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ARTICLE
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A cautionary message on combining physiological thermal limits with macroclimatic data to predict species distribution

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Abstract

Macroclimatic data are widely used to estimate the realized environmental niche of species and predict the current or the future spatial distribution of species. Because the realized niche is a subset of the fundamental niche—constrained by biotic interactions and dispersal limitations—proxies of the fundamental niche (e.g., thermal limits obtained from physiological experiments) are sometimes combined with macroclimatic data under the assumption that areas predicted as unsuitable from a realized niche perspective may belong to the species' fundamental niche. However, it is unclear whether this assumption is valid and whether thermal limits can be combined with macroclimatic data. Here, we explored these questions using available physiological thermal limits measured for 151 ectotherms. Specifically, we explored whether physiological thermal limits are larger than observed (realized) thermal limits measured using macroclimatic data, and what would be the effect of considering the physiological niche in addition to the realized niche for current and future predictions. Our results confirm previously raised concerns, as physiological limits can delimit a narrower range of thermal tolerance than the realized niche, particularly at the cold end of the thermal gradient where adaptive and/or facilitative mechanisms could allow species to survive in temperatures below physiological limits. These findings show that combining data on physiological thermal limits with macroclimatic data is dubious and that spatial predictions should be interpreted with caution because data on physiological thermal limits do not fit well with macroclimatic data that do not capture the conditions that organisms experience in the wild. While estimated physiological thermal limits are likely of value to complement species distribution studies, they are likely more useful in biophysical models that account for additional processes including the animal's behavior.

Mathieu Chevalier and Vincent Pignard contributed equally to the work reported here.

KEYWORDS
climate change, experimental measures, geographic range, physiological niche, realized niche, species distribution, thermal limits

INTRODUCTION

The environmental niche (Austin, 1985; Grinnell, 1917; Pulliam, 2000; Soberón, 2007) is a key ecological concept to understanding the distribution of species and their response along environmental gradients, which has regained prominence in the context of climate change (Guisan & Thuiller, 2005). Hutchinson (1957), in his conceptual definition of the niche, distinguished (1) the fundamental niche which defines the set of abiotic conditions allowing individuals to survive and reproduce (i.e., where the population growth rate is positive), and (2) the realized (or ecological) niche which is the fundamental niche constrained by biotic interactions and dispersal limitations (Chase & Leibold, 2003; Pulliam, 2000). The realized niche is therefore expected to be a subset of the fundamental niche (Araujo & Guisan, 2006; Soberon & Arroyo-Peña, 2017).

Overall, two strategies are commonly employed to predict species distributions, one mechanistic based on the fundamental niche and the other correlative based on the realized niche. Mechanistic niche models based on the principles of biophysical ecology use physiological data to capture the balances of heat, water, and other aspects of energy and mass exchange between organisms and their microclimate to capture the processes behind the species' response to the environment (Briscoe et al., 2023; Kearney & Porter, 2004). These mechanistic biophysical models require data on the relationship between the species' environmental conditions and its performance under the assumption that a particular set of processes are influencing the phenomena of interest (e.g., the spatial distribution of species and its response along environmental gradients; Burrows et al., 2011). Because these mechanistic niche models are based on experimental data, explicitly account for physiological mechanisms, and do not account for biotic interactions, it is usually considered that they model the fundamental niche (Briscoe et al., 2023). The second approach is phenomenological in nature and uses empirical species distribution data together with macroclimatic data to find relationships between the phenomena of interest and predictor variables (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). These correlative niche models are widely used to predict distributional responses to changing climate (Guisan & Thuiller, 2005). It is assumed that correlative models estimate the realized niche since they rely on the current distribution of species which is constrained by biotic interactions and dispersal limitations (Guisan et al., 2017). Both approaches have advantages and drawbacks. On the one hand, biophysical models are supposedly more accurate in predicting the response of species along environmental gradients since they explicitly integrate the physiological response of species to changing conditions (Kearney & Porter, 2004; Urban et al., 2016). However, the data necessary to calibrate such models are difficult and costly to acquire, precluding their use to a large number of species (Briscoe et al., 2023). On the other hand, while correlative models are easy to use and can be applied to numerous species, they mostly rely on macroclimatic data although the effect of microclimatic conditions is increasingly recognized as important (Haesen, Lenoir, et al., 2023), and does not account for the physiological processes behind species distribution changes (Guisan et al., 2017).

A main goal of both approaches is to provide predictive maps of the effect of various anthropogenic pressures (e.g., climate change) on species distribution (Briscoe et al., 2023) at a macroecological scale under the assumption that a drastic reduction in the species range implies a higher risk of extinction (Guisan & Thuiller, 2005; Kearney & Porter, 2004). Due to their spatial underpinnings, both approaches are frequently referred to as species distribution models (SDMs) and some studies have shown that they can yield similar predictions regarding, for example, the effect of climate change on species (e.g., Kearney et al., 2010). However, other studies have shown the opposite. Specifically, because mechanistic SDMs neglect the effect of biotic interactions and dispersal limitations, they tend to overestimate species ranges and therefore underestimate species extinction risks (Kearney & Porter, 2009). In contrast, correlative SDMs usually face extrapolation and transferability issues (Yates et al., 2018) because biotic interactions and dispersal limitations do not allow covering the full response of species along environmental gradients (Broennimann et al., 2021; Veloz et al., 2012). A related consequence is that correlative SDMs cannot predict the distribution of species if biotic interactions change (Jiménez et al., 2019; Wisz et al., 2013) and therefore also assume that biotic interactions are stable over time (Pearman et al., 2008). However, under climate change, mounting empirical evidence indicates that species are tracking suitable environmental conditions at a different pace (Burrows et al., 2011; Lenoir et al., 2020), implying potential changes in biotic interactions (Blois et al., 2013; Montoya & Raffaelli, 2010). These changes may lead species to occupy sites with abiotic conditions previously not included within their realized niche but that belong to their fundamental niche, for example, if there is a release of the competition pressure that allows species to colonize and thrive in new abiotic conditions (Catullo et al., 2015). Such examples of niche shifts have been documented for a number of invasive species (Broennimann et al., 2007; Guisan et al., 2014; Petitpierre et al., 2012). Hence, the use of the fundamental niche in correlative SDMs is increasingly recognized as potentially useful for the interpretation of distribution patterns (Catullo et al., 2015; Gong et al., 2023; Gouveia et al., 2014; Kearney & Porter, 2009; Martínez et al., 2015; Pearson & Dawson, 2003), and some studies have shown that including physiological data (e.g., estimated thermal limits, considered in this context as a proxy for the fundamental niche) as predictors in correlative SDMs can reduce the estimated impact climate change can have on the distribution of species (Gamliel et al., 2020). However, previous studies have raised concern regarding this approach because it is unclear whether physiological data accurately reflect the limits of the fundamental niche. Indeed, physiological limits are related to particular aspects of the metabolism (e.g., for reptiles, thermal requirements for egg development, thermal preferences and tolerances, metabolic and evaporative water loss rates; Kearney & Porter, 2004), can vary throughout the year (Bozinovic et al., 2011), the life stages (Pottier et al., 2022), between individuals (Kearney, 2006), and are measured under controlled conditions that do not account for the covariation with other important factors (e.g., humidity; Briscoe et al., 2023). Despite these limitations, physiological data are sometimes included as predictors (or priors when models are fitted within the Bayesain framework; Gamliel et al., 2020) in correlative SDMs (Martínez et al., 2015; Rodríguez et al., 2019) or used to set up parameter values in some mechanistic models (e.g., CLIMEX models; Sutherst & Maywald, 1985) fitted with macroclimatic data. Recently, physiological data were also used to asses to which extent species overfill or underfill their distribution limit by comparing physiological limits to macroclimatic data (Kirk & Rahel, 2022).

Beyond these practical aspects, recent studies showed that the realized niche estimated by correlative SDMs can sometimes look larger than the putative fundamental niche measured experimentally (Soberon & Arroyo-Peña, 2017). This contrasts with theory (Hutchinson, 1957) and may happen if (1) there are suitable, but not quantifiable, microhabitats nested within macrohabitats that are overall perceived as nonviable by the available data (e.g., too coarse environmental data; Kennedy, 1997), (2) there are sink populations outside the fundamental niche (Pulliam, 2000), or (3) because of phenotypic plasticity or local adaptation (Mottola et al., 2022). For instance, a recent study showed that the physiological range of tolerance to aridity was narrower than the range of aridity conditions experienced by eight water beetle species over their range suggesting that other nonphysiological factors (i.e., not related to aridity tolerance) can have an important influence in shaping species distributions (Pallarés et al., 2022). Overall, while the realized niche can seem larger than the fundamental niche in real-case studies, the conditions associated with this pattern are likely not tailored to the intrinsic characteristic of the study system in itself but rather to data features. From a theoretical perspective, if one had access to appropriate biological (e.g., only fit populations) and environmental data (e.g., appropriate spatiotemporal resolution given the study species), making it possible to accurately capture the microclimatic conditions experienced by a given species over its range and across its life cycle, then the realized niche should always be narrower than the fundamental niche (Araujo & Guisan, 2006; Pulliam, 2000; Soberón, 2007). When this is not the case, combining physiological data with macroclimatic data to account for the fact that the environment can be suitable beyond realized niche limits no longer applies and can lead to inappropriate predictions, notably by increasing extinction risk predictions.

The GlobTherm database (Bennett et al., 2018) contains information about the physiological thermal limits (PTLs) of hundreds of species of plants, fungi, and animals collected from different studies. Given that temperature is at the basis of most ecological processes (Brown et al., 2004) and is one of the main drivers of the distribution of animal and plant species (Román-Palacios & Wiens, 2020), this database represents a great opportunity for exploring whether and to which extent physiological limits estimated from experiments differ from realized limits estimated from observed data and whether the latter can be used as a proxy for fundamental niche limits in macroecological studies. In this study, we used global geographic databases (GBIF [Global Biodiversity Information Facility] and IUCN [International Union for Conservation of Nature]) to estimate the realized niche thermal limits of 151 ectotherms, while physiological data were considered as putative estimates of the fundamental niche thermal limits of these species. By comparing realized and putative fundamental niche limits, we first tested whether the former is a subset of the latter, considering separately the limits taking place at the cold and the warm ends of the thermal gradient (Figure 1). We then evaluated how and to which extent these differences in thermal limits translated in the geographical space (i.e., influenced the species distribution), and what would

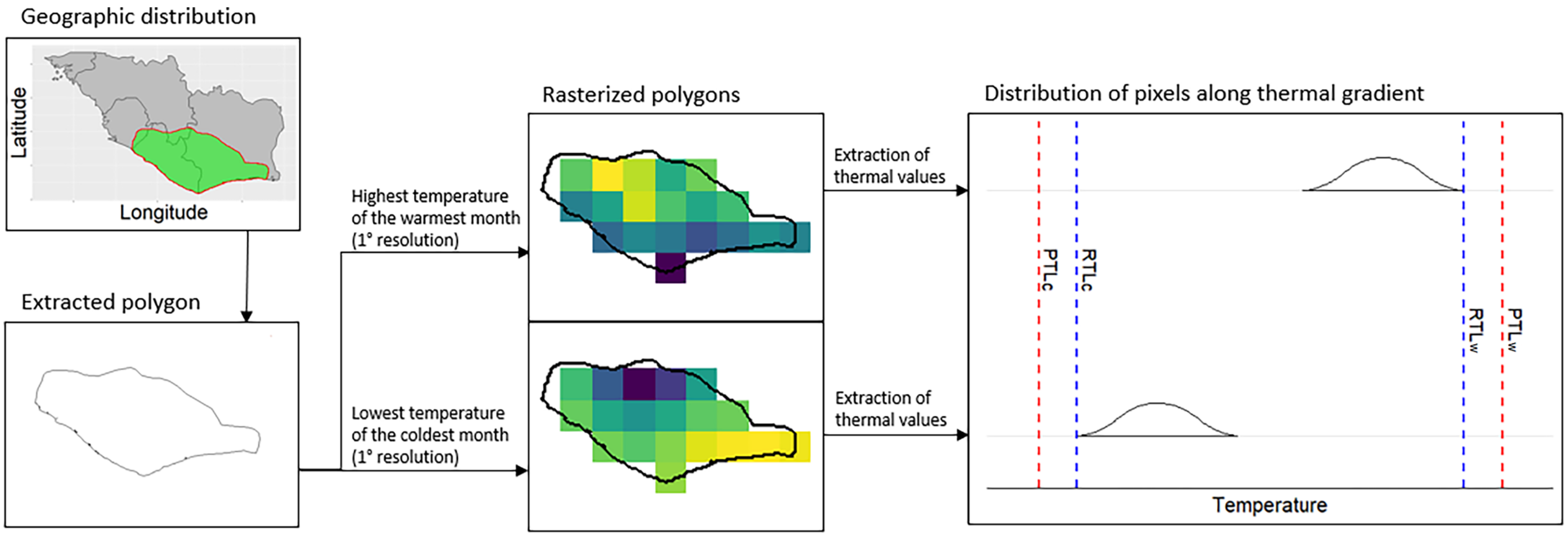

FIGURE 1 Determination of realized thermal limits (RTL) from IUCN (International Union for Conservation of Nature) data. Physiological thermal limits (PTL) were directly extracted from the GlobTherm dataset. PTL_c, PTL at the cold end; PTL_W, PTL at the warm end; RTL_c, RTL at the cold end; RTL_W, RTL at the warm end.

be the effect of considering physiological limits instead of (or in addition to) realized niche limits for current and future predictions. Under the assumption that the realized niche is a subset of the fundamental niche, we predict that some areas predicted as unsuitable in the future according to the realized niche would be predicted as suitable according to physiological limits. If true, this would theoretically open up the possibility to define geographic areas potentially suitable for species under specific physiological assumptions, providing additional interpretation to traditional SDM outputs (Kirk & Rahel, 2022; Rodríguez et al., 2019). However, given the spatial (1°) and the temporal (average climatic conditions over a period of 30 years) resolution of the climatic data used in this study (and in studies of the same type), departures from theoretical expectations (i.e., if the realized niche is larger than the fundamental niche) can be observed and call for caution. In this case, it is unclear how spatial predictions obtained by combining physiological data with macroclimatic data should be interpreted spatial predictions obtained physiological data.

MATERIALS AND METHODS

Datasets

Physiological data

Physiological data were retrieved from the GlobTherm database (Bennett et al., 2018). This dataset contains information on PTLs for six taxonomic groups (Actinopterygii, Amphibia, Gastropoda, Malacostraca, Mammalia, Reptilia), collated from 567 studies. Several metrics were used to determine PTLs depending on the taxonomic group and study. The most common metric was the "Critical Threshold" which is the temperature at which individuals can no longer perform basic functions, such as feeding or moving. For some species, "Lethal Temperatures" (LT50, when 50% of the individuals died; LT100, when 100% of the individuals died) were reported. For mammals, the thermal limit was measured as the "Thermal Neutral Zone" which is the limit above (for the warm end) and below (for the cold end) which an individual must actively regulate its body temperature to maintain a fixed internal temperature. As noticed in previous studies, the thermoneutral zone does not reflect tolerance limits but rather describes the boundaries between which homeothermic endotherms, living under basal-like conditions, would have to react (e.g., by increasing food and water intake), to maintain thermal homeostasis (Mitchell et al., 2018). Hence, mammals were not considered in this study. We also removed freshwater species because no appropriate environmental layers (i.e., describing the climatic conditions within lakes or rivers) exist to accurately characterize the realized thermal range for these species. For the remaining species, we extracted physiological (i.e., putatively estimating the fundamental niche) thermal limits (hereafter PTL) from the GlobTherm database (see dashed red lines in Figure 1). Species for which only information on the warm ($\mathrm{PTL_w}$) or cold ($\mathrm{PTL_c}$) physiological limit was available were retained.

Observed spatial distribution data

Distribution data for the species present in the GlobTherm database were recovered from two databases widely used in the literature: IUCN (https://www.iucnredlist.org/en) and GBIF (https://www.gbif.org/en/). IUCN data are expert-based and come in the form of coarse polygons representing the global geographic distribution of a given species (Herkt et al., 2017; Hurlbert & Jetz, 2007). GBIF data, on the other hand, are citizen science based and come in the form of point coordinates with a high resolution, but whose spatial coverage is limited (Chandler et al., 2017). For each species, GBIF data were cleaned by removing non-georeferenced occurrences, missing observations, duplicated coordinates, and coordinates that had both a latitude and a longitude equal to zero.

Temperature data at macroecological scale

To recover the observed thermal limits at the warm and cold ends of the gradient for each species (i.e., realized niche thermal limits), we used two different raster layers representing the "maximum temperature of the warmest month" (named BIO5 and Max for terrestrial and marine realms, respectively) and the "minimum temperature of the coldest month" (named BIO6 and Min for terrestrial and marine realms, respectively). For terrestrial and freshwater species, we downloaded "Worldclim" raster layers at a 2.5′ resolution (WorldClim; https://worldclim.org/) whereas for marine species we downloaded surface raster layers at a 5′ resolution from "Bio-ORACLE" (Bio-ORACLE: Marine data layers for ecological modeling; https://www.bio-oracle.org/).

To study species range changes from realized or PTLs in the future, we used the same temperature layers as for the current period (i.e., BIO5 and BIO6 for terrestrial species; Max and Min for marine species) considering two Representative Concentration Pathways (RCP) by 2100: RCP 2.6 and RCP 8.5. RCP 2.6 predicts the weakest changes (i.e., mitigation scenario), whereas RCP 8.5 is the scenario that predicts the most significant changes (i.e., business as usual scenario; van Vuuren et al., 2011). For terrestrial environments, we used climatic layers for the years 2081–2100 at 2.5′ resolution derived from the Climate System Model of Beijing Climate Center (BCC-CSM2-MR retrieved from WorldClim). For marine environments, we used layers at 5′ resolution recovered from Bio-ORACLE for the years 2090–2100.

Statistical analyses

Overall, data from 151 species were used in this study. Yet, not all species had information on PTLs at both ends of the thermal gradient. Hence, 135 species were considered to compare PTLs and realized thermal limits (RTL) at the warm end of the thermal gradient, whereas 92 species were considered regarding the cold end. When considering both ends, 76 species were considered. All analyses were performed in R version 4.0.4 (R Core Team, 2019) using the raster package version 3.5 (Hijmans, 2021).

Determining realized niche thermal limits

To determine RTLs from IUCN polygons, we extracted the temperature values of pixels contained within the polygon of each species—thus assuming that the species is present everywhere within the polygon—for both the raster of minimum (to determine the limit at the cold end of the gradient) and maximum (to determine the limit at the warm end of the gradient) temperatures (see Figure 1). The highest and lowest values were then retrieved to determine the RTL at the warm (RTL_w) and the cold end (RTL_c) of the thermal gradient, respectively (dashed blue lines in Figure 1). Due to their low precision (Akçakaya et al., 2006), IUCN polygons were rasterized at a low spatial resolution (1°) for both terrestrial and marine environments (Hurlbert & Jetz, 2007). For GBIF data, occurrences were projected on higher resolution temperature rasters (2.5′ for terrestrial species, 5′ for marine species) and maximum and minimum temperature values extracted.

We tested differences between PTL and RTL (for IUCN and GBIF data) considering both the cold and warm ends of the thermal gradient using Wilcoxon paired tests. Regarding terminology, we use the term “larger” (resp. “narrower”) to describe a larger (resp. lower) tolerance to temperature at both ends of the thermal gradient (e.g., a value of −25°C for RTL_c relative to +2°C for PTL_c would translate as RTL_c being larger than PTL_c).

Determining thermally tolerable geographic ranges from RTL, PTL, and both

In order to measure how the geographic range of each species would change in the future, we computed the proportions of pixels of the current range of species that was included within thermal limits (i.e., the thermal tolerance range) under each projection (current, RCP 2.6, and RCP 8.5) using rasters of 2.5′ resolution (or 5′ for marine species). Indeed, while a coarse resolution is needed to determine RTL owing to the coarse resolution of IUCN polygons, spatial projection can be done at any resolution. This was done separately for both RTL and PTL. Pixels were then classified in three categories: thermally tolerable according to both RTL and PTL (green horizontal arrows in Figure 2), thermally tolerable according to RTL only (yellow horizontal arrows in Figure 2), and thermally tolerable according to PTL only (light-blue horizontal arrows in Figure 2). We also distinguished whether differences in the thermal tolerance range emerged from differences at the cold or at the warm end of the thermal gradient (Figure 2).

For each of the three above-defined categories, we tested differences in the thermal tolerance range (i.e., the proportion of pixels of the species distribution within thermal limits) across the three climatic scenarios (current, RCP 2.6, and RCP 8.5) using Kruskal–Wallis nonparametric tests considering separately the cold and the warm ends of the thermal gradient.

RESULTS

Comparing thermal limits

We found that RTL is on average narrower than PTL at the warm end of the thermal gradient (PTL_w: mean = 41.4°C, SD = 3.4°C; RTL_w: mean = 35.9°C, SD = 4.2°C; paired Wilcoxon test, $p < 0.001$) whereas the opposite occurred at the cold end of the gradient (PTL_c: mean = 7.1°C, SD = 3.6; RTL_c: mean = −4.3°C, SD = 11.3°C; paired Wilcoxon test, $p < 0.001$; Figure 3). Similar results were obtained when RTL were estimated with GBIF data (Appendix S1: Figure S1).

Predicted changes in species’ thermal tolerance range under climate warming

A typical example

Considering as an example the species *Pseudonaja textilis*, we illustrate how combining information on RTL and

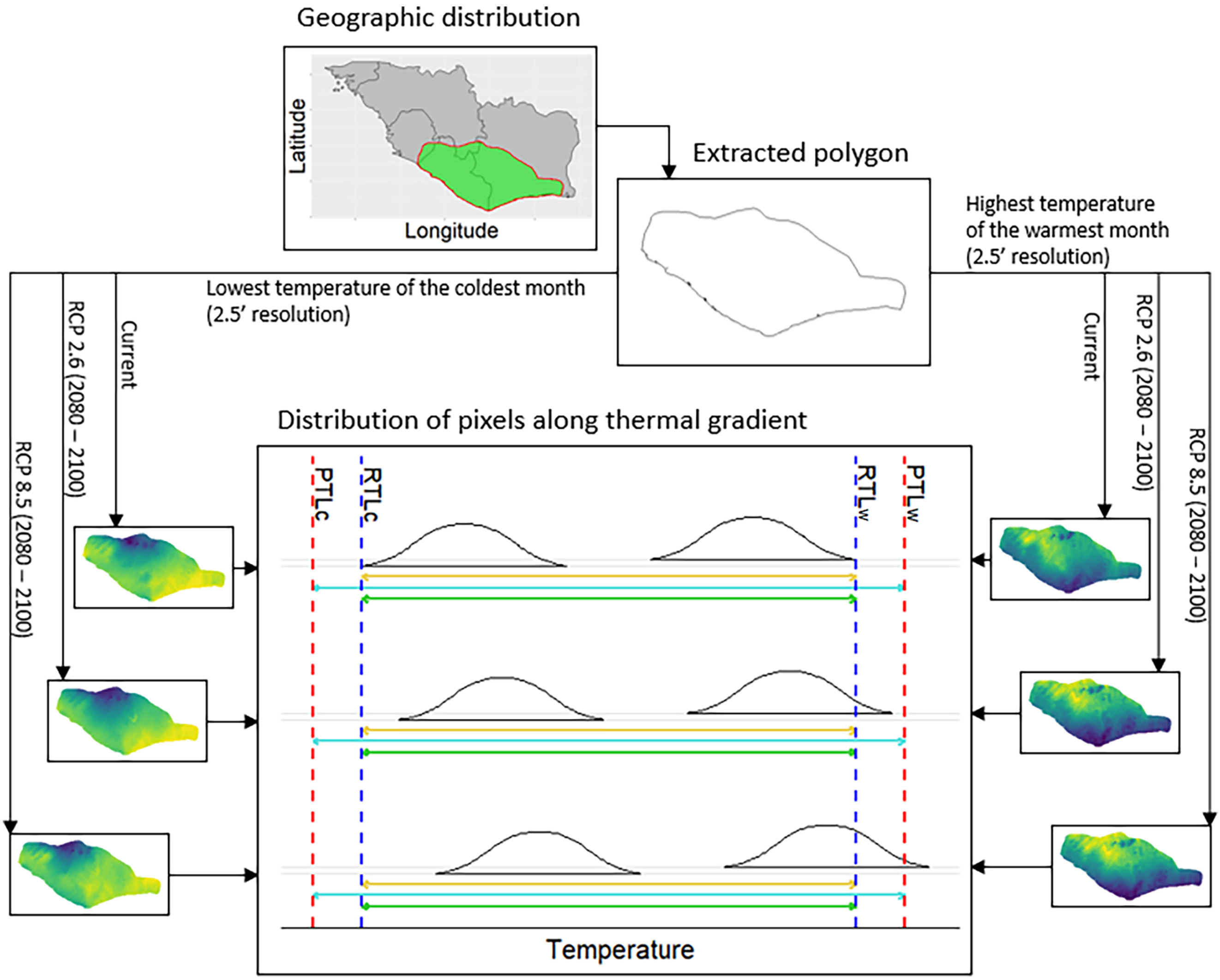

FIGURE 2 Determination of the thermal tolerance range from thermal tolerance values according to physiological thermal limits (PTL) and realized thermal limits (RTL) determined from IUCN (International Union for Conservation of Nature) data. Following theory, PTL should be larger than RTL. Yellow, light-blue, and green horizontal arrows show the thermal tolerance range used to compute the proportion of pixels included within RTL, PTL, and both, respectively. If data are in line with theory, the thermal tolerance range obtained when combining PTL and RTL should equal the thermal tolerance range of RTL (because PTL is expected to be larger than RTL at both ends of the thermal gradient). $\mathrm{PTL_c}$, PTL at the cold end; $\mathrm{PTL_w}$, PTL at the warm end; RCP, Representative Concentration Pathways; $\mathrm{RTL_c}$, RTL at the cold end; $\mathrm{RTL_w}$, RTL at the warm end.

PTL translates in the geographic space (Figure 4). This species is representative of the set of species considered, presenting a larger PTL than RTL at the warm end of the gradient but a narrower PTL than RTL at the cold end of the gradient. Under current climatic conditions, a higher proportion of the IUCN geographic range (98.01%) is thermally tolerable according to RTL relative to both PTL (82.65% of the geographic range) and the combination of PTL and RTL (81.1% of the geographic range). By 2100, and under RCP 2.6, the thermal tolerance range of *P. textilis* is predicted to increase by 10.57% according to PTL, whereas it is predicted to decrease for both RTL (30.69% decrease) and the combination of PTL and RTL (17.42% decrease). Under RCP 8.5, the thermal tolerance range is predicted to decrease with regard to RTL (61.05%), PTL (17.07%), and their combination (56.97%) owing to a decrease in the proportion of pixels included within thermal limits at the warm end of the gradient (61.12% for $\mathrm{RTL_w}$, 29.2% for $\mathrm{PTL_w}$, 61.23% for their combination) not compensated by a similar increase at the cold end of the gradient (0.47% increase in the proportion of pixels included within thermal limits for $\mathrm{RTL_c}$, 18.26% for $\mathrm{PTL_c}$, 18.26% for their combination). Note that some pixels (2.45% of the IUCN geographic range) currently too cold are predicted to become too warm by 2100, considering the combination of RTL and PTL.

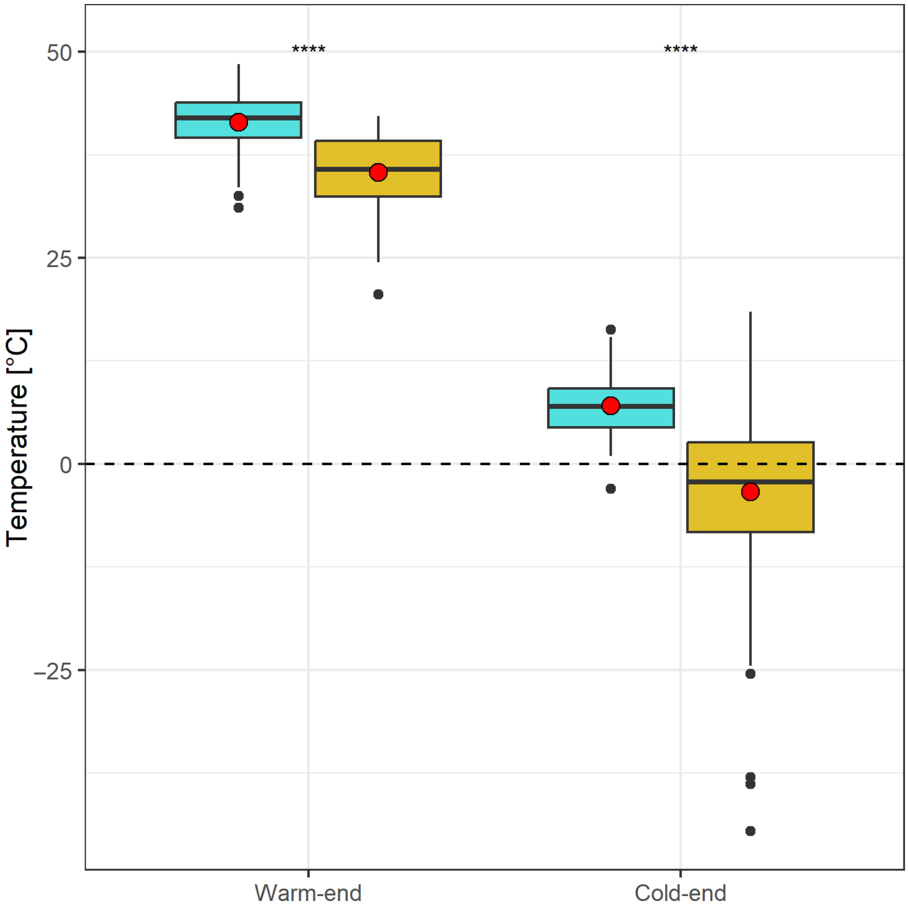

FIGURE 3 Comparison of species' physiological thermal limits (PTLs) and realized thermal limits (RTLs) at both ends of the thermal gradient. PTLs are shown in blue and RTLs are shown in orange. Red points represent average values. For the boxplots, the center line represents the median, the box limits define the upper and lower quartiles, the whiskers define 1.5× the interquartile range, and the points represent outliers. RTL were estimated from IUCN (International Union for Conservation of Nature) polygons rasterized at a 1° resolution. For a similar figure with RTL estimated from GBIF (Global Biodiversity Information Facility) data see Appendix S1: Figure S1.
$^{****}p < 0.0001$.

General trends

The thermal tolerance range is predicted to increase significantly in the future at the cold end of the gradient for RTL ($p < 0.01$) but not for PTL ($p = 0.07$) or the combination of RTL and PTL ($p = 0.06$; Figure 5). In contrast, a significant decrease is predicted to occur in the future at the warm end of the gradient for RTL, PTL, and their combination (all $p < 0.001$; Figure 5). Thermal stress is therefore predicted to decrease in the coldest areas (pixels currently too cold will become thermally tolerable in the future), but to increase in the warmest areas (pixels currently thermally tolerable will become too warm) by 2100. Considering both ends of the gradient, the thermal tolerance range is predicted to decrease significantly for RTL ($p < 0.001$) but not for PTL (where the trend is rather toward an increase; $p = 0.24$) or the combination of PTL and RTL ($p = 0.88$).

DISCUSSION

Physiological data on thermal limits have been widely used to calibrate biophysical models fitted with microclimatic data to account for the physiological processes driving species distributions and related changes (Briscoe et al., 2023). However, these data have also been used as surrogates for fundamental niche limits in correlative SDMs (Gamliel et al., 2020; Martínez et al., 2015; Rodríguez et al., 2019) or in mechanistic SDMs fitted with macroclimatic data (e.g., CLIMEX; Ramirez-Cabral et al., 2017) under the assumption that they can account for environmental conditions existing beyond realized niche limits that can potentially become available to species under climate change, for example, through a release of the competition pressure (Bush et al., 2019; Catullo et al., 2015; Gong et al., 2023; Kearney & Porter, 2009). In this study, we first aimed to assess whether available estimates of PTLs (taken as a proxy for fundamental niche limits)

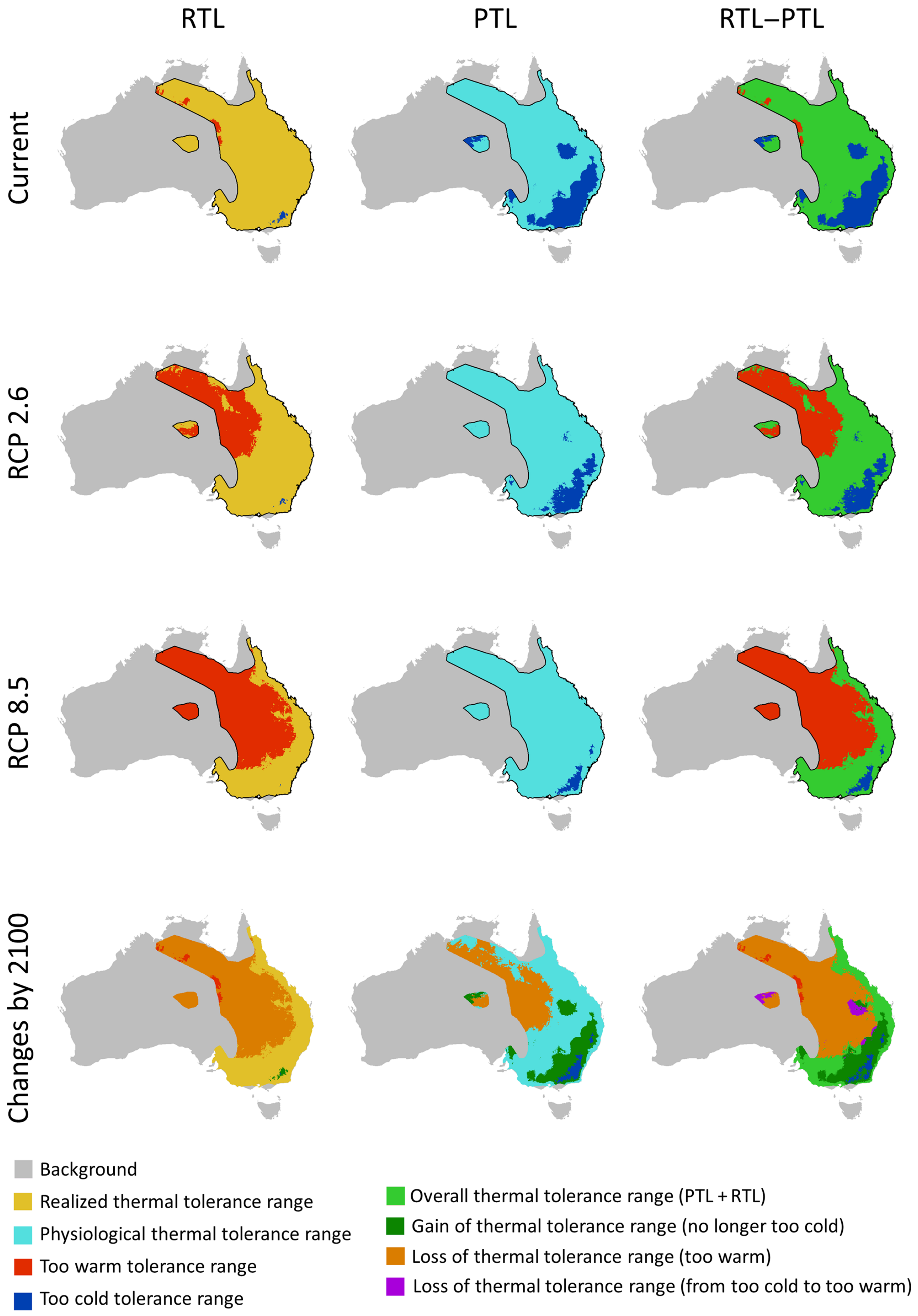

FIGURE 4 Legend on next page.

for 151 ectotherms were expectedly larger than RTLs estimated by coupling distribution data with macroclimatic data (as done in correlative SDMs). Second, we aimed to assess how differences between RTLs and PTLs translate in the geographical space and whether PTL can be used to provide additional insights regarding species current and future distributions, as recently done (Hoffmann et al., 2021; Kirk & Rahel, 2022). At the warm end of the thermal gradient, we found that PTL is, as expected, larger than RTL. However, for the cold end of the thermal gradient, we found that PTL is narrower than RTL which contradicts theory stating that the fundamental niche should be larger than the realized niche. This result invalidates the main motivation for considering physiological data in combination with macroclimatic data to account for the fact that the environment can still be suitable beyond realized niche limits, for example, through a release of the competitive pressure.

At least three reasons can explain why RTL can be larger than PTL in real case studies. First, PTL may be a poor proxy of fundamental limits for several reasons. For instance, the fundamental niche is essentially multidimensional, and should ideally be estimated considering all environmental variables (e.g., water availability) affecting the fitness of species (Kearney & Porter, 2004). Unfortunately, these aspects of the fundamental niche are usually not considered owing to a lack of data (Soberon & Arroyo-Peña, 2017). Furthermore, most studies do not account for (1) the environmental requirements (including thermal limits) associated with different components of the life cycle (e.g., juvenile or adult survival), (2) the demographic parameters directly related to fitness (e.g., fecundity, survival, but see Pironon et al., 2018), or (3) niche differentiation and local adaptation that can exist between races/ecotypes/subspecies (Kearney & Porter, 2004; Pearman et al., 2010). However, whether incorporating these various aspects would lead to a better estimate of the fundamental niche is unclear. Second, our estimates of RTL are conditioned on the environmental data considered and it would be interesting to consider data that better approximate the actual temperature experienced by species across their range. For instance, the coarse resolution of the raster classically used in macroecological studies does not allow accounting for the microclimatic conditions that can act as refugia and allow species to survive in areas estimated as unsuitable from a macroclimatic perspective (Scheffers et al., 2014; Sunday et al., 2012). Furthermore, even if considered at the highest possible resolution (1 km^2), global climatic data (e.g., Worldclim) can still fail to represent the conditions individual species face in reality because these data are produced by interpolating climatic measurements (e.g., rainfall, temperature) from climate stations that measure parameters at standardized heights (2 m above ground) and which are averaged over a 30-year period (Fick & Hijmans, 2017). However, in many situations, ground temperature can deviate from the temperature measured 2 m above ground by more than 10°C (Foken & Napo, 2008) which is problematic for the numerous species that live close to the ground. Hence, although very powerful for species distribution modeling, global climatic data may fail to represent the temperature individual species experience in reality which can lead one to overestimate the magnitude of range shifts under climate change (Maclean & Early, 2023). One way to account for microclimatic conditions would be to use mechanistic microclimatic modeling approaches (e.g., NicheMapR) that calculate the microclimates to which organisms are exposed using principles of micrometerology, soil physics, and hydrology (Kearney et al., 2014). However, these models are extremely data-demanding, requiring as inputs the maximum and minimum daily values of air temperature, wind speed, relative humidity, and cloud cover, the timing of the maxima and minima relative to dawn or solar noon, soil properties as well as the roughness height, slope, and aspect. As such, their applicability remains limited. Another possibility would be to use increasingly available new microclimate datasets such as soilTemp (Lembrechts et al., 2022) or forestTemp (Haesen, Lembrechts, et al., 2023) that correct macroclimate temperature interpolated from weather station records at 2 m height with a temperature offset map derived from temperature loggers placed at different heights on the field (Zellweger et al., 2019). However, although datasets compiled at the continental scale are starting to emerge (Haesen, Lenoir, et al., 2023), their applicability is so far limited owing to a limited temporal or spatial extent and their accuracy remains to be seen (but see Haesen, Lenoir, et al., 2023).

FIGURE 4 Spatial transcription of the thermal tolerance range of *Pseudonaja textilis* according to physiological thermal limits (PTL), realized thermal limits (RTL), and their combination under three climatic scenarios (current, Representative Concentration Pathways [RCP] 2.6 and RCP 8.5). Thermal tolerance range projection obtained from RTLs, PTLs, and their combination under the three projections (current, RCP 2.6, RCP 8.5; first three rows) are represented. The predicted difference in thermal tolerance range between the present and 2100 according to RCP 8.5 is also provided (last row). Thermally unsuitable areas are differentiated according to whether pixels are unsuitable with regards to the cold or the warm end of the thermal gradient. Some pixels currently predicted as too cold are predicted to become too warm by 2100.

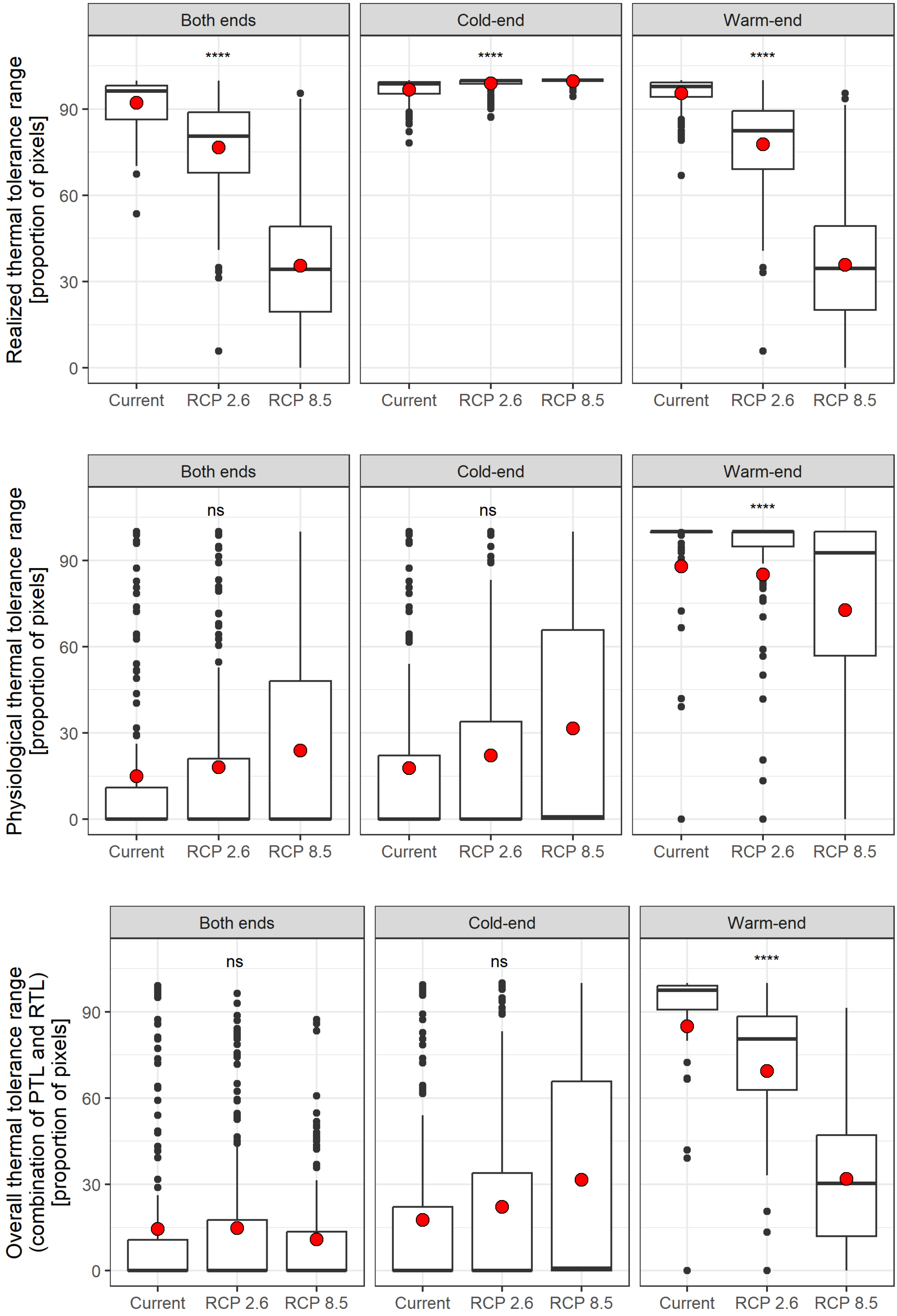

FIGURE 5 Legend on next page.

To be conservative in our assessment of RTL, we focused on the coldest/warmest temperatures of the coldest/warmest month which potentially inflated the thermal limits for most species (84 out of 92 with a RTL_c larger than PTL_c; 9 out of 135 with a larger RTL_w than PTL_w). Beyond methodological issues, a third reason that can explain why RTL can be larger than PTL relates to behavioral, physiological, and/or evolutionary mechanisms. For example, some amphibians have behavioral adaptations to overwinter in water (Boutilier et al., 1997), while others have physiological adaptations allowing them to endure periods of freezing by storing cryoprotective molecules (Storey & Storey, 1986). Marine actinopterygians have also been shown to migrate to avoid cold temperatures (Hurst, 2007; Jansen & Gislason, 2011) but we have not considered (and most distributional studies do not) seasonal changes in geographical distribution which can affect estimates of RTL (Zurell et al., 2018). Similarly, reptiles can migrate over short distances to find overwintering habitats (Southwood & Avens, 2010) where temperatures remain above their PTL_c. These various strategies, only measurable at the microscale, and thus undetectable given the coarse resolution used in this study (and in most SDM studies), probably explain why our results indicate that RTL_c is globally larger than PTL_c.

Data on PTL are used for various purposes such as informing species distributions (Gamliel et al., 2020), evaluating the ability of SDM to inform species fundamental niche limits (Paz & Guarnizo, 2020), assessing species vulnerability to climate change (Hoffmann et al., 2021; Wagner et al., 2023), estimating the fundamental niche (Jiménez et al., 2019), understanding biogeographical patterns (Sklenář et al., 2023), or evaluating the extent to which species overfill or underfill their distribution (Kirk & Rahel, 2022). Most of these studies rely on the assumption that physiological limits are a proxy for fundamental niche limits and that these limits can be used to refine predictions obtained from macroclimatic data. Yet, our results show that combining physiological data with macroclimatic data can lead to inappropriate predictions and erroneous conclusions. This is because critical temperatures obtained from laboratory experiments are not easy to compare to macroclimatic data, as temperature estimates from coarse-grained macroclimatic data do not correlate well with the temperatures organisms actually experience in the wild (Kennedy, 1997). Overall, physiological data are relevant to characterize when individuals are active (daily and seasonally) and how they respond to local-scale microhabitats (e.g., sun vs. shade), an information that is crucial in biophysical models and that can be used to inform large-scale distributions and how species ranges will change under climate change since these models rely on microclimatic data (Briscoe et al., 2023; Kearney & Porter, 2004). These physiological data are, however, of limited use to inform large-scale patterns estimated with macroclimatic data because they do not necessarily represent climatic conditions that exist beyond realized niche limits.

Given that the main motivation behind the inclusion of physiological data in correlative SDMs or in some mechanistic SDMs (e.g., CLIMEX) does not hold for most of the species considered in this study, it is unclear whether differences between PTL and RTL can be used to interpret the spatial structure of species geographical ranges under current and future environmental conditions. For instance, areas currently predicted as unsuitable according to PTL but as suitable according to RTL have recently been interpreted as "distribution overfilling," and suggest that factors unrelated to temperature are affecting species' distribution limits (Kirk & Rahel, 2022). Yet, these factors can be of multiple origins, providing limited insights regarding the mechanisms at play. For instance, while physiological (e.g., thermoregulation) and/or behavioral (e.g., hibernation) mechanisms can explain why populations are found in areas presenting conditions outside PTLs, an alternative explanation could be that these areas are inhabited by sink populations (Pulliam, 2000; Soberon & Arroyo-Peña, 2017) or that populations have locally adapted to the conditions prevailing in the area (Eliason et al., 2011). Regarding areas currently predicted as suitable according to PTL but not RTL, this could suggest that changes in biotic settings (e.g., release of competition or predation pressures) could allow some species to take advantage of existing

FIGURE 5 Estimated thermally tolerable geographic ranges. Proportion of pixels within species IUCN (International Union for Conservation of Nature) geographic ranges classified as thermally suitable according to realized thermal limits (RTL, first row), physiological thermal limits (PTL, second row), and both (RTL–PTL, third row) across all species under the three projections (current, Representative Concentration Pathways [RCP] 2.6, RCP 8.5), considering both ends (left panels), the cold end (middle panels), and the warm end (right panels) of the thermal gradient. The realized thermal tolerance geographic range was estimated using IUCN polygons rasterized at a 1° resolution. For the boxplots, the center line represents the median, the box limits define the upper and lower quartiles, the whiskers define 1.5× the interquartile range, and the points represent outliers. Red points highlight average values. For a similar figure with the realized thermal tolerance range estimated from GBIF (Global Biodiversity Information Facility) data, see Appendix S1: Figure S2. ns, not significant. $^{****}p < 0.0001$.

resources (Brose et al., 2017) and extend their geographic range. For future changes, areas presenting a higher suitability according to PTL_w than RTL_w imply that species could theoretically survive over a larger portion of their geographic range, provided that competition (Bolnick et al., 2010) or predation (Antiqueira et al., 2018) pressures do not change in the future. Yet, it could also point to areas that could become suitable (i.e., pixels currently too cold that become warm enough to be within PTL), provided biotic settings are suitable. Overall, the myriad possible interpretations associated with differences between PTL and RTL make their comparison unlikely to provide any useful insights about the mechanisms at play within species geographical ranges (e.g., dispersal, biotic interactions) or regarding how ranges will evolve under climate change, unless additional information is available to disentangle the potential causes underlying differences between PTL and RTL.

Overall, we showed that RTL is not necessarily more restrictive than currently available estimates of PTL. This result can be explained by several non-mutually exclusive explanations including adaptive/behavioral mechanisms, inflated RTL estimates, inappropriate measures of PTL, the coarse resolution of the environmental data, or the presence of sink populations. This does not mean that one measure is better than another, but rather that their combination with macroclimatic data may lead to an inappropriate interpretation of distribution patterns. Hence, if one wants to model species distributions using physiological measurements, the best way would be to use biophysical models that go into the details of the actual behavior of the species and that explicitly consider the microclimatic and microhabitat conditions experienced by the species (Kearney et al., 2014; Lembrechts et al., 2019), while also accounting for all aspects of the thermal (and other abiotic such as hydric) relationship across the species life cycle (Briscoe et al., 2023). The use of these models is however restricted to some well-known species making SDMs fitted with macroclimatic data still a useful alternative to illuminate global trends across taxa. Such SDMs should however not consider physiological data to refine predictions unless combined with microclimatic data to generate a predictor that reasonably approximates the conditions experienced by the species (see e.g., Gong et al., 2023).

AUTHOR CONTRIBUTIONS

Mathieu Chevalier, Olivier Broennimann, and Antoine Guisan developed the idea. Vincent Pignard and Mathieu Chevalier processed the data, ran the analyses, and wrote the first draft of the manuscript. All authors provided critical comments on previous versions of the manuscript and contributed to the writing of the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are available from Bennett et al. (2018), the Global Biodiversity Information Facility: https://www.gbif.org/, the International Union for Conservation of Nature Red List https://www.iucnredlist.org/resources/spatial-data-download, and Worldclim: https://www.worldclim.org/. Details are provided in *Materials and methods*.

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SUPPORTING INFORMATION

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

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