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RESEARCH ARTICLE

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# Can thermoregulatory traits and evolutionary history predict climatic niches of thermal specialists?

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## Abstract

**Aim:** Predictions of future species distributions rest on the assumption that climatic conditions in the current range reflect fundamental niche requirements. So far, it remains unclear to what extent this is true. We tested if three important factors determining fundamental niche—ecophysiology, morphology and evolutionary history—can predict the realized niche, using thermal specialist ants. They are suitable model organisms because their body temperature, metabolism and fitness are closely tied to the habitat temperatures.

**Location:** Iberian Peninsula and Maghreb.

**Time period:** 2013–2015.

**Major taxa studied:** Ants (Hymenoptera:Formicidae).

**Methods:** We measured heat tolerance, chill coma recovery, body size and phylogenetic relationships in 19 desert specialist ants in the genus *Cataglyphis* to test if these important determinants of fundamental niches are good predictors of species realized niches. We modelled species climatic niches using 19 bioclimatic variables from WorldClim for recorded occurrence of each species.

**Results:** None of the determinants of the species' fundamental niche were linked to their realized climatic niche, modelled using species distribution models. However, both heat tolerance and chill coma recovery were highly correlated with body size and all three thermoregulatory traits were phylogenetically constrained, suggesting they reflect fundamental requirements of each species.

**Main conclusions:** Our results challenge the basic assumption of climatic niche modelling, that the realized niche can be used as a proxy for determining fundamental niche requirements. These findings are particularly concerning for studies that use the species' current realized niche to predict their responses to climate change.

KEYWORDS
ants, ecological niche, fundamental niche, geographic distributions, macrophysiology, thermal tolerance

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Cleo Bertelsmeier and Raphaël Boulay contributed equally to this study.

Raphaël Boulay passed away on 27/06/18. His contributions as an author are listed in the author contribution section.

## 1 | INTRODUCTION

Climatic niches have been the focus of research for over a century because of their importance for understanding species range dynamics in time and space (Chase & Leibold 2003; Elton 1927; Grinnell, 1917). The fundamental niche comprises the entire set of environmental conditions under which a species can survive and reproduce (Hutchinson, 1957), which is determined by the species eco-physiological adaptations (Guisan et al., 2014). It can be represented as an *n*-dimensional hypervolume comprised of species' abiotic requirements (Colwell & Rangel, 2009; Hutchinson, 1957). The realized niche is a part of the fundamental niche actually occupied by the species. Thus, the realized niche is usually narrower than the fundamental niche because biotic interactions (Bolnick et al., 2010; MacArthur & Levins, 1967) and dispersal limitations (Soberon & Peterson, 2005) restrict species ranges.

Although many factors constrain the realized niche, it is generally assumed to reflect, at least to some extent, fundamental niche requirements, that is eco-physiological adaptations. This is an important premise of climatic species distribution models (SDMs) which are widely used in global change biology to predict species' ranges following climate change (Lenoir et al., 2020; Parmesan & Yohe, 2003; Thuiller et al., 2005; Trisos et al., 2020). These models are usually correlative, relying exclusively on occurrence data and climates that species experience throughout their range (Broennimann et al., 2007; Fraimout & Monnet, 2018; Guisan & Thuiller, 2005; Wiens et al., 2009). Thus, they base their predictions of species responses to future climate change on the realized niche and not the fundamental niche which is more difficult to measure. However, if differences in realized niches across species are not linked to differences in eco-physiological adaptations, SDM predictions might not be biologically meaningful.

So far, only few comparative studies have tested the link between realized and fundamental niches across species (Helaouët & Beaugrand, 2009). Functional traits like body size and thermal tolerance reflect fundamental niche requirements and have been shown to be linked to realized niches of mussels (Feng et al., 2020; Kearney et al., 2010), copepods (Helaouët & Beaugrand, 2009) and frogs (Enriquez-Urzelai et al., 2020). Because functional traits have evolved over time in response to the environment, species with a long shared evolutionary history should have similar fundamental niche requirements. As a consequence, a certain degree of niche conservatism across species is expected (Losos, 2008; Wiens & Graham, 2005). Here, our aim is to test to what extent variation in realized niches across species is explained by functional traits and evolutionary history.

To achieve that, we chose ants (Formicidae) as a model system. Ants like all ectotherms are likely to have a climatic niche tightly linked to their fundamental requirements, because their metabolism and fitness are governed directly by environmental temperatures (Angilletta, 2009; Deutsch et al., 2008; Shik et al., 2019). Despite the immense diversity of insects and their importance for ecosystem functioning, they are rarely used to test the contribution of functional traits and evolutionary history in determining realized climatic niches (Kellermann et al., 2012). Insect thermal limits can predict species climatic niches (Arnan & Blüthgen, 2015; Lancaster et al., 2015), and this relationship should be more pronounced in thermal specialists, because their physiology mirrors habitat temperatures. As a result, predictive modelling of climatic niches for species with narrow environmental tolerances is thought to be particularly accurate (Hernandez et al., 2006). However, measuring experimentally an *n*-dimensional fundamental niche is almost impossible. Therefore, we have to rely on measuring species' fundamental requirements that are known to be important aspects of the fundamental niche. Thus, we tested if three factors relevant for determining fundamental niche—ecophysiology, morphology and evolutionary history—can predict the realized niche in thermal specialists.

To do so, we modelled species' realized niches using SDMs, measured thermoregulatory traits and phylogenetic relatedness of thermophilic ants. We used 19 thermal specialist species in the ant genus *Cataglyphis*. *Cataglyphis* ants are desert specialists whose heat tolerance and behaviour are adapted to daily thermal maxima (Boulay et al., 2017; Cerdá & Retana, 2000). We focused on functional traits important for ant thermoregulation—thermal limits and morphology (Baudier et al., 2018; Cerdá & Retana, 2000; Hurlbert et al., 2008; Kaspari et al., 2015; Penick et al., 2017). Generally, ant heat tolerance predicts foraging temperature during which ants acquire resources (Cerdá et al., 1998; Roeder et al., 2018), suggesting an important role of heat tolerance in determining local persistence in relation to climatic variables. Additionally, ants from warmer habitats have higher heat tolerance (Kaspari et al., 2015), and heat tolerance is generally higher in large ants (Baudier et al., 2018), including in some *Cataglyphis* species (Cerdá & Retana, 2000). Thus, we hypothesized that thermal tolerance, morphology and evolutionary history (i.e. phylogenetic relatedness) will be linked to the variation in realized climatic niches among thermal specialist species.

## 2 | MATERIALS AND METHODS

We collected 19 *Cataglyphis* species across their range in Spain and Morocco, mostly between April and June of 2014 (Table S1). We excavated whole colonies, including the queen and brought them to the laboratory. In cases where it was not possible to excavate the whole colony, we collected a colony subset of 100–250 workers. Most colonies were at least 50 m apart and considered to be separate colonies. In the laboratory, we placed the colonies in 20 × 15 × 12 cm plastic boxes lined with Fluon® to prevent ants from escaping. The ants were provided with two 20 × 2 cm test tubes, half filled with water, and sealed with a cotton plug, that ants used a nest. Before using the colonies in thermal assays we kept them at 25°C, 50%–60% relative humidity with ad libitum access to dead mealworms (*Tenebrio molitor*) and 10% sugar water. Colonies were tested one month after collection. This is a sufficient amount of time to remove the effect of field acclimatization, as 7 to 10 days is enough for ants in the laboratory to acclimate new thermal conditions (Chown et al., 2009; Clusella-Trullas et al., 2010; Coulin et al., 2019). We used the same colonies to measure heat and cold tolerance, but each worker was tested only once. Our focal *Cataglyphis* species were: *C. albicans albicans*, *C. albicans vaucheri*, *C. bicolor*, *C. bombycina*, *C. cubica*, *C. emmae*, *C. floricola*, *C. gadeai*, *C. hispanica*, *C. iberica*, *C. mauritanica*, *C. cursor_nr*, *C. rosenhaueri*, *C. savignyi*, *C. tartessica*, *C. theryi*, *C. velox*, *C. viatica*, *C. rubra agilis*. The *albicans* species were defined following the recently published phylogeny (Villalta et al., 2018). The taxonomical identifications of other species groups, particularly the ones from Morocco, were provided by the expert Henri Caignant.

## 2.1 | Measuring thermal tolerances

### 2.1.1 | Heat tolerance

We used lethal temperature at which 50% of the workers in a sample died after heating ($LT_{50}$) as a measure of heat tolerance (Oms et al., 2017). To measure $LT_{50}$, we collected workers of laboratory colonies outside the test tubes. We tested a total of 30 workers from each laboratory colony on a Selecta Plactronic hot plate, using Fluon lined bottomless plastic containers. We used a static assay to record the mortality rate starting at 56°C and ending at 70°C. This temperature range was chosen based on the previous knowledge of *Cataglyphis* heat tolerance, and ground temperatures experienced by *Cataglyphis*, that reach up to 70°C (Cerdá & Retana, 2000; Cerdá et al., 1998). At each temperature, we heated the plate, then placed two ants in the container and recorded mortality after 10 min. We tested, on average, 4 colonies for each of the 19 *Cataglyphis* species (mean ± SE = 4.2 ± 0.8). Overall, we measured $LT_{50}$ for a total of 2391 workers from 80 colonies. Generally, ant lethal temperatures ($LT_{50}$) strongly correlate with measures of critical thermal maxima (Arnan & Blüthgen, 2015). We used $LT_{50}$ because ants frequently experience temperatures close to their thermal maximum while foraging on the hot desert sand, and because its connection to optimal foraging of *Cataglyphis* and other xerothermic ants is well documented (Cerdá & Retana, 2000; Cerdá et al., 1998). We used a logistic regression to estimate $LT_{50}$ for each species (Figure S1) which is the variable used in subsequent analyses.

### 2.1.2 | Chill coma recovery time

To assess lower thermal limits we measured chill-coma recovery time (CCR)—the time required for an individual to recover from exposure to the extremely low temperatures (Castañeda et al., 2005). We used an established protocol for measuring ant CCR (Angilletta et al., 2007; Boyles et al., 2009). We placed 6 ants from each colony in a Petri dish which was completely embedded in ice for 20 min. The temperature inside of the Petri dish stabilizes after 1 min to 0.1°C. After this cold exposure, we moved all ants to the centre of a printed 45 mm diameter circle, placed them on their backs, and measured the time needed for each ant to upright itself and move out of the circle. Air temperature directly above the paper was 23 ± 1°C in all trials. We repeated chill coma recovery tests five times for a single colony thus measuring 30 workers per colony. For each colony, we calculated mean chill coma recovery time, which we used in our analyses (Figure S2).

## 2.2 | Morphological measurements

Each worker used in the $LT_{50}$ trials was preserved in ethanol for morphological measurements. *Cataglyphis* spp. exhibit a various level of polymorphism, with only some species being highly polymorphic (bicolor, altisquamis and emmae). We did not select workers according to their size, so we randomly collected 30 workers from the colony that were used for $LT_{50}$ trials. Workers were individually mounted on a microscope slide with Vaseline and photographed together with a millimetre ruler using a digital camera Canon 30D with MP-E 65 mm macro lens. We measured standard morphological ant traits that are considered ecologically important (Parr et al., 2017) using ImageJ software (Schneider et al., 2012). For each worker, we took 6 measurements: head length, inter eye distance (the distance between the eyes), mesosoma length (measured in lateral view from the edge of the pronotum to the most distant part of the propodeum), tarsus length, femur length and tibial length of the hind leg. This resulted in 180 morphological measurements per colony, and we used species level means for each morphological trait (Figure S3). Because we did not have a priori expectation as to which of the variables will best explain the variation in *Cataglyphis* body size we used all 6 important morphological variables in the subsequent analyses.

## 2.3 | Phylogenetic analyses

### 2.3.1 | DNA extraction, amplification and sequencing

We collected workers from focal colonies that were immediately preserved in 96% ethanol. We extracted DNA from the thorax and legs of one worker per species using a Wizard® Genomic DNA Purification Kit (Promega). We amplified 503 bp portion of the mitochondrial cytochrome oxidase subunit I (COI), 656 bp of the long wavelength rhodopsin (LWRh), and 769 bp of the ribosomic RNA (28S) with 6 different primers (for extraction and primer details see Villalta et al., 2018). After purification, polymerase chain reaction (PCR) templates were sequenced on an automated ABI 3730XL sequencer using Big Dye® Terminator cycle sequencing kit (Applied Biosystems) at the Genoscreen facility (http://www.genoscreen.fr/).

### 2.3.2 | Sequence analysis and phylogenetic inference

We corrected, aligned and analysed all sequences in Geneious v. 8.0 (Kearse et al., 2012) using the MAFFT plugin (Katoh et al., 2002) with the auto option for other parameters set as default and then refined manually. We used DnaSP v. 5.1 (Librado & Rozas, 2009) to retrieve haplotypes through the algorithms provided by PHASE. All sequences were deposited in GenBank (Table S2). We implemented Bayesian phylogenetic analyses on the concatenated DNA matrix in MrBayes 3.2.6 (Ronquist et al., 2012) via the CIPRES Science Gateway (Miller et al., 2010). To determine the best fitting substitution model for each partition, we used PartitionFinder v. 1.1.1 (Lanfear et al., 2012), with the following parameters: linked branch length, models available in MrBayes, BIC model selection, and greedy search algorithm. We used *Proformica nasuta* as an outgroup using DNA sequences retrieved from GenBank (DQ3539311, DQ353195, DQ353581). Two independent runs of the Bayesian analysis were run for 20,000,000 generations, using four chains per run. Chains were sampled every 1000 generations, using a burn-in fraction of 10%. The consensus tree was generated using the 'allcompat' option.

## 2.4 | Species distribution modelling

For the focal 19 species of *Cataglyphis* distributed across the Iberian Peninsula and Maghreb, we assembled an occurrence data set including 1039 data points. This data set is comprised of localities sampled by the authors (Table S1), acquired from the literature (see Supporting Information for references) and from AntWeb (www.antweb.org. Accessed 2016–2017). For each occurrence point, we extracted 19 bioclimatic variables from WorldClim averaged from 1970 to 2000 (Hijmans et al., 2005). These bioclimatic variables are frequently used in species distribution modelling because they are considered biologically meaningful. They represent annual trends (e.g. mean annual temperature, annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme climatic factors (e.g. temperature of the coldest and warmest months), and precipitations of the wet and dry quarters (Hijmans et al., 2005). The spatial resolution of the GIS layers was approximately 18.5 × 18.5 km (10 arcmin).

For each species, we tested the variable importance with the variable selection procedure in the *Biomod2* package v.3.3.7 (Thuiller et al., 2009). We averaged relative variable importance across all available algorithms in this package. After assessing pairwise correlations among all 19 bioclimatic variables, for each of the 19 species, we selected the three most important uncorrelated variables per species (Pearson's $r < .75$). We then used these three variables (Table S3) in ensemble forecasting to calculate the climatic suitability for each of the 19 *Cataglyphis* species. The models were calibrated and projected with the *Biomod2* package which included 10 statistical and machine learning methods: (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) generalized boosted models (GBM), (4) classification tree analysis (CTA), (5) flexible discriminant analysis (FDA), (6) multivariate adaptive regression splines (MARS), (7) random forests (RF), (8) maximum entropy (Maxent), (9) surface range envelopes (SRE), and (10) artificial neural networks (ANN). To validate the models, we performed 10-fold cross-validation where at each run 70% of randomly selected occurrences are selected to train the model, and the remaining 30% are used for model evaluation (Guisan & Thuiller, 2005). After determining the climatic suitability across the range, we examined individual presence–absence predictions spatially, and by scaling the value to 1, produced a suitability index that can indeed be interpreted as the probability that the grid cell presents favourable environmental conditions for the species (Araújo & New, 2007). Thus, for each species, we created a climatic suitability map (Figure S4) which was then used in subsequent analyses.

## 2.5 | Data analysis

We examined the relationship between morphological and thermal traits by first log transforming the 6 morphological measurements and then reducing them with principal components analysis (PCA). PCA is the most common ordination method used in morphometry to represent body size, and in ants it is extensively used to assess ants' ecological requirements (Oliveira et al., 2022; Sosiak & Barden, 2021; Weiser & Kaspari, 2006). The first two PC axes accounted for the majority of variation in ant morphology so we used them in subsequent analyses. The first principal component (PC1) captured 97.3% of variation in ant body size among the 19 *Cataglyphis* species, which accounted for variation in thorax length and total leg length (Figures S5 and S6). A small proportion of variation (2.2%) was explained by PC2 which accounts for the effect of body shape with highest loadings for head size and inter eye distance.

To assess the relationship of body size (PC1), shape (PC2) and thermal tolerance ($LT_{50}$ and CCR time), we used the Procrustean randomization test (Jackson, 1995) with 999 permutations. This permutation test can compare raw data matrices with ordination solutions to find the optimal superimposition and detect the degree of association under a variety of scenarios (Peres-Neto & Jackson, 2001). We used Procrustean randomization test because of its power to test ecological and evolutionary relationships across a diverse set of traits. We also tested the relationship between body size and $LT_{50}$ with a linear model, and we used generalized linear model ('glm' function) with Poisson family distribution to explore the effect of body size on CCR time.

We analysed the differences among SDM predictions using a distance-based method approach (Wilson, 2011). This analysis uses pixel-by-pixel comparison between image pairs of SDM maps of climatically suitable areas for each species (Figure S4). We calculated Euclidean distances between pixels creating a distance matrix that reflects dissimilarities of the SDM predictions (Wilson, 2011). After generating a Euclidean distance matrix for our SDM pairs, we used a principal coordinate analyses (PCoA) to compare the relationships between these SDM maps displaying predicted realized niches. Then, we tested if interspecific differences in niche predictions were linked to interspecific differences in morphological traits and thermal tolerance. To achieve that, we overlaid the results of the PCoA of SDMs dissimilarities and the matrix of thermal tolerances ($LT_{50}$, CCR) and compared the two data sets using a Procrustean randomization test. Lastly, we tested if morphology (PC1 and PC2) or phylogeny are good predictors of species distributions also using Procrustean randomization tests with 999 permutations. All functions used in ordination analyses were from the *ade4* package (Dray & Dufour, 2007).

We tested if a phylogenetic signal was present in physiological and morphological traits using the Abouheif Moran test. This analysis examines the trait of interest by focusing on the topology of the phylogenetic tree and not on branch lengths (Pavoine et al., 2008). We ran separate Abouheif Moran tests to examine phylogenetic signal in thermal tolerance ($LT_{50}$ and CCR time) and morphology (PC1 and PC2). All the analyses were performed in R version 3.6.3 (R Core Team, 2020).

## 3 | RESULTS

### 3.1 | No link between realized niche and species' thermal tolerance, morphology or phylogeny

We used a principal coordinate analysis (PCoA) to explore the variation in SDM predictions representing the species' variation in realized climatic niches (Figure 1). The position of each species in the ordination (Figure 1) is based on a distance matrix reflecting dissimilarities among SDM maps. We found no link between the variation in thermal tolerance traits and SDM maps across the 19 *Cataglyphis* species (Procrustean randomization test: $m_{obs}$ = 0.29, $p$ = .394). Likewise, we found no link between morphological traits (PC1 and PC2 of the morphological PCA) and variation in SDM maps (PCoA) (Procrustean randomization test: $m_{obs}$ = 0.28, $p$ = .322). For example, several species with similar SDM maps and therefore similar realized climatic niches (Figure 1, e.g. *C. bombycina* and *C. rubra*, or *C. emmae* and *C. savignyi*), had extremely different thermal limits and body sizes (Figure 2). Conversely, some species with similar morphological traits and thermal tolerance (e.g. *C. rosenhaueri* and *C. albicans)* had dissimilar realized niches (Figure 1; SDMs maps of the two species located far apart along the 1st PCoA axis).

Moreover, we found no link between the species' phylogeny and variation in SDM maps (Procrustean randomization test: $m_{obs}$ = 0.08, $p$ = .91, Figure 3). Instead, the PCoA revealed an influence the geographic origin of species (Iberian Peninsula vs. Maghreb) on the predicted realized niches (Figure 1). The SDM maps of species distributed across the Iberian Peninsula differed from those of species disturbed across Maghreb on both PCoA axes (Mann–Whitney $U$ test, Axis 1: W = 76, $p$ < .01, Axis: W = 69, $p$ = .04). In their range, ant species

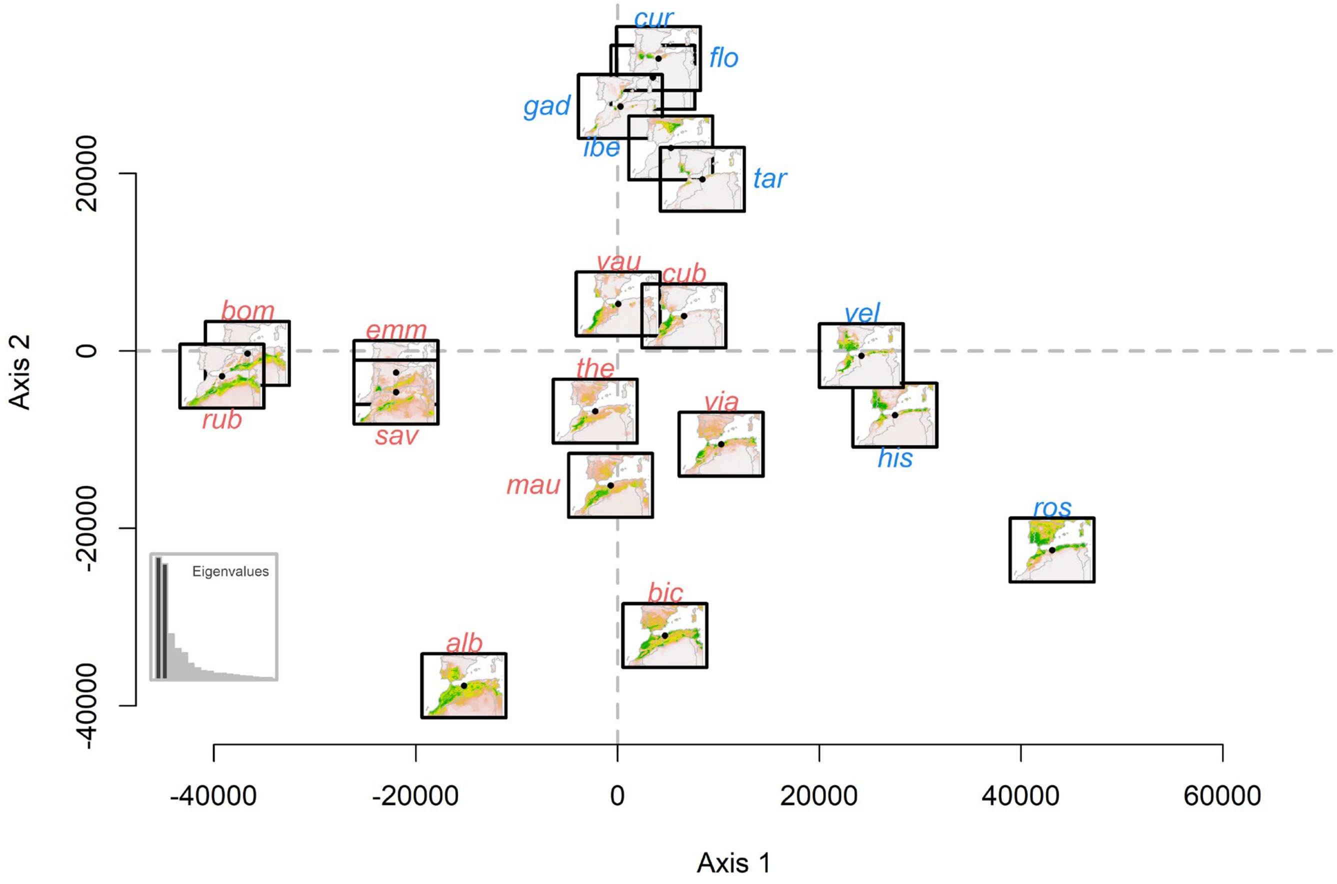

**FIGURE 1** Principal coordinate analysis (PCoA) of species distribution model comparisons across 19 *Cataglyphis* species. Each map represents a predicted climatic niche of a species coded with three first letters of the species name. Variability on each axis is structured by geographic origins, opposing Iberian Peninsula (blue) to Maghreb (in red). Black dot in the middle of the map marks the exact ordination position of each species

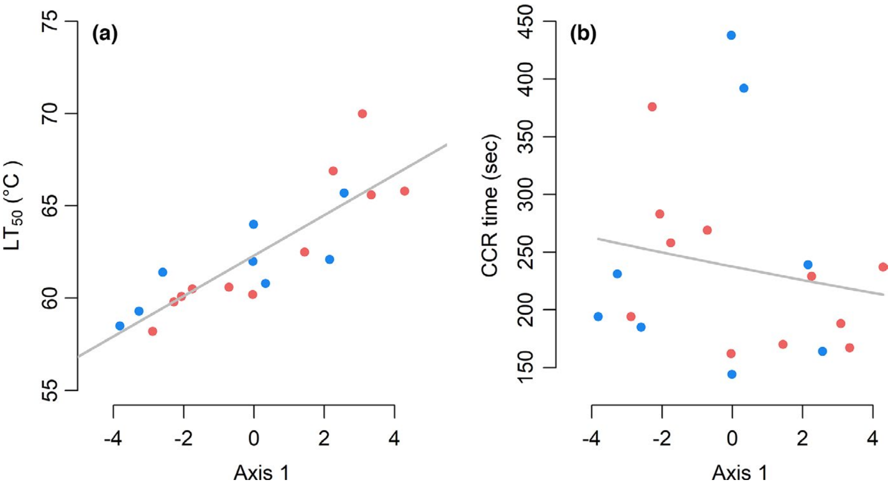

FIGURE 2 Relationship between species body size (PC1 = Axis1) and (a) upper thermal limit ($LT_{50}$); (b) chill coma recovery time (CCR time). Species are color-coded based on their geographic origin—the Iberian Peninsula in blue, Maghreb in red

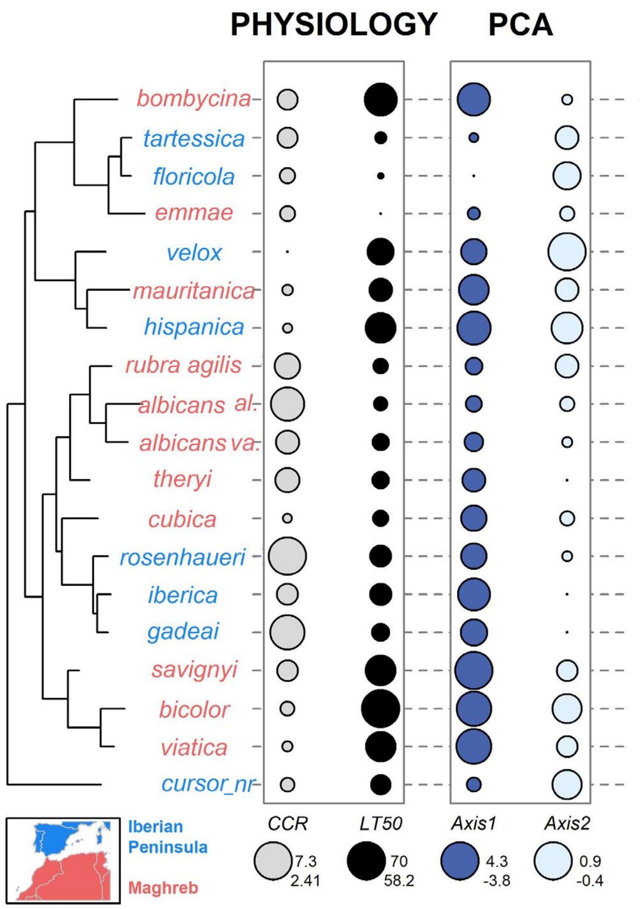

FIGURE 3 Phylogenetic tree of 19 *Cataglyphis* species color-coded by their geographic origin: Maghreb (red), Iberian Peninsula (blue). For each species, mean chill coma recovery time (CCR) in minutes is shown in grey, and mean upper lethal temperature ($LT_{50}$) in ° C in black. Morphological variables were reduced to two axes PC1—representing variation in body size (dark blue), and PC2—representing variation in body shape (light blue). Bubble size corresponds to the average value of the trait. Maximum and minimum values of each trait are listed below the trait names

from Maghreb experienced higher annual mean temperatures than ant species from the Iberian Peninsula (mean ± SE = 17.2 ± 0.2 °C vs. 15.0 ± 0.1 °C, W = 208,709, $p < .001$).

## 3.2 | Thermal tolerance and morphology are strongly correlated

Thermoregulatory traits were highly correlated, as there was a significant concordance between morphological and thermal traits—heat tolerance and chill coma recovery time (Procrustean randomization test: $m_{\text{obs}} = 0.81$, $p < .001$). Body size accounted for 82% of the variation in heat tolerance with upper lethal temperatures ranging from 58.2 to 70.0°C. Larger ants tolerated higher temperatures (Figure 2a; $R^2 = .82$, $F_{1,17} = 36.8$; $p < .001$) and were also faster to recover from chill coma, although this relationship was weaker (Figure 2B; GLM: $\beta = -0.03$, SE = 0.05, z (−13.3), $p < .001$). Thermal tolerances and morphological traits did not differ between species from the Iberian Peninsula and Maghreb (Figure 2, $W_{LT50} = 47$, $p = .84$; $W_{CCR} = 44$, $p = 1$; $W_{PC1} = 54$, $p = .44$). We found no phylogenetic autocorrelation in the residuals of the two linear models used to examine the relationship of $LT_{50}$ and body size (Abouheif Moran test: $p = .16$), and CCR time–body size relationship (Abouheif Moran test: $p = .77$).

## 3.3 | Thermal tolerance and morphology are both linked to phylogeny

Heat tolerance and chill coma recovery time showed a strong phylogenetic signal across the 19 *Cataglyphis* species (Figure 3; Abouheif Moran test: $p < .01$). Moreover, we found a phylogenetic signal in morphological traits (PC1, Abouheif Moran test: $p < .01$).

## 4 | DISCUSSION

Contrary to expectations, none of the three important determinants of species fundamental niche—thermal tolerance, morphology and phylogeny—were good predictors of realized climatic niches across 19 ant species. This contrasts with the basic assumption of climatic niche modelling, that the realized niche can be used as a proxy for determining fundamental niche requirements. Our findings are even more surprising given that we studied a set of thermal specialist species (Lenoir et al., 2009; Wehner & Wehner, 2011) that forage during the hottest parts of the day during which the ants avoid predation and competition (Boulay et al., 2017; Wehner & Wehner, 2011). Because of this pronounced thermophilia, we expected that their realized climatic niche would be strongly linked to the thermoregulatory traits that determine species fundamental niche, as suggested by previous work on another set of Mediterranean species adapted to high temperatures (Arnan & Blüthgen, 2015).

Our findings are consistent with earlier work showing that SDMs were not good predictors of physiological tolerances in vertebrate ectotherms (frogs and lizards) (Paz & Guarnizo, 2020). Similarly, another study identified a mismatch between the fundamental and realized niche in specialist butterflies which were unable to shift their ranges in response to climate change because they relied on the presence of particular host plants with restricted ranges (Schweiger et al., 2012).

Here, we found that all thermoregulatory traits examined were strongly correlated with each other and were strongly linked to the species' phylogeny, thus reflecting the evolutionary history and the fundamental biological requirements of these species. This is consistent with previous studies across distantly related ant species which found phylogenetic constraints in upper thermal limits (Bujan et al., 2020) or both upper and lower thermal limits (Diamond & Chick, 2018). We are aware that phylogenetic signal must be cautiously interpreted, because closely related organisms are more likely to live in similar conditions that can impact thermal limits and acclimation ability (Hoffmann & Sgrò, 2018). There are several reasons why we believe we recovered a true phylogenetic signal. First, we did not test the ants directly from the field, but after laboratory acclimation, during which the effects of field-related acclimatization were removed, and all 19 species were experiencing the same temperature. Second, all studied *Cataglyphis* species are diurnal, thermophilic, ground foragers living in similar habitats (Lenoir et al., 2009), and their local adaptations related to the microhabitat should not differ. Lastly, morphology is often used for species delimitation, and our phylogenetic analysis shows a strong congruence with morphology lending further support to robustness of phylogenetic relatedness recovered.

Thermal tolerances of *Cataglyphis* were highly correlated with body size, as larger ants were more likely to withstand higher temperatures and faster to recover from a chill coma. This is in accordance with strong effect of body size on ant thermal limits recorded for ants (Kaspari et al., 2015), including at an intra-specific level in polymorphic ant species (Baudier et al., 2018; Ribeiro et al., 2012). In some polymorphic *Cataglyphis* species, larger workers are also more heat tolerant than smaller workers and will forage during the hottest parts of the day (Cerdá & Retana, 2000). Considering high thermophilia in *Cataglyphis* one might predict a strong trade-off with cold tolerance, which was suggested for ectotherms (Angilletta, 2009) and found to be true for ants (Diamond & Chick, 2018). But here, we showed that, despite the high thermophilia, large ants were also faster to recover from chill coma. The absence of a trade-off between heat and cold tolerance in *Cataglyphis* may be explained by higher levels of constitutive heat shock proteins (Gehring & Wehner, 1995; Willot et al., 2017). Heat shock proteins (HSP) are molecular chaperones that protect cells from thermal damage, or other stressors (Sørensen et al., 2003). Insects predominantly use HSP70 in their response to environmental stress (Zhao & Jones, 2012), including chill coma recovery in *Drosophila* (Colinet et al., 2010), and ants (Maisov et al., 2007). Upregulation of HSP70 has been related to cold tolerance during diapause of some insects (Cheng et al., 2016; Rinehart et al., 2007), and HSP70 is proposed to have a role in the chilling injury repair (Koštál & Tollarová-Borovanská 2009). Thus, thermally tolerant species of *Cataglyphis* might be also well equipped to recover from a chill coma.

We found that variation in realized climatic niches was not linked to any of abovementioned thermoregulatory traits. This begs the question: What does determine variation in realized climatic niches? Realized niches are often constrained by dispersal barriers (Wiens & Donoghue, 2004), and indeed, we found striking differences between the realized niches of ants from the Iberian Peninsula and those from Mahgreb (Figure 1). This suggests that the geographic origin of species influences the realized niche more than thermoregulatory traits, perhaps because ant species are unable to fill their entire fundamental niche due to dispersal limitations.

The *Cataglyphis* species we studied were distributed either across the Iberian Peninsula or Maghreb, but never both, suggesting that the sea poses a potential dispersal barrier. This is plausible given that many *Cataglyphis* species evolved dependent colony founding in which newly mated queens need help of nestmate workers to establish a colony, at a relatively short distance from their mother colony (Boulay et al., 2017). In these species, queens underwent a wing reduction and loss of wing muscles, so dispersal is exclusively done on foot (Peeters & Aron, 2017). Such short-distance dispersal was documented for at least seven out of 19 *Cataglyphis* species we studied (Boulay et al., 2017; Leniaud et al., 2013; Lenoir et al., 1988; Peeters & Aron, 2017). Like many plants (Dullinger et al., 2004; Hanspach et al., 2011), these ants might not be able to naturally disperse to certain areas presenting suitable climate. Perhaps SDMs offer a more realistic estimation of suitable climatic niches for species with high dispersal ability.

However, the geographic origin of *Cataglyphis* species is not the only factor explaining the discrepancy between species' thermoregulatory traits and their realized niches. For example, some species from the same range (either Maghreb or the Iberian Peninsula) had extremely similar realized niches while possessing strikingly different morphology and thermal tolerances (Figures 1 and 3). Similarly, some species with similar morphology and thermal tolerance, living in the same range, presented extremely divergent realized niches (Figures 1 and 3). Some of these differences might be explained by other biotic constraints like competition, predation or parasitism. Biotic interactions like interspecific competition or parasitism can limit species distributions and prevent the species from occupying a whole extent of the realized niche (Gouveia et al., 2014; Soberón, 2007). Resource availability and soil biogeochemistry (e.g. sodium availability (Clay et al., 2017)) could also constrain the realized niche. To test this, we would need experimental evidence, measuring each species' fitness under different abiotic and biotic conditions. This could be achieved with reciprocal-transplant experiments, settling experimental ant colonies within and beyond their current range and measuring factors supposed to limit their current distribution (such as soil elemental chemistry). These manipulative experiments have so far mostly been done with plants, but it would be interesting to conduct them using ants.

Although it is beyond the scope of this study to attempt to identify the precise factors limiting the species' distributions experimentally, we could show that thermal tolerance and morphology do not constrain the realized climatic niches among *Cataglyphis* species in Maghreb and the Iberian Peninsula. Even though it is well recognized in the literature that many other biotic and abiotic factors influence species distributions (Bolnick et al., 2010; Guisan et al., 2014), one would still expect a link between these determinants of the fundamental niche and the realized niche. Therefore, our findings caution against forecasting species responses to climate change using correlative SDMs. When climatic conditions change within a species' range, the species' persistence will be determined by the size of its fundamental niche and capacity to adapt (Bellard et al., 2012). Therefore, forecasting species responses to climate change should perhaps be directly based on thermoregulatory traits (Bishop et al., 2019).

We focused on thermal tolerance and morphological traits because they are historically used to assess survival and performance in different climates (Roeder et al., 2021). However, additional traits such as pilosity, cuticle reflectance and colour contribute to insect thermal tolerance (Bishop et al., 2016; Shi et al., 2015). Most of our ant species were of moderate pilosity, except *C. bombycina* whose cuticle is covered with a dense layer of triangular hairs that enhance reflectivity and reduce heating rate (Shi et al., 2015). Highest heat tolerance, however, was recorded for *C. bicolor*, although this species is mostly hairless, except for a portion of mesosoma. Thus, a complex interaction cuticle properties, heat tolerance and body size (Willmer & Unwin, 1981) merits further investigation in ants.

Here, we used WorldClim variables which are used in the overwhelming majority of studies predicting future species distributions (van Beest et al., 2021; Carvalho et al., 2021; Chu et al., 2021). But, these variables might not reflect microclimatic conditions near the ground surface experienced by ants. Ants are small, cursorial ectotherms and microclimate availability might be more important for their physiological adaptations than the climate provided by the meteorological stations (Pincebourde & Salle, 2020). But so far, a global soil temperature dataset is only starting to develop (Lembrechts et al., 2020) and will hopefully be available for climatic niche studies in the near future.

Using a comprehensive data set of physiological, morphological, phylogenetic and bioclimatic data, we showed that realized niches predicted with SDMs do not correspond to species' thermoregulatory traits in a genus of thermal specialist ants. This suggests that even for insects whose foraging activity and distribution are strongly tied to temperature, species distribution models should be used with caution when predicting climatic niches and distributions under climate change.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available in Figshare https://doi.org/10.6084/m9.figshare.16400790

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## BIOSKETCH

**Jelena Bujan** is interested in ecophysiological adaptations and the role they play in structuring insect communities and distributions. Her current research explores physiological and behavioural plasticity of ants in thermally stressful environments.

Author contributions: CB and RB conceived the ideas and designed the methodology. XC, FA, AT, AD, RB conducted fieldwork, collected distribution and physiological data. IV and SD collected molecular, physiological and morphological data. SO, CB, IV and JB analysed the data. JB led the writing of the manuscript, CB and SO provided detailed edits. Authors contributed critically to the drafts and gave final approval for publication.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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