microclimate model (function *micro_ncep*) that integrates historical 6-hourly macroclimatic data sets from the National Center for Environmental Predictions. The function *micro_ncep* is connected to the package *microclima* (Maclean et al., 2019), which downscales macroclimatic data

to microclimatic conditions, accounting for variation in radiation, wind speed, altitude, surface albedo and cold air drainage. The *micro_ncep* function also accounts for topographic effects (amount of shade via terrain slope) in association with the package *elevatr* (Hollister et al., 2017), which is connected to Amazon Web Services Open Data. We used *micro_ncep* to model microclimatic conditions with locally estimated slope and aspect, with the 'soil moisture routine' turned on (Kearney & Maino, 2018), and with soil properties drawn from the SoilGrids data set (Hengl et al., 2017). Our model ran under unshaded conditions, in order to capture the hottest conditions that could affect distribution limits (Enriquez-Urzelai et al., 2019). We ran the microclimate model for a period of 3 years (2018–2020).

Using the physiological data collected in this study, we computed the heat and water budget of each species in this study across the latitudinal gradient in eastern Australia. We modelled a lizard-like model at steady-state body temperature with thermoregulatory behaviour, using the function *ectotherm*. We set activity as diurnal and allowed the ectotherm to seek shade in burrows (maximum depth of 100cm). For each skink species, we used the data collected for body mass, T_{pref} and $CT_{max/min}$ to parametrize the models (see details in Table S2), enabling us to generate species-specific simulations (Kearney et al., 2013). We then used the physiological data collected for metabolic rate, evaporative water loss, and sprint speed to fit different curves as a function of temperature, including simple linear regression, exponential and quadratic functions. We selected the best fit via Akaike's information criteria (AIC). We then used the best fit function (Table S3) to predict the metabolic rate, evaporative water loss, and sprint speed of each species as a function of the hourly body temperatures simulated in NicheMapR (Kearney et al., 2008). We ran the models for 3713 coordinates in eastern Australia, spaced at 0.25°, using QGIS (version 3.10.11). These coordinates were extracted as regular points, which were bound by the range maps of each species available at the International Union for Conservation of Nature (IUCN) (Tingley et al., 2019). The westernmost limit of the selected coordinates was the eastern side of the Great Diving Range, which is known to limit the distribution of *Lampropholis* (Chapple, Chapple, et al., 2011; Wilson & Swan, 2021). Thus, for each coordinate, we were able to predict the sprint speed, evaporative water loss, and metabolic rate (which were averaged) of each species in our study.

2.8 | Distribution modelling

We assigned the presence or absence of each species to each of the coordinates used to model physiological rates. To do that, we used extent of occurrence range maps available from IUCN species assessments (<https://www.iucnredlist.org/resources/spatial-data-download>) to draw regular points (spaced by 1 km) across the range of each species. Hence, for each coordinate and species combination, we obtained a data set consisting of predicted physiological traits, as well as the presence (1) or absence (0) of the species for the eastern coast of Australia. We then fit a logistic regression model, in which species presence/absence was

the response variable, and the simulated physiological traits (mean of evaporative water loss, metabolism, and sprint speed for each cell) and all possible interactions were predictors. We selected the most parsimonious logistic regression model using AIC. From the best-fitting model, we predicted, for each cell, the probability of occurrence of each skink species based on its physiological traits (see Table S4). In order to compare models based on physiological traits to models using only macroclimatic data without biophysical transformations, we fitted logistic regression including variables (air temperature, relative humidity, wind speed, solar radiation) extracted from the NCEP macroclimate data and all possible interactions. From these regressions, we predicted the probability of occurrence based on macroclimatic variables (Table S5).

2.9 | Phylogenetic tree

We constructed a phylogenetic tree containing all the species in our study using the mitochondrial DNA gene, ND4. ND4 sequences for each species/population were obtained from GenBank, or from unpublished research that used the methods outlined in Chapple, Hoskin, et al. (2011). GenBank accession numbers for all sequences are provided in Table S6. Sequences were edited and aligned (using default parameters of Clustal W; Larkin et al., 2007) in Geneious 7.1.5 (Kearse et al., 2012). We translated all coding region sequences in MEGA X (Kumar et al., 2018) to ensure none contained premature stop codons. The closely related *Carinascincus pretiosus* was used as an outgroup (Table S6). We used jModelTest 2.1.10 (Darriba et al., 2012) to identify the most appropriate model of sequence evolution based on the Bayesian Information Criterion (BIC). This model was then implemented in MEGA X to generate a maximum likelihood (ML) tree ($-\ln L = -3467.90$). Node support was estimated using 1000 bootstrap replicates.

2.10 | Phylogenetic analyses

We fitted phylogenetic generalised linear mixed models (PGLMM), using the package *phyr* (Li et al., 2020) in R (R Core Team, 2021), to compare the physiological traits between range-restricted and widespread species along the latitudinal gradient of Eastern Australia. Importantly, we considered the three populations of *L. delicata* as different 'species', since they are divergent lineages and are exposed to different environmental pressures (Chapple, Chapple, et al., 2011; Chapple, Hoskin, et al., 2011).

First, we examined whether thermal sensitivity of physiological traits (metabolism and evaporative water loss) differ between range-restricted and widespread species, and whether it varies along the latitudinal gradient. To do that, we extracted for each individual the slope coefficient from linear model fit between logarithm metabolic rates, or evaporative water loss, and temperature. We used this slope as our response variable in a PGLMM model, which included the interaction of latitudinal position (North Queensland, South Queensland, and New South Wales)

and range (range-restricted vs widespread). As random factors, we set individual identification and the block of experiments an individual was tested in (i.e. the year in which they were tested, time of the day).

Similarly, to compare field body temperatures, thermal preference, critical thermal minimum and maximum, thermal performance breadth and thermal optimum, we fitted a PGLMM for each trait including the interaction between latitudinal site and geographic range as predictor. For all the models, we evaluated the good-of-fitness using the package *rr2* (Ives, 2019).

To compare the presence probability maps generated using mechanistic models (i.e. with physiological data) to maps generated only with macroclimatic data, we quantified the area under the receiver operating characteristic curve (AUC) using the package *PresenceAbsence* in R (Freeman & Moisen, 2008). In this case, AUC is a measure of how well predicted probabilities of occurrence distinguish sites where a species is present from where it is absent. Higher AUC values (closer to 1) indicate better performing models. To calculate AUC, we trained our models by performing 10-fold cross-validation using the package *caret* in R (Kuhn, 2008). We used all available data produced by the cross-validation to predict the presence probability of skinks in each cell. The AUC was then calculated from the probability of presence after the cross-validation process.

3 | RESULTS

3.1 | Thermal sensitivity of metabolic rates and evaporative water loss

We did not find significant differences between the thermal sensitivity of metabolic rates of range-restricted and widespread species (PGLMM = 0.021 ± 0.029 SE, Z score = 0.729, $p = 0.465$), and no significant effects of the interactions between range and latitudinal sites (Table S7; Figure 1a). However, we found an effect of latitude, with species from south Queensland showed significant lower sensitivities than species from other sites (PGLMM = -0.045 ± 0.022 SE, Z score = 2.024, $p = 0.042$). Furthermore, we did not find significant effects of the interaction between latitude and range (Table S7).

Thermal sensitivity of evaporative water loss did not differ between range-restricted and widespread species (PGLMM = 0.022 ± 0.040 SE, Z score = 0.558, $p = 0.576$), neither along the latitudinal gradient (Table S7; Figure 1b). Furthermore, we did not find significant effects of the interaction between latitude and range (Table S7).

3.2 | Thermal performance curves

Thermal performance curves significantly differed between widespread and range-restricted *Lampropholis* skinks (Figure 2; Table S8).

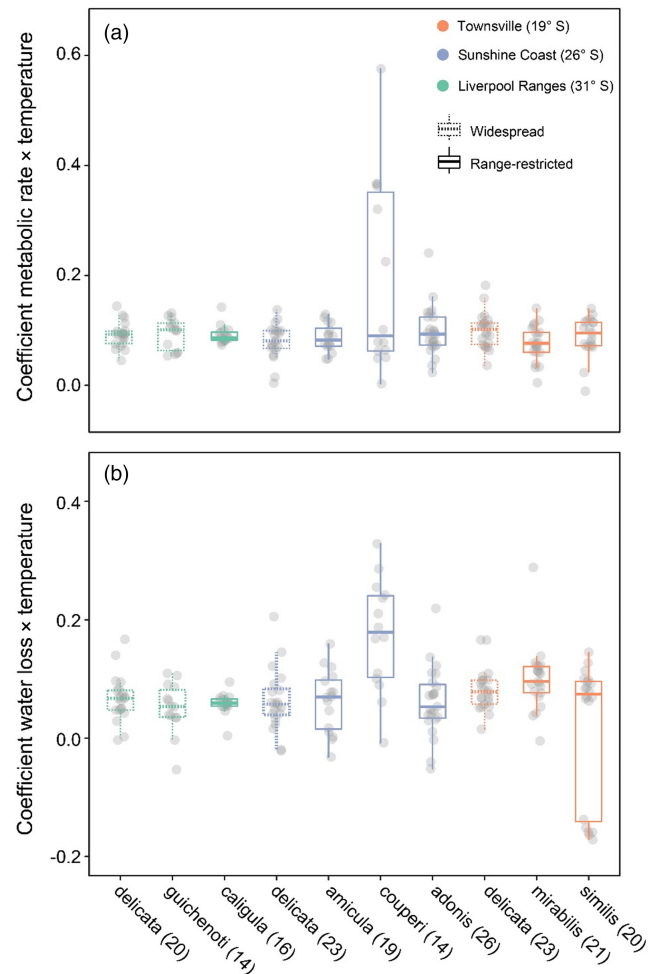


FIGURE 1 Sensitivity of metabolic rates (a) and evaporative water loss (b) to changes in temperatures of widespread and range-restricted *Lampropholis* skinks distributed across the latitudinal gradient of Eastern Australia. Boxes represent the interquartile range (i.e. the range between the 25th and 75th percentile), whiskers the minimum and maximum values within 1.5 times the interquartile range, and the cross bar in the boxes the median. Numbers in the parentheses are sample sizes.

We found that widespread species had lower optimum temperatures (PGLMM = -1.656 ± 0.454 , Z score = -3.642 , $p < 0.001$) and wider thermal performance breadth (PGLMM = 2.004 ± 0.577 , Z score = 3.471 , $p < 0.001$) than range-restricted species (Figure 3). Although we did not find significant effects of latitude in optimum temperatures nor thermal performance breadths (Table S8), there was significant effects of the interaction between range and latitude (Table S8).

3.3 | Thermal physiology

We found that field body temperatures of *Lampropholis* skinks were significantly different between range-restricted and widespread species, with the latter showing lower body temperatures (PGLMM = -1.368 ± 0.461 , Z score = -2.962 , $p = 0.003$; Figure 4a). We also found effects of latitude, with South Queensland

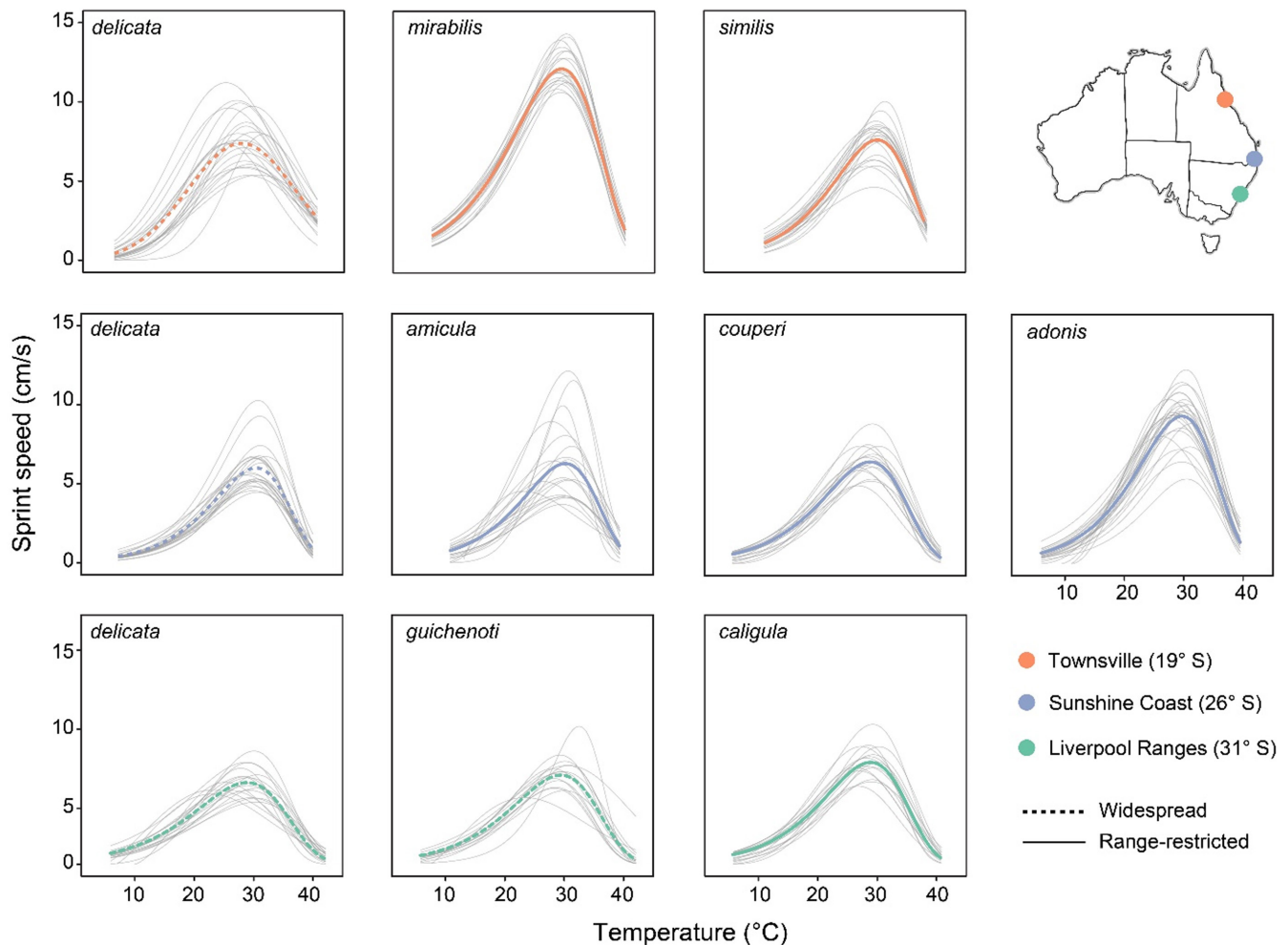


FIGURE 2 Thermal performance curves for locomotor ability (sprint speed) of range-restricted and widespread species of *Lampropholis* skinks. Animals were collected from three different latitudes along eastern Australia. The grey lines indicate thermal performance curves fitted for each individual, and the coloured line represents the overall for the whole species/population.

(PGLMM = -0.802 ± 0.346 , Z score = -2.311 , $p = 0.020$) and NSW species (PGLMM = -2.719 ± 0.520 , Z score = -2.316 , $p < 0.001$) showing reduced body temperatures compared to North Queensland species (Table S9). The interaction between range (widespread) and latitude (New South Wales) was also significant (PGLMM = 1.723 ± 0.771 , Z score = 2.423 , $p = 0.015$; Table S9).

Thermal preference was also similar between widespread and range-restricted species (PGLMM = 1.405 ± 0.980 , Z score = 1.434 , $p = 0.151$; Figure 4b), but it differed among latitudes, with species from NSW exhibiting significant higher thermal preference (PGLMM = 2.022 ± 1.005 , Z score = 2.010 , $p = 0.044$; Table S9). We also found a significant interaction between range and latitudes (PGLMM = -2.86 ± 1.345 , Z score = -2.126 , $p = 0.033$; Table S9).

Critical thermal temperatures differed between range-restricted and widespread species (Figure 5). Critical thermal minimum was lower for widespread species than for range-restricted ones (PGLMM = -2.698 ± 0.608 , Z score = -4.435 , $p < 0.001$), and varied across latitudes, with species from NSW exhibiting lower critical minimum than species from other latitudes (PGLMM = -2.921 ± 0.628 , Z score = -4.655 , $p < 0.001$). The interaction between range

(widespread) and latitude (New South Wales) was also significant (PGLMM = 3.222 ± 0.880 , Z score = 3.664 , $p < 0.001$; Table S10). Critical thermal maximum was higher for widespread than for range-restricted species (PGLMM = 0.494 ± 0.223 , Z score = 2.206 , $p = 0.02$). However, we did not find effects of latitude nor of interactions between range and latitude (Table S10).

3.4 | Distribution predictions

The AUC metrics indicated that physiological traits, estimated through biophysical modelling (Table S4; Figure S1), and macroclimatic variables (Table S5; Figure S2) predicted the distributions of *Lampropholis* species with high accuracy (all models with AUC > 0.8) (Figure 6; Figures S3 and S4; Table 1). However, for all range-restricted species except *L. caligula*, physiological models had a higher predictive power than models incorporating only macroclimatic data (Table 1). For widespread species, physiological and macroclimatic models had similar performance. Values of AUC were above 0.9 for all species when physiological traits were used as model inputs.

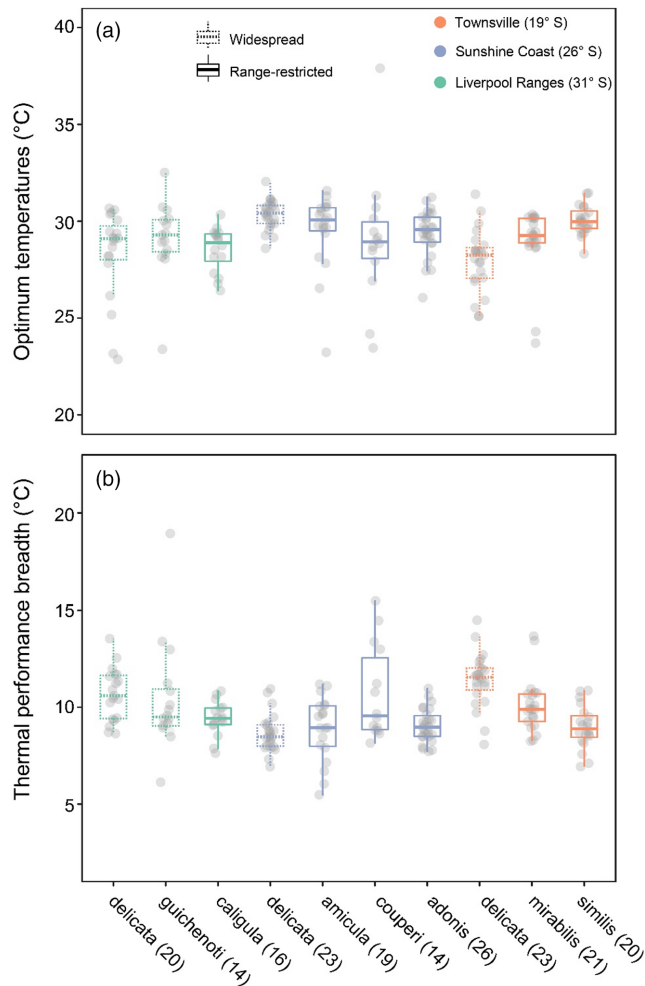


FIGURE 3 Parameters of the Thermal Performance Curves of *Lampropholis* skinks collected from three different latitudes across eastern Australia. (a) Optimum temperature for the sprint speed of the skink. (b) Thermal Performance Breadth, which indicates the range of temperatures within which the skinks attained 80% of the maximum performance. Boxes represent the interquartile range (i.e., the range between the 25th and 75th percentile), whiskers the minimum and maximum values within 1.5 times the interquartile range, and the cross bar in the boxes the median. Numbers in the parentheses are sample sizes.

4 | DISCUSSION

We first tested CVH predictions by investigating correlations between distribution of *Lampropholis* skinks and their physiological traits. Although we did not find support for the CVH in metabolism and water loss, thermal physiological traits and thermal performance curves differed between range-restricted and widespread species. This suggests that thermal relationships are key drivers of physiological adaptations to climate, and consequently shape skinks distributions. Latitude (here used as a proxy of thermal variation), and the interaction between range size and latitude, were also important factors influencing physiology. In general, widespread species from higher latitudes exhibited physiological responses (e.g., lower

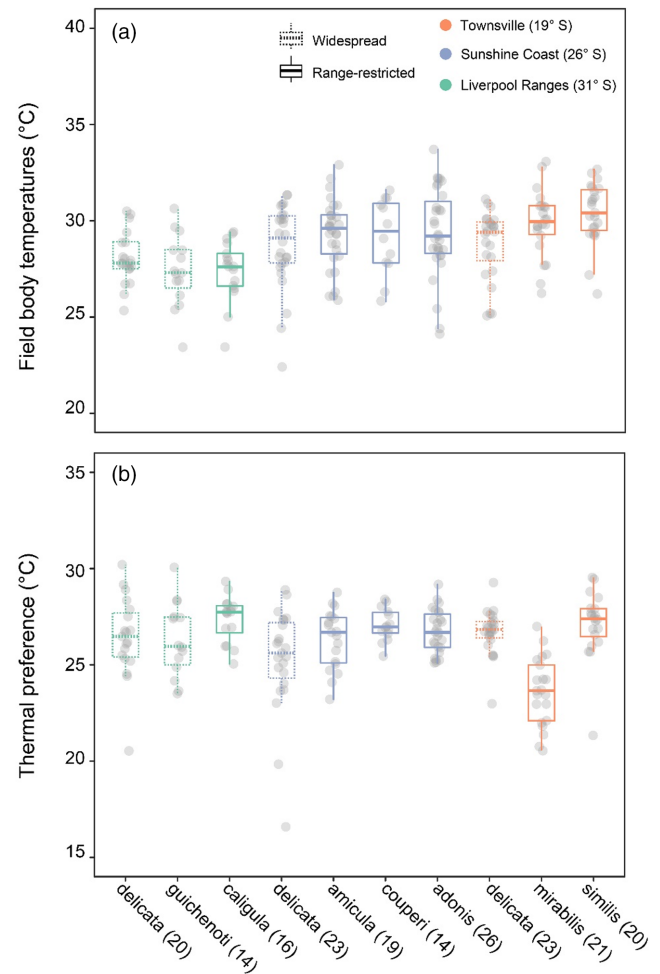


FIGURE 4 Field body temperatures (a) measured for active *Lampropholis* skinks collected from three different latitudes across eastern Australia, and thermal preference (b) measured in thermal gradient in the laboratory, without biotic or abiotic constraints. Boxes represent the interquartile range (i.e., the range between the 25th and 75th percentile), whiskers the minimum and maximum values within 1.5 times the interquartile range, and the cross bar in the boxes the median. Numbers in the parentheses are sample sizes.

thermal limits, wider thermal performance breadths and lower optimum temperatures) expected according to CVH predictions.

Second, we tested the hypothesis that physiology and behaviour play a significant role in shaping the distribution of *Lampropholis* skinks. We found that mechanistic models can better predict the probability of presence than sole climatic layers, suggesting that integrative approach and organismal information is key for enhancing distribution models (Kearney & Porter, 2009; Muñoz & Bodensteiner, 2019).

4.1 | Physiology, climate, and distribution

We were able to pinpoint physiological aspects that might be key in interacting with climate to establish range limits. Contrary to our

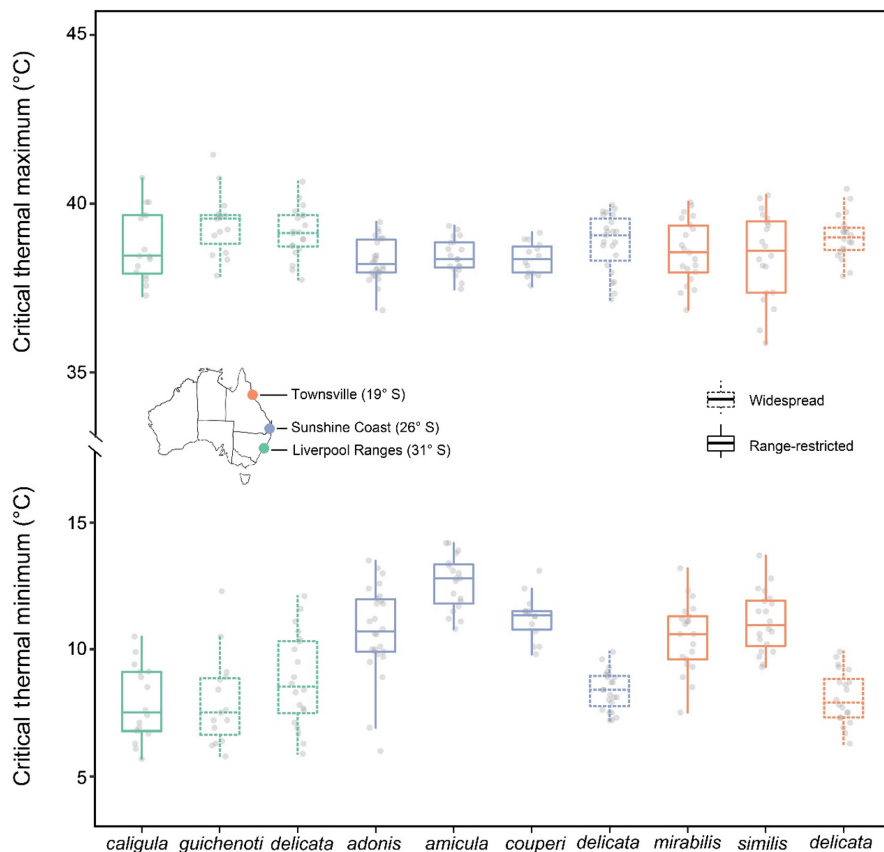


FIGURE 5 Critical thermal minimum (lower boxplots) and maximum (upper boxplots) of *Lampropholis* species from three different latitudes across eastern Australia.

predictions, thermal sensitivity of evaporative water loss and metabolic rates did not differ between widespread and range-restricted species. Despite variations of these traits in lizards are known to occur at regional (Angilletta, 2001; Withers et al., 2000) and global scales (Anderson, White, et al., 2022; Cox & Cox, 2015), such variation does not appear to be related to distribution size of *Lampropholis* skinks. In this group, metabolic rate and evaporative water loss are known to respond to climatic variation across geographic gradients (Anderson, Alton, et al., 2022), but these observations are mostly from intraspecific comparisons (Llewelyn et al., 2016; Phillips et al., 2016). This could be likely due to phylogenetic conservatism of metabolic rates and evaporative water loss in this genus, and that these traits are not exposed to strong natural selection forces across their range (Llewelyn et al., 2016; Martins et al., 2019). Similar observations have been made for invertebrates, in which resistance to desiccation was not correlated with range size (Pallarés et al., 2022) and thermal sensitivity of metabolic rates did not change across tropical and temperate species of stoneflies (Shah et al., 2021). Our results suggest that the *Lampropholis* species might conserve low thermal sensitivities for metabolism and water loss (Pallarés et al., 2022), perhaps due to behaviour buffering effects of climatic variation and reducing selective pressures on thermal sensitivities (Muñoz & Losos, 2018).

According to the CVH, thermal performance curves are expected to be broader in species with large distributions (Hertz et al., 1983; Navas, 1996, 2002). This can reflect a trade-off between being a specialist in one specific climate versus a generalist able to survive

in a variety of conditions (Angilletta et al., 2010; Huey & Kingsolver, 1989). Our findings support this trend, with widespread species having broader thermal breadths than range-restricted species, which is also seen in other ectotherms (Gvoždík & Van Damme, 2008; Huey & Slatkin, 1976). This suggests that broader performance breadth contribute to range expansion as widespread species can perform near maximum levels in more habitats than specialised species (Jacob et al., 2018). Moreover, the lower optimum temperatures of wide-spread species indicate that thermal performance curves track thermal variation the skinks experience in the field (Angilletta Jr et al., 2002), and support the idea that range-restricted species are thermally specialised (Angilletta et al., 2010). Indeed, broad thermal performance curves and lower optimum temperatures are reported for other ectotherms exposed to climatic variation, such as anurans living at high elevations (Navas, 1996) and temperate tree frogs (John-Alder et al., 1988). These changes in thermal performance curves are likely key responses of widespread species to occupy areas with high environmental constraints (e.g. colder temperatures), whereas range restricted species are adapted to narrow environmental conditions (Jacob et al., 2018). Finally, although we did not find a strong effect of latitude on thermal performance, there was a significant interaction between range and latitude (see also van Berkum, 1988). This supports the idea that climate influences the distribution of species through affecting their thermal performance. For example, tropical range-restricted species exhibited a narrow range of optimal temperatures compared with widespread species from southern distributions (Deutsch et al., 2008).

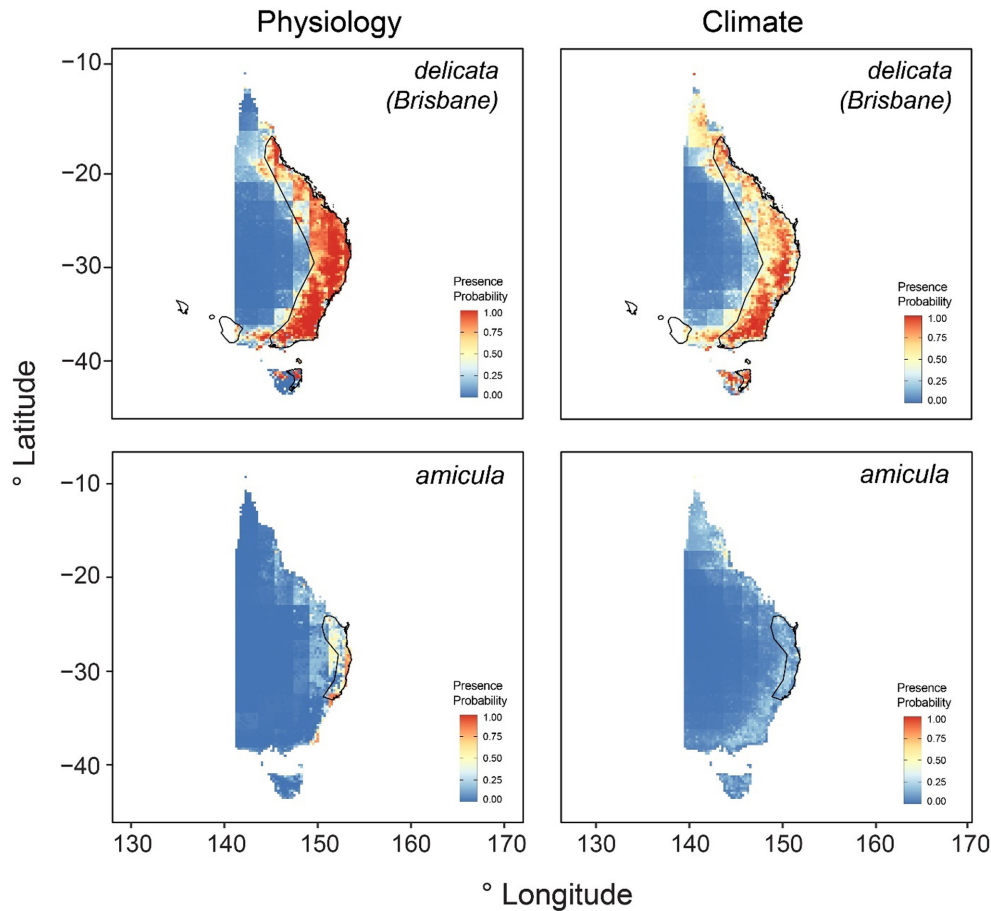


FIGURE 6 Probability of presence predicted by physiology (left panels) and climate (right panels) of a widespread (*Lampropholis delicata*) and a range-restricted (*L. amicula*) species inhabiting eastern Australia. The black polygon indicates the observed occurrence of the species. Distribution maps for all species can be found in [Figures S3 and S4](#).

TABLE 1 Area under the curve (AUC) of distribution maps generated from physiology and macroclimate for widespread and range-restricted species of the *Lampropholis* skinks. The AUC values indicate how well predicted probabilities of occurrence distinguish sites where a species is present from where it is absent. Higher AUC values (closer to 1) indicate better performing models.

Species	Distribution	Physiology AUC (\pm SD)	Macroclimate AUC (\pm SD)
<i>L. adonis</i>	Range-restricted	0.944 (\pm 0.009)	0.885 (\pm 0.008)
<i>L. amicula</i>	Range-restricted	0.941 (\pm 0.007)	0.833 (\pm 0.008)
<i>L. caligula</i>	Range-restricted	0.916 (\pm 0.029)	0.972 (\pm 0.011)
<i>L. couperi</i>	Range-restricted	0.960 (\pm 0.005)	0.833 (\pm 0.008)
<i>L. similis</i>	Range-restricted	0.973 (\pm 0.005)	0.956 (\pm 0.01)
<i>L. delicata</i> (Brisbane)	Widespread	0.967 (\pm 0.002)	0.958 (\pm 0.003)
<i>L. delicata</i> (New South Wales)	Widespread	0.948 (\pm 0.003)	0.958 (\pm 0.003)
<i>L. delicata</i> (Townsville)	Widespread	0.921 (\pm 0.004)	0.958 (\pm 0.003)
<i>L. guichenoti</i>	Widespread	0.977 (\pm 0.002)	0.981 (\pm 0.001)

Many studies have found interspecific variations of lizards' thermal preference and field body temperatures at local and global scales and it is often attributed to be an influence of climate (Anderson, White, et al., 2022; Clusella-Trullas et al., 2011; Meiri et al., 2013). For *Lampropholis* skinks, we also observed effects of latitudinal trends in both field body temperatures and thermal preferences. This indicates that these ectotherms actively thermoregulate to compensate for detrimental environmental conditions, as observed

along geographic gradients (Anderson, Alton, et al., 2022; Llewelyn et al., 2017). Although thermal preferences of skinks were similar between widespread and range-restricted species, field body temperatures differed. In the laboratory, they showed similar thermal preferences, which indicate that, in the absence of abiotic and biotic constraints, both widespread and range-restricted species converge to a similar preferred temperature. However in the field, widespread species had lower field body temperatures than range-restricted

species, even at low latitudes. This discrepancy between field body temperatures and thermal preferences indicates that ecological interactions (e.g. competition) and behavioural thermoregulation might be driving divergence in field body temperature of skinks (Lelièvre et al., 2011; Michelangeli et al., 2018). As these skinks occupy microhabitats varying in thermal characteristics, ecological pressures might have pushed them to select microenvironments to which they became physiologically adapted. For example, tropical and subtropical range-restricted species are typical rainforest-associated *Lampropholis* species, generally active in canopy gaps, where they can maintain high body temperatures. While widespread species can be found in a more variety of habitats (e.g. forest edges, wet sclerophyll forest) and perform at a broad range of temperatures.

Thermal tolerances of *Lampropholis* skinks correlated with their distributions, that is, widespread species showed, respectively, lower and higher CT_{min} and CT_{max} than range-restricted species. This result confirms that thermal tolerances are key for the distribution of ectotherms, as suggested by the CVH (Calosi et al., 2008; Gutiérrez-Pesquera et al., 2016; Phillips et al., 2016). In fact, in invertebrates (Calosi et al., 2008; Polato et al., 2018) and vertebrates (Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022) interspecific variation of thermal limits can explain range sizes. The limited range of temperatures in the environments inhabited by range-restricted species drive physiological adaptations to narrow ranges of temperature (Araújo et al., 2013). Whereas for widespread species, the occupancy of more diverse habitats and consequently the exposure to wide climatic variation likely selects for a broader thermal tolerance range (i.e. difference between CT_{max} and CT_{min}). The expansion of thermal tolerance in ectotherms is often due to increased tolerance to cold temperatures, as some organisms cannot regulate their body temperature through behaviour (e.g. aestivating animals; Bodensteiner et al., 2021). However, we also observed that CT_{max} is key for the widespread distribution of these skinks. Although upper thermal limits are phylogenetically constrained in many ectotherms (Araújo et al., 2013), and CT_{max} variation can be prevented by behaviour thermoregulation (Muñoz et al., 2016), the increased heat tolerance of widespread skinks likely aided them to colonise new, hot environments.

4.2 | Impacts of organismal information on distribution models

When modelling skink distributions, mechanistic models, informed by physiological and behavioural data, could better predict the distribution ranges of most range-restricted species of *Lampropholis* compared to macroclimatic models. However, both model types exhibited similar performance for widespread species.

Especially for range-restricted species, models based on physiology and behaviour were more accurate than macroclimatic models. This may be because physiological constraints of range-restricted species are captured by the species-specific physiological models. These models also incorporate behavioural

and microenvironmental aspects that govern the interaction between organism and environment (Anderson, White, et al., 2022; Enriquez-Urzelai et al., 2019). However, for widespread species, macroclimatic and mechanistic models had similar predictive power. This is hard to interpret, but it might suggest that the large niche of most widespread species is easily captured by climatic layers (Tingley et al., 2016). This also highlights potential limitations of mechanistic models. For instance, aspects such as ecological interactions (e.g. competition, predation) are not included in our models, yet such interactions are key in determining the spatial niche of ectotherms (Jacob et al., 2018). Furthermore, we did not account for thermal opportunities (e.g. number of activity hours) or stressful events (e.g. amount of time temperatures were outside the thermal tolerance limits), which could limit the presence of skinks in certain regions (Anderson, Meiri, et al., 2022; Sinervo et al., 2010). These aspects when not incorporated into mechanistic models might limit their predictive power for widespread species, and a mix of correlative and physiological models might be the solution (Enriquez-Urzelai et al., 2019).

Overall, our results agree with previous studies that have also found that physiology is key for mapping distributions of ectotherms (Enriquez-Urzelai et al., 2019; Tingley et al., 2014). Incorporating species-specific physiology and behaviour can account for mechanistic processes that are omitted in standard correlative distribution models that consider only macroclimate (Kearney & Porter, 2009). Given that organisms interact with their environment via physiology (Tracy, 1976), and that they can buffer deleterious effects of climate (Kearney et al., 2009), incorporating physiological data into species distribution models can bring insights that are sometimes overlooked.

5 | CONCLUSIONS

Using an integrative approach encompassing several physiological aspects of Australian skinks, we showed how different traits can be incorporated into a single framework to test hypotheses regarding the processes underlying species distributions. Our result supports CVH, showing that species with widespread distributions exhibit a wider physiological tolerance than species with range-restricted distributions, but also that processes occurring at lower spatial scales (e.g. behaviour) can enrich our understanding of species distribution. For instance, future studies can incorporate species interactions, behaviour and stressful events (e.g. heatwaves) to better resolve climatic determinants of organisms range sizes.

AUTHOR CONTRIBUTIONS

Rodolfo O. Anderson, Craig R. White, Reid Tingley and David G. Chapple designed the study. Rodolfo O. Anderson and Conrad J. Hoskin collected the data. Rodolfo O. Anderson analysed the data. Rodolfo O. Anderson wrote the first version of the manuscript. All authors contributed to and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw physiological data of *Lampropholis* skins and R scripts used for biophysical modelling are available at Bridges Monash University data repository (Anderson & Chapple, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Logistic fit of the presence of *Lampropholis* species in function of their modelled physiological traits. Logistic regressions predict the probability of finding the species according to their physiological responses to environmental conditions.

Figure S2: Logistic fit of the presence of *Lampropholis* species in function of climate. Logistic regressions predict the probability of finding the species according to their physiological responses to environmental conditions.

Figure S3: Probability of presence of widespread *Lampropholis* species across eastern Australia.

Figure S4: Probability of presence of range-restricted *Lampropholis* species across eastern Australia.

Table S1: Information of the collection sites, and the number of the lizards collected.

Table S: Parameters for the *ectotherm* function for the biophysical modelling. These values were estimated through the thermal preference and critical temperature experiments.

Table S3: Equations used to estimate ecophysiological traits of skinks in function of the body temperature (T ; °C) simulated through biophysical modelling. For each species, the equations were the best fit of the ecophysiological data (sprint speed, water loss, and metabolic rates) collected in the laboratory at a range of ecologically relevant temperatures.

Table S4: Logistic models fitted for the Presence of skinks in function of their ecophysiological traits. Comparison of the best-scored model (following Akaike Information Criteria) with a null model (Presence ~ 1) using likelihood ratio test.

Table S5: Logistic models fitted for the Presence of skinks in function of climate. Comparison of the best-scored model (following Akaike

Information Criteria) with a null model (Presence ~ 1) using likelihood ratio test.

Table S6: Sample information and GenBank accession numbers for the *Lampropholis* samples used in the phylogenetic analysis.

Table S7: Output of Phylogenetic Generalised Mixed Models for metabolic rates and evaporative water loss.

Table S8: Output of Phylogenetic Generalised Mixed Models for optimum temperatures and thermal performance breadth.

Table S9: Output of Phylogenetic Generalised Mixed Models for field body temperatures and thermal preference.

Table S10: Output of Phylogenetic Generalised Mixed Models for critical thermal limits.

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