

RESEARCH ARTICLE

Precipitation shapes colour polymorphism in a widespread spider

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Abstract

1. Colour polymorphism, the presence of multiple colour variants within a population, is a common example of intraspecific phenotypic variation and has served as a model for studying drivers of diversity.
2. Climatic factors can influence the distribution of colour variants, but effects may vary depending on the lineage-specific functions of colour. Colour polymorphism is widespread in arachnids, in which colour functions in intra- and interspecific interactions such as prey-luring; yet, the drivers of colour diversity in this lineage remain largely unexplored.
3. Here, we investigated climatic factors influencing colour polymorphism in a widely distributed colour polymorphic spider (*Austracantha minax*) using a combination of controlled experiments, field measurements and tests for macroecological associations.
4. We showed that although different colour morphs occupy distinct climatic niches across Australia, in the laboratory and field, dark colouration is unlikely to provide biologically relevant thermal benefits. Instead, precipitation, rather than temperature, appears to be the strongest driver of colour morph frequencies: there were higher frequencies of dark individuals in regions with higher precipitation while orange individuals were more common in drier areas.
5. We discuss potential mechanisms related to background matching and pathogen protection in humid environments. Our findings highlight the role of climatic factors in shaping colour variation and demonstrate the value of combining macroecological, field and laboratory approaches.

KEYWORDS

colour variation, geographic variation, Gloger's rule, humidity, thermal melanism hypothesis

1 | INTRODUCTION

Species with discrete within-population phenotypic variation (i.e. polymorphism) provide an ideal model to understand how

environmental factors shape intraspecific variation across different geographical scales (Ford, 1945; Gray & McKinnon, 2007; Jamie & Meier, 2020). A range of factors—including climate, habitat structure, predator–prey interactions and sexual selection—can

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shape phenotypic variation within and between populations (Dreiss et al., 2012; Endler, 1977). These drivers are commonly studied by examining large-scale correlations between traits and environmental variables among populations or focussing on adaptive variation within populations (McLean & Stuart-Fox, 2014; Svensson, 2017). However, few studies examine both within- and between-population variation or integrate analyses across different geographic scales. Thus, it remains unclear whether the same environmental factors maintain polymorphism within populations and explain larger scale patterns of diversity.

Colour polymorphism typically refers to discrete, within-population colour variation that is genetically based (Gray & McKinnon, 2007; Svensson, 2017), although the term is also used more broadly in the literature to encompass cases where the causal genetics are unknown (e.g. Evans et al., 2020; Goutte & Boissinot, 2025; Leimar, 2009). Because discrete colour variants can be reliably scored, and genetic pathways underlying colouration often influence behavioural and physiological traits (Dijkstra et al., 2017; Pérez i de Lanuza et al., 2017; Sinervo & Svensson, 2002), colour morphs can be functionally linked to particular behavioural or physiological traits that confer fitness advantages under distinct environmental conditions (e.g. Mullen & Hoekstra, 2008; Tate et al., 2016). At the within-population level, variation in local environmental conditions can maintain discrete phenotypes by generating morph-specific fitness differences across microhabitats (Nosil et al., 2024; Villoutreix et al., 2023)—for example, colour polymorphic Mediterranean wrasses select distinct colour microhabitats that match their colouration for optimal camouflage in heterogeneous environments (Fark et al., 2022). Such fine-scale environmental selection on coloration is expected to be replicated at larger scales, generating variation among populations in the relative frequency or presence of morphs among populations (Koskenpato et al., 2023; Romano et al., 2024).

At the macroecological scale, temperature and humidity are two of the most important environmental variables shaping animal colouration. Spatial variation in these two variables has been linked to colouration diversity across a wide range of taxa and is known as Bogert's rule (or the thermal melanism hypothesis) and Gloger's rule, respectively (Goldenberg et al., 2022). According to the thermal melanism hypothesis (Clusella Trullas et al., 2007), darker individuals should be more abundant in environments with low ambient temperatures (e.g. higher latitudes or shadier microhabitats), given the thermoregulatory benefits of dark colours—higher heating rates due to increased solar absorption—especially for ectotherms (Meredith & Sarna, 2006; Watt, 1968). Even though this pattern has been observed in multiple taxa, such as lizards, snakes, ants and moths (Azócar et al., 2016; Bishop et al., 2016; Broennimann et al., 2014; Clusella-Trullas et al., 2008; Dalrymple et al., 2018; Hantak et al., 2022; Heidrich et al., 2018; Muri et al., 2015; Pinkert et al., 2017), in many cases, we ignore how ambient temperature is mechanistically associated with the presence of dark colouration, and whether the degree of colour variation in the wild can lead to biologically relevant differences in thermoregulation across morphs.

In other words, large-scale correlations supporting the thermal melanism hypothesis are often not supported by experimental evidence (e.g. Bishop et al., 2016; Heidrich et al., 2018; Law et al., 2020).

Similar to ambient temperature, humidity shapes the geographic distribution of colouration at macroscale—both within and between species—in many taxa, including birds, ants and butterflies (Delhey, 2019; Friedman & Remeš, 2017; Kang et al., 2021; Koskenpato et al., 2023; Lopez et al., 2021; Romano et al., 2024). Darker individuals appear to be more abundant in places with higher humidity or precipitation than in drier places (Delhey, 2019). This pattern does not have a clear causal explanation; it is possible that it emerges as a consequence of improved background matching (Cheng et al., 2018; Stevens & Merilaita, 2008), pathogen protection (Mackintosh, 2001; Nosanchuk & Casadevall, 2003) or pleiotropic effects (Ducrest et al., 2008). In addition to the lack of clarity on the mechanisms, there are some taxa, such as amphibians and arachnids, that are notably underrepresented in the available empirical evidence supporting these macroecological patterns (Delhey, 2019). Furthermore, some studies have demonstrated in insects support for an opposite pattern—that higher melanisation levels are associated with greater desiccation resistance (melanism–desiccation hypothesis; Parkash et al., 2009; King & Sinclair, 2015)—suggesting that darker individuals should be more abundant in drier places (Kalmus, 1941).

Web-building spiders offer an ideal system to examine how climatic variables shape the presence or abundance of discrete colour variants within and between populations. They are a diverse group (>6000 species in the families Theridiidae and Araneidae alone) with at least 140 colour polymorphic species, some of which have large geographical distributions (Salgado-Roa, Stuart-Fox, White, & Medina, 2024). Unlike many other taxa, colour in web-building spiders may be shaped more strongly by interspecific interactions than by intraspecific interactions. Specifically, colour often functions in prey-luring, camouflage or possibly aposematism (Messas et al., 2021, 2025; Robledo-Ospina & Rao, 2022; White & Kemp, 2015), but this group of spiders may lack colour vision (Tiedemann et al., 1986; Yamashita, 1985) and relies on other sensory modalities (olfaction, mechanoreception) in mating interactions (Gaskett, 2007; Huber, 2005). Consequently, web-building spiders provide an interesting comparison to more intensively studied groups, such as birds, reptiles and damselflies (Delhey, 2019; Roulin & Bize, 2007; Wellenreuther et al., 2014).

Here, we combined controlled experiments, field measurements and macroecological analyses to examine the climatic drivers that influence the presence and abundance of light and dark colour morphs within and between populations of the widespread colour polymorphic spider (*Austracantha minax*; Figure 1). We hypothesize that if ambient temperature is a key climatic factor shaping colour polymorphism in spiders, dark individuals should heat more rapidly than lighter individuals under controlled conditions, exhibit higher body temperatures in the field and be more common in colder environments where dark coloration would provide a thermal advantage. This would provide support for the thermal melanism hypothesis in

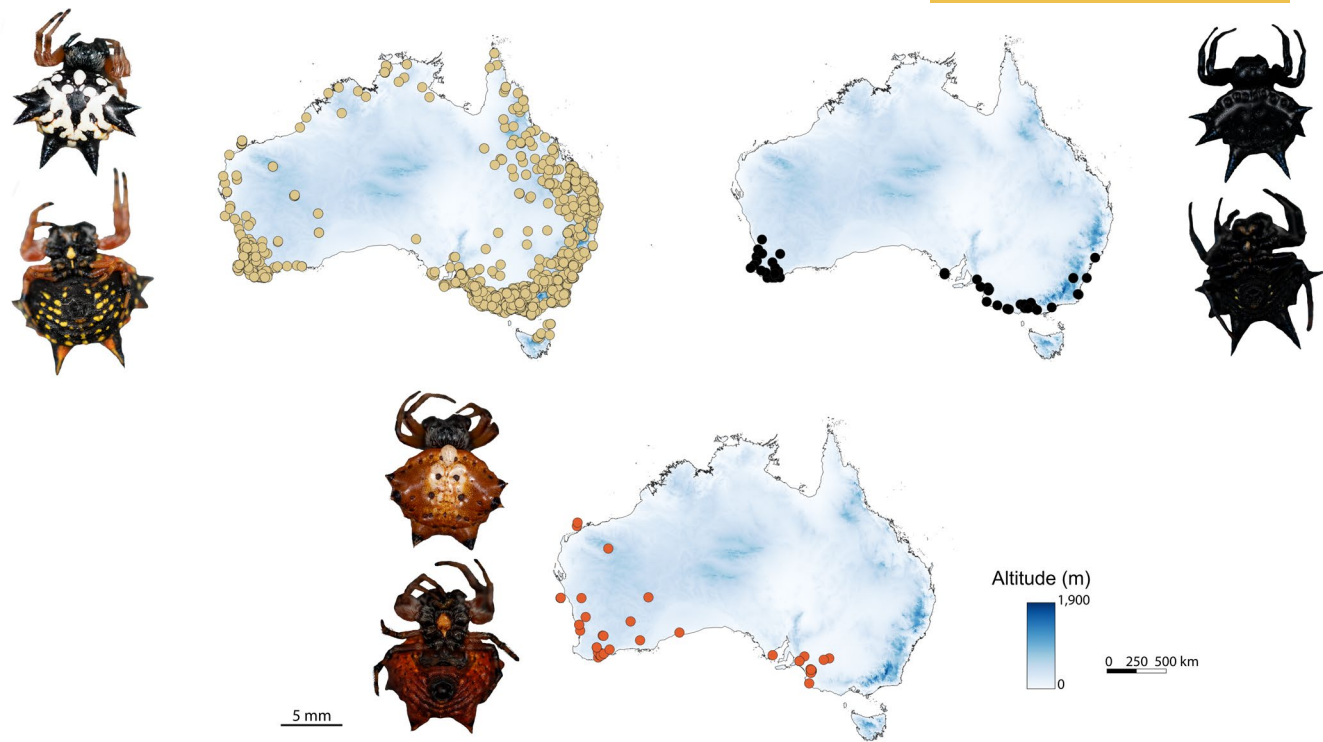


FIGURE 1 *Austracantha minax* colour variation and morph distribution. Each map represents the geographical records collated for each female colour variant plotted on an altitude background. The top-left panel corresponds to the black-and-white morph (1097 records), the top-right to the black morph (123 records) and the bottom panel to the orange morph (34 records).

polymorphic systems. We also considered whether colour morph frequency was associated with precipitation and whether darker morphs were more prevalent in humid environments, which would support some of the predictions of Gloger's rule. Our study integrates experimental, field-based and macroecological approaches to investigate the climatic drivers of phenotypic diversity at different scales in an underexplored taxonomic group.

2 | MATERIALS AND METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Population	Colour morph	20 individuals per colour morph in the heating rates laboratory experiment.
Population	Colour morph	15 individuals per colour morph in the field measurements of body temperature.
Species	Colour morph	1254 occurrence records categorized by colour morph, used for macroecological analyses

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Population	49 replicates/locations with a total of 15,214 spiders categorized by morph. Used for colour morph frequency analyses.

2.2 | Study species

Austracantha minax, the Christmas spider, is a common colour polymorphic species widely distributed in Australia, yet little is known about its biology or the mechanisms underlying its colour polymorphism, which is expressed in both sexes. Females exhibit two main colour morphs that segregate from a single egg sac regardless of climatic conditions (personal observation; and we have observed a similar pattern in the related species *Gasteracantha cancriformis*), suggesting a genetic basis for this variation: one morph is completely dark on both the dorsal and ventral sides; and the other presents black, white and yellow on the dorsal side, and a mosaic yellow pattern ventrally (Waldock, 1991). A third colour morph has been described for this species; however, the reports are limited to only a few places in Western Australia (Hogg, 1914; Waldock, 1991). This colour variant appears to be orange and white on its dorsal side and completely orange on its ventral side (Waldock, 1991). Based on previous museum and field observations, as well as early studies (Elgar

& Bathgate, 1996; Lloyd & Elgar, 1997; Mascord, 1996; Waldock, 1991), females of the Christmas spider tend to be bigger, more abundant, live longer and exhibit clearer phenotypic variation than males. These observations prompted us to explore the effect of climatic variables on the colour polymorphism, focussing exclusively on females. Work on this species did not require ethical approval.

2.2.1 | Heating rates experiment

Correlations between colour variation and climate can be driven by several factors, one of the most important being thermal needs. To investigate potential functional explanations for ecogeographical patterns, we quantified heating rates under a solar simulator in the two most common morphs—the black morph and the black-and-white morph. These morphs represent two extremes of colour variation in terms of reflection of solar radiation (Supporting Information), so they provide an indication of the extent to which colour may affect body temperature across the colour variants. The experiments quantified radiative heating while minimizing effects of convection and conduction under a solar simulator that closely approximates the spectral power distribution of sunlight. They therefore enabled a precise quantification of differences in heating rate between the morphs due to differences in colour. We exposed a total of 20 black females and 20 black-and-white females to radiative heating from a solar simulator on both their ventral and dorsal sides for 15 min. The equipment and protocol for this experiment are based on and fully described in Wang et al. (2021) and Ospina-Rozo et al. (2022) (Figure S1; set up detailed in the Supporting Information: Methods). Because we sacrificed the spiders immediately before the experiment using a CO₂ chamber (Supporting Information), we acknowledge that our experimental approach quantifies exclusively the effects of colouration and body size without considering physiological or behavioural thermoregulation.

To compare heating rates between the colour morphs on each side, we employed two methods. The first involved calculating the total temperature differences between the initial and final measurements after 5 min (ΔT), while the other measured the maximum change in temperature in 20-s intervals ($\text{maxHR} = \Delta T/s$). Additionally, considering that larger objects are expected to heat up more slowly, we recorded the weight and width of each sample before the start of each trial. Because both measurements were highly correlated (Pearson's $r = 0.82$), we only used weight as a covariable. To test for differences in heating rates between morphs, we built linear models per side (dorsal/ventral) in R v4.2.0 (R Core Team, 2021) using either ΔT or maxHR as response variables and colour morph and weight as predictors. The assumptions of the linear model were verified using diagnostic plots.

2.2.2 | Field thermal measurements

To explore whether our controlled heating rates measurements were biologically relevant in the field under natural conditions of wind,

solar radiation and physiological thermoregulation, we compared body temperatures of the same two morphs used in laboratory experiments—black and black-and-white individuals—in their natural environment. We measured the body temperature of 15 black and 15 black-and-white females from facultative aggregations of individuals on active webs near Ballarat, Victoria, Australia (latitude: -37.8215 , longitude: 143.7585). We conducted all measurements at noon—when radiation is highest—on a cloudless, still day along a transect of less than 50 m. Although microclimate conditions (air temperature, wind and illumination) can vary substantially, we chose still cloudless conditions at noon to maximize any potential effect of colour on body temperature, while ensuring similar sunlight exposure of all individuals. Windy or cloudy conditions would reduce any effect of colour on heating or cooling (Clusella Trullas et al., 2007); thus, the comparison of body temperatures under the conditions we chose provides an indication of the potential importance of colour for thermoregulation. All spiders were found on webs constructed on the plant *Ficinia nodosa* and were selected opportunistically, with no deliberate selection based on colour morph or body size.

We measured the body surface temperature of the individuals on their dorsal and ventral side using an infrared thermal camera (FLIR t540). Raw images were processed with the manufacturer software (FLIR Tools v6.4) to extract average temperatures per side. Simultaneously, we recorded wind speed with an anemometer (BTMETER BT-100), air temperature with a thermometer (Center 521, Center Technology Corp., Taiwan) and the luminosity level (measured in lux) using a digital illuminance device (Model: LX1330B-Dr. meter; spectral sensitivity ranging from 400 to 700 nm). These devices were positioned parallel to the individuals. We also measured the height of the web of every spider.

We analysed each body side (dorsal and ventral) independently by building linear models in R v4.2.0 (R Core Team, 2021). The models included body temperature as the response variable and colour morph (black or black-and-white), air temperature, wind speed, luminosity and web height as predictors. We checked for collinearity between the predictors using the function *check_collinearity* from the R package *performance* v0.10 (Lüdtke et al., 2021) and calculating their Pearson's correlation. Diagnostic plots were used to confirm the assumptions of the linear model. To evaluate whether our field sample size was adequate to detect biologically relevant temperature differences between colour morphs, we conducted a series of power analyses (see Supporting Information: Methods and Results, for full details).

2.2.3 | Geographical records data collection

To test whether and which climatic variables can explain colour variation in *A. minax*, we obtained female geographical records from three different sources. First, we visited four of the main arachnological collections in Australia: Western Australian Museum, Queensland Museum, Australian Museum and Museums Victoria, obtaining records from 1960 to 2010. Second, we collated all the research-grade

records of the species on iNaturalist spanning from 2019 to 2023 (data accessed on the 11th of November 2023; $n = 2297$). Finally, we also added new geographical records from our own surveys of locations across south-east and south-west Australia (details in colour morph frequency section below). With these records, we performed automated data cleaning and removed occurrence points that were too close together to reduce spatial autocorrelation and sampling bias (details in [Supporting Information](#)). Our final data set consisted of 1254 records, 1097 records for the black-and-white colour morph, 123 records for the black morph and 34 records of the orange morph ([Figure 1](#)).

2.2.4 | Climatic niche variation among colour morphs

We tested whether the three colour morphs of the Christmas spider differ in the range of climatic conditions where they are found (i.e. realized climatic niche; Peterson et al., 2011). To extract climatic data that represent the conditions in which adults are found in the field, we focussed on the months when the species shows the highest number of geographical records (95% of the records were from October to May). Using these months, we downloaded six climatic variables from CHELSA v2.1 (Karger et al., 2017) that we hypothesised could be linked to morph variation: mean daily maximum and minimum air temperature (both extracted automatically at 2 m), precipitation, surface downwelling shortwave flux in air (i.e. solar radiation), potential evapotranspiration and climatic moisture index. Because the studied species is not active throughout the entire year, we accounted for temporal variation and biases due to extreme conditions by generating raster layers for Australia for each variable, averaging the values for the months of peak geographic reports of the species (October to May) over the last decade of available data (2009–2019). The values for each record were extracted using the function *extract* from the R package *terra* v1.7 (Hijmans, 2023).

Using the climatic data, we implemented uni- and multivariate comparisons between the colour morphs of the Christmas spider. For the univariate comparisons, we computed the density profiles per colour morph of every climatic variable and Tukey honest significant difference (Tukey HSD) tests to determine which of the colour morphs were significantly different from one another across the six climatic variables. For the multivariate analysis, we implemented a COUE (Centroid shift, Overlap, Unfilling and Expansion) scheme (Guisan et al., 2014). This framework is commonly used to test differences in the climatic niche of different populations of the same species (Farquhar et al., 2022; Wang et al., 2023).

For the COUE scheme, we first delimited the geographical range of each colour morph by adding a buffer of 20 km radius to every geographical record, and defined the spatial extent of their environmental background (Methodological details in the [Supporting Information Methods](#)). We then summarized climatic variation from all records (presence and background) in two principal components

(PCs), which explained 95.4% of the climatic variation and represented the environmental space of the whole species (i.e. including both observations and possible suitable areas for all the morphs; [Figure S2](#)). This information was used as an input for the R package *ecospat* (Di Cola et al., 2017), where we implemented the COUE scheme to explore the similarity of the climatic niche of the colour morphs. First, we created grids of 100 × 100 cells per colour morph that represented the occurrence density of each morph over the environmental space of the whole species (summarized in the two PCs). Then, using the grid topology of all the colour morphs, we compared their climatic niche estimating the *D* index (Schoener, 1968) and the similarity statistic *I* (Warren et al., 2008) between all the colour morphs with *ecospat* (Di Cola et al., 2017). The values of *D* and *I* range between 0 and 1, where 0 indicates no niche overlap between the niche occupied by colour morphs, and 1 represents complete overlap.

To evaluate the statistical significance of *D* and *I*, we performed tests of niche equivalency and similarity using 10,000 permutations (pseudo-replicates) to create a null distribution of similarity values based on the background environment of each morph. This allowed us to compare the observed values of *D* and *I* against a null distribution to implement a one-tailed hypothesis test. We tested this for niche conservatism (niche overlap is more equivalent/similar than random expectations) and for niche divergence (niche overlap is less equivalent/similar than random expectations).

2.2.5 | Climatic factors shaping colour morph frequency

The analysis of geographical distribution of the colour morphs described above provides a broad scale comparison between the environments where morphs are found, but multiple morphs can be found within the same population. To gain insights into the drivers of abundance for each colour morph at the population level, we measured their frequency in the field. We sampled 49 locations encompassing 36 degrees of longitude and 6 degrees of latitude in south-eastern and south-western Australia during the summer of 2022 and 2023 ([Figure 2](#)). Taking advantage of the capacity of this species to form facultative aggregations (Lloyd & Elgar, 1997), we searched for aggregations of individuals of *A. minax* at these locations. When these aggregations were found, we conducted an exhaustive search of females within a radius of 1 km, including solitary and aggregated individuals in our surveys. We categorized the individuals found at each location as black, black-and-white or orange ([Figure 1](#)). In total, we counted 15,214 spiders, with a mean of 310.49 spiders per location, a minimum of 85 individuals and a maximum of 817.

We used the colour morph frequency information from the field to test whether variation in morph frequency was associated with climatic factors. Climatic data were obtained from the Australian Gridded Climate Data / Australian Water Availability Project dataset (AGCD/AWAP; Jones et al., 2009), which offers higher regional specificity, making it ideal for this finer-scale analysis

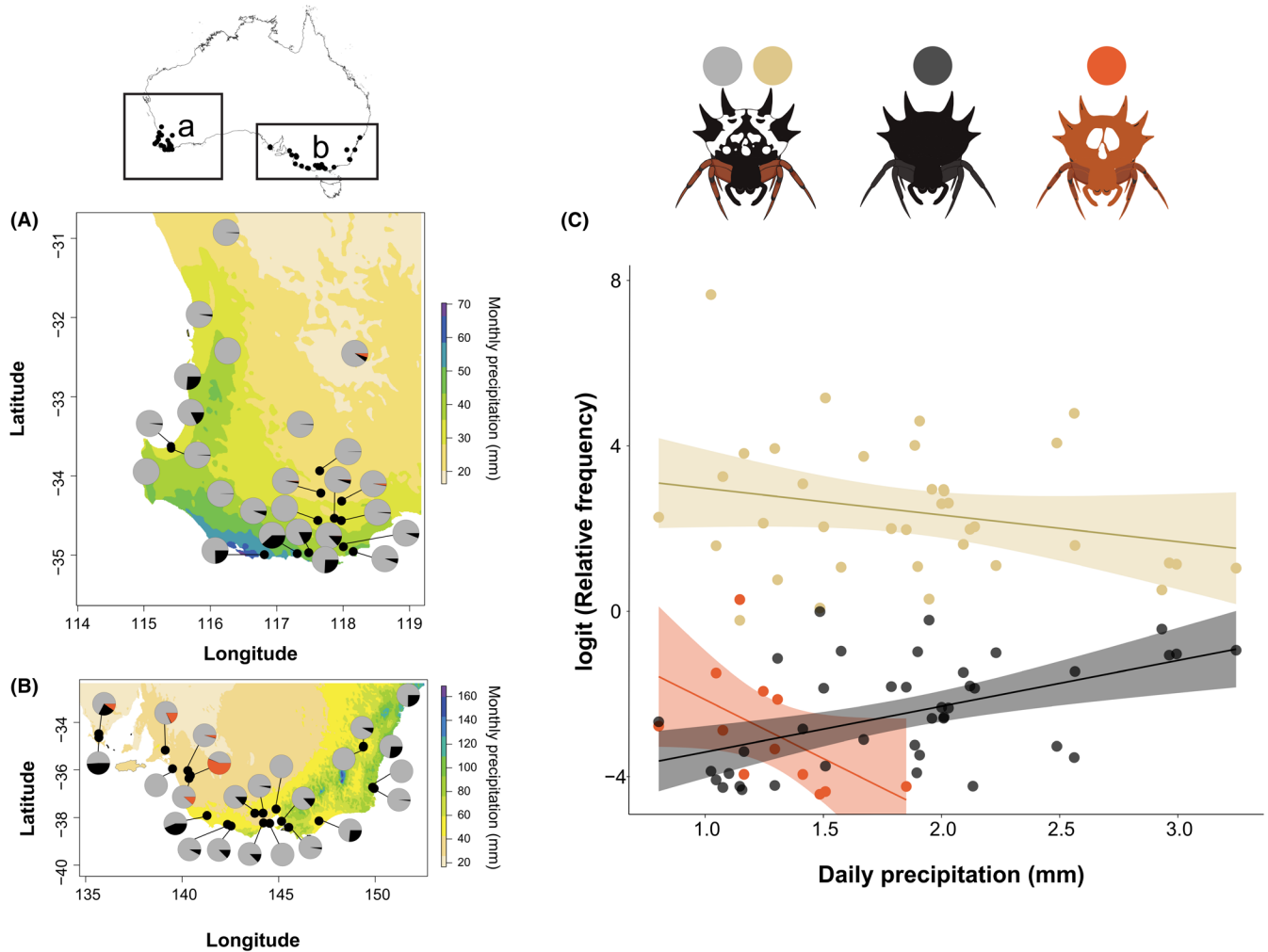


FIGURE 2 Variation in relative frequency for each colour morph and its association with precipitation. The maps show the relative frequency of the black-and-white (grey colour), black and orange morphs across 49 locations in (A) south-western and (B) south-eastern Australia. (C) Linear model association between the relative frequency of each colour morph and daily precipitation. Line represents estimate from the model and shaded area represents the confidence interval of the regression.

(a comparison between the use of CHELSA and AGCD datasets is given in [Supporting Information: Methods](#)). We downloaded daily values (entire day) of five climatic variables: vapour pressure, minimum temperature, maximum temperature, precipitation and solar radiation. To account for temporal bias, we averaged each location's data for the species' peak activity months (October–May) over the last decade (2011–2021). Before the analyses, we assessed potential collinearity between the climatic variables using Pearson correlation and performed hierarchical clustering to identify independent climatic variables. A pairwise distance threshold of >0.5 was used to determine independence (variable selection and collinearity test in [Supporting Information: Methods](#)).

We constructed multiple matrix regression (MMR) models using non-collinear variables with the R package *ecodist* v2.1 (Goslee & Urban, 2007). Predictors included Euclidean distance matrices for each climatic variable and geographic distances between sampling locations, calculated with the R package *geosphere* v1.5 (Hijmans, 2016). The response variable was the Euclidean distance

in colour morph frequencies between pairs of locations, calculated as follows:

$$\text{dist}(A, B) = \sum_{i=1}^n \sqrt{(fA_i - fB_i)^2}$$

Here, fA_i and fB_i represent the relative frequency of morph i in locations A and B, respectively. Predictors were log-transformed if their distribution significantly deviated from normality, and all matrices were scaled and centred before analysis. Two MMR models were conducted for the three colour variants of the Christmas spider, avoiding highly correlated predictors in the same model. One model included precipitation, minimum temperature, maximum temperature and geographical distance, while the second included precipitation, vapour pressure, solar radiation and geographical distance. If a model contained a statistically significant predictor, we performed pairwise comparisons between morphs to determine whether certain variables strongly influenced specific morphs by directly comparing the coefficient estimates and significance levels of the predictors across all models.

Since distance measures can reduce statistical power (Legendre & Fortin, 2010), we also built linear models for each colour morph using morph frequency as the response and significant climatic predictors from the MMR models. We applied the logit transformation to the relative frequency of each morph and examined model assumptions by assessing residual normality and heteroscedasticity.

3 | RESULTS

3.1 | Thermal differences between black and black-and-white morph

Under controlled conditions, the black morph heated faster than the black-and-white morph on both the dorsal ($F_{1,41}=6.44$, p -value=0.01, $R^2=0.18$) and ventral sides ($F_{1,41}=7.24$, p -value=0.01, $R^2=0.1$). The same pattern was supported by the two methods of calculating heating rate (Tables S1 and S2; Figure S3). The difference in heating rate was small, varying in less than 1 degree after 5 min of solar exposure on both ventral and dorsal sides. Colour variants differ in their final body temperature (after 5 min) only on their ventral side, where black individuals had on average 0.71°C (95% CI: 0.70–0.71°C, p -value=0.017) higher body temperatures than black-and-white individuals. Our field measurements revealed no temperature difference between the black and black-and-white morphs on either the dorsal (Figure 3) or ventral sides (Figure 3). Air temperature, wind speed and light intensity appear to be the most important factors explaining the variation in body temperature in our field data (Table S3). Power analyses confirmed that our field sample size was sufficient to detect the strong effect of air temperature on body surface temperatures ($R^2=0.25$ –0.40)

and colour morph temperature differences $\geq 1.80^\circ$ (see Supporting Information, for details).

3.1.1 | Climatic niche variation among colour morphs

In the different sources of geographical records that we accessed (public records, museum collections and field observations), the black-and-white morph was the most prevalent colour morph (87.5%), followed by the black morph (9.8%). The orange morph was rare, with a prevalence of only 2.7% (Figure 1).

Visual examination of the climatic niche of all colour morphs in a density space per climatic variable, along with the pairwise significance test (Tukey HSD), suggests that the black and orange morphs exhibit differences across all variables except for mean minimum temperature (Figure 4, Table S4, Figures S3 and S4). We also observed a similar pattern when comparing the black-and-white with the orange morph; however, they showed similar values of mean maximum temperature. (Table S4). Notably, the niches of the black and black-and-white morphs significantly (p -value <0.05) differ in potential evapotranspiration, precipitation, solar radiation and air temperature, but not in climatic moisture index (Table S4).

We found that the climatic niche of the orange morph was the most dissimilar, presenting low-to-medium overlap values when compared with the black ($D=0.25$, $I=0.45$) and black-and-white ($D=0.21$, $I=0.39$) morphs (Table S5). In contrast, the climatic niches of the black and the black-and-white morphs were more similar, with high-to-medium overlap values ($D=0.64$, $I=0.82$). These results are consistent with a visual inspection of the density of occurrences in the environmental space (reduced multivariate dimensions to two PCs) where the black-and-white morph has a higher overlap with

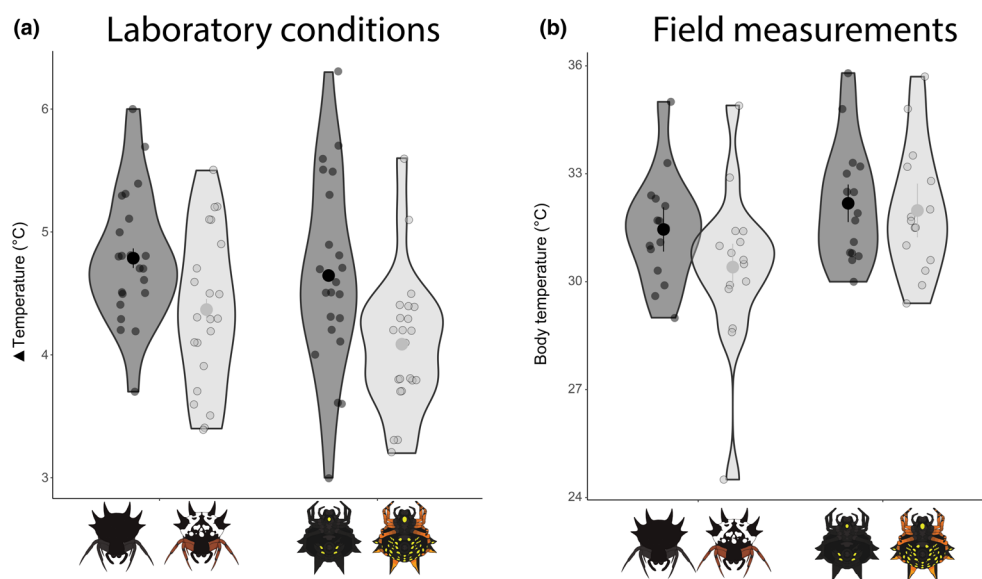


FIGURE 3 Differences in temperature between the black-and-white and black colour morphs on their ventral and dorsal sides.

(a) Heating rates experiment under controlled laboratory conditions. (b) Field temperature measurements. The dots represent measured values per individual per morph, while the big circles and bars represent the mean $\pm$ standard error of the predicted values from the linear models.

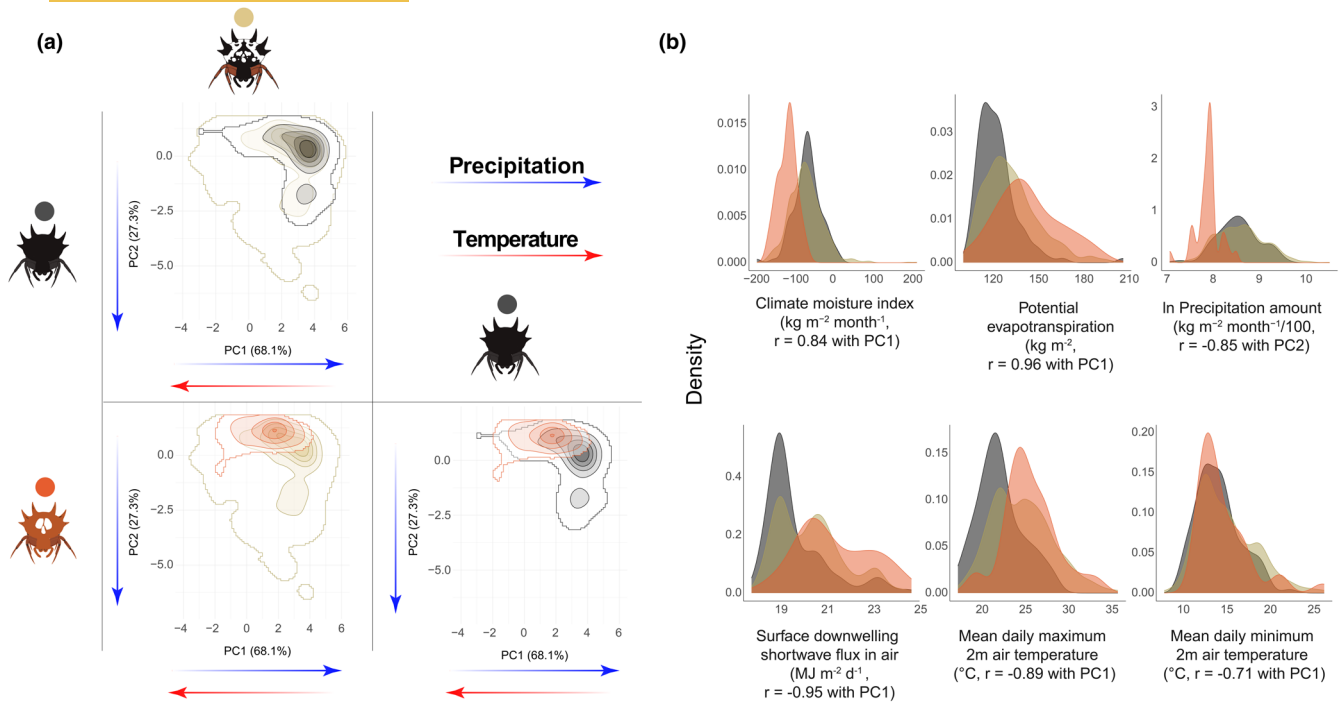


FIGURE 4 Realized climatic niche of the colour morphs of the Christmas spider. (a) Multivariate pairwise comparison of the climatic environment of the black-and-white (yellow), black (black) and orange (orange) morphs. Darker colours represent a higher density of records. Blue arrows represent the direction of increase of precipitation, climatic moisture index and potential evapotranspiration values in both PC1 and PC2. Red arrows symbolize the increase of solar radiation and temperature values on PC1. (b) Density distribution of the records of each climatic variable and their correlation with the principal components in plot (a). All density plots per variable are available in Supporting Information (Figures S5 and S6).

the black morph than with the orange morph (Figure 2). When comparing the environmental densities of the black and orange morphs, the segregation is even clearer (Figure 2); the black morph is more frequent in areas with higher precipitation ($F_{1,142}=64.2$, p -value <0.0001 , $R^2=0.31$) and climatic moisture index ($F_{1,142}=64.3$, p -value <0.0001 , $R^2=0.31$), and the orange morph has a higher density of points in areas with more solar radiation ($F_{1,142}=36$, p -value <0.0001 , $R^2=0.2$) and higher temperature ($F_{1,142}=41.3$, p -value <0.0001 , $R^2=0.22$; Figure 2).

Our test for niche conservatism and niche divergence supports the idea that the black-and-white and black morph share more similar niches than expected by chance ($D=0.64$, $I=0.82$, p -value <0.001 ; Table S5). Conversely, we found that the orange morph's climatic niche is less equivalent than expected by chance when compared to the black morph ($D=0.25$, $I=0.45$, p -value $=0.003$; Table S5) and the black-and-white morph ($D=0.21$, $I=0.39$, p -value $=0.003$; Table S5).

3.1.2 | Climatic factors shaping colour morph frequency

In the field, we observed that the black-and-white morph was the most abundant colour variant in most locations, exhibiting a mean relative frequency of 88% (min=43.5% to max=100%). The black morph ranked as the second most abundant morph in our sampling,

showing a mean relative frequency of 11.8% (0.3% to 48.8%). Lastly, the orange morph appeared as the least frequent, with a mean relative frequency of 9% (0.18% to 56%, Figure 2).

Our MMR models indicate that precipitation is the strongest predictor of morph frequency change across our sampling, and there was little effect of geographical distance and temperature (Figure 4; Table S6). Pairwise models suggest that the effect of precipitation is reduced ($r_{\text{partial}}=0.087$, p -value $=0.051$) when only comparing black and black-and-white morphs. However, the effect of precipitation is stronger when comparing only the orange morph and black morph ($r_{\text{partial}}=0.37$, p -value <0.001 ; Table S7) or the orange morph and the black-and-white morph ($r_{\text{partial}}=0.16$, p -value <0.001 ; Table S7). Similar results were obtained with the CHELSA dataset (Table S7).

Given that precipitation had the strongest effect in the analysis above, we explored the effect of precipitation on the frequency of each colour variant using linear models. Precipitation did not predict the frequency of the black-and-white morph ($F_{1,33}=2.12$, p -value $=0.15$, $R^2=0.02$; Figure 2) but had a significant positive effect on the frequency of the black morph ($F_{1,36}=14.77$, p -value <0.001 , $R^2=0.30$), which was more abundant in places with higher precipitation (Figure 2). The orange morph seems to follow the opposite pattern, with higher relative frequency in places with lower precipitation (Figure 2), but there is only marginal statistical support, possibly due to lower sample size ($F_{1,8}=4.64$, p -value $=0.06$, $R^2=0.31$, morph present in 13/49 populations). We obtained similar results with the CHELSA dataset for all the colour morphs (black:

$F_{1,37}=9.43$, p -value=0.003, $R^2=0.24$; black-and-white: $F_{1,34}=1.77$, p -value=0.19, $R^2=0.05$), except for the orange morph ($F_{1,9}=0.11$, p -value=0.74, $R^2=0.01$).

4 | DISCUSSION

Integrating macroecological patterns, within-population trends, experiments under controlled conditions and field observations, we identified climatic drivers that shape the distribution and frequency of the colour morphs of a widespread colour-polymorphic spider. We found little evidence for thermal benefits of dark colouration, or that temperature drives variation in morph frequency or presence at the macroecological scale. Instead, differences in the realized climatic niche of colour morphs, and their frequency and presence, were strongly linked to precipitation. Specifically, there is a higher frequency of dark individuals in wetter areas and a higher frequency of orange individuals in drier areas. Our results highlight the crucial role of environmental factors in shaping the presence and frequency of discrete phenotypes within and between populations.

Under controlled conditions, the black morph had a slightly higher heating rate than the black-and-white morph. However, we detected no difference in body temperature between these two colour morphs under field conditions (average air temperature $30.32 \pm 0.2^\circ\text{C}$ SE). Our results are consistent with previous evidence that discounted, under field or laboratory conditions, any thermal differences between light and dark colour variants in other arthropods (Kuyucu et al., 2018; Umbers et al., 2013), or between colour morphs in other spiders (Rao & Mendoza-Cuenca, 2016). This pattern likely occurs because body temperature in very small animals is driven primarily by convection rather than radiation (Parry, 1951; Rubalcaba & Olalla-Tárraga, 2020; Shine & Kearney, 2001; Umbers et al., 2013), meaning that other factors such as convective and evaporative heat loss can have a greater impact on body temperature than body colouration (Roberts et al., 2025; Turner & Lombard, 1990; Umbers et al., 2013). Supporting this, our field measurements showed that body temperature variation was mostly explained by air temperature and wind speed (Table S3).

The absence of differences in body surface temperatures in the field accompanied by minimal differences in heating rates in the laboratory aligns well with our realized climatic niche comparison, which shows that colour morphs differ in almost all climatic variables except for minimum temperature. However, we acknowledge that our evidence only partially discards thermoregulation as a factor shaping colour variation between the morphs, and its potential role should be further explored. For instance, since our field measurements represent a single snapshot, it remains possible that the small differences in heating rate observed under controlled conditions could become biologically relevant through cumulative effects over extended time periods, or under specific environmental conditions not captured in our study. Additionally, we were unable to include the orange morph in our heating rate and body surface temperature experiment. Therefore, it is possible that thermoregulation

could be relevant for the distribution of the orange morph, given its high reflectance in the near-infrared compared to the black morph (Supporting Information).

The black and black-and-white morphs are the most similar in their climatic niche, while the orange and black morphs are the most climatically distinct, replacing each other throughout our sampling areas (only nine of 38 populations with black individuals also have orange individuals). Our colour frequency measurements across multiple populations also indicated that precipitation is the most important climatic factor affecting the distribution of colour morphs in the Christmas spider. Specifically, higher precipitation favours a greater abundance of black individuals while limiting the presence of the orange morph in the same areas. Higher abundance of darker individuals in wetter areas has been reported in other taxa (Delhey et al., 2019; Friedman & Remeš, 2017; Kang et al., 2021; Koskenpato et al., 2023; Lopez et al., 2021; Passarotto et al., 2022; Romano et al., 2024). This pattern may arise as a consequence of the role of melanin in antimicrobial protection (Mackintosh, 2001; Nosanchuk & Casadevall, 2003), assuming higher pathogen density in high-humidity environments. However, in spiders, black and browns are usually produced by ommochrome pigments (a combination of ommatins and ommins) (Seligy, 1972); in fact, melanin was only recently reported in spiders for the first time (Hsiung et al., 2015). While our macroecological results partially support the predictions of Gloger's rule, the underlying mechanism remains uncertain due to lack of knowledge on the pigmentary basis of black coloration in spiders. More work on spider pigmentation and its physiological and ecological consequences is needed to understand the potential protective role of dark colour in humid environments in spiders.

A potential explanation for the frequency variation of the black and orange morphs of the Christmas spider across a precipitation gradient is that it could arise, at least partly, as a consequence of local adaptation associated with background matching (Cheng et al., 2018; Stevens & Merilaita, 2008). Background matching in web-building spiders is crucial to reduce predation (Pekár, 2014; Robledo-Ospina & Rao, 2022) and increase prey capture (Nakata, 2021; Nakata & Shigemiyu, 2015) because they are restricted to their webs. A post-hoc exploration of the association between soil brightness and colour variation suggests that the black morph is more prevalent in forested locations with darker soils, while the orange morph is more abundant in areas with lighter soils characteristic of the most arid regions of Australia (Figure S5). Available data on background colour are very coarse, which hinders a formal analysis, and there are inescapable links between soil colour and climatic variables, but background matching could be behind the association between precipitation and colouration in this system. In fact, background matching to reduce predation or enhance prey capture can promote colour variation both within and between populations across multiple lineages and types of environments (Bond, 2007; Fark et al., 2022; Nosil et al., 2018; Tate et al., 2016). However, the background matching hypothesis needs to be formally tested by collecting more detailed data on background and spider colours in the field. We also note that the sources of selection could be different between the

alternative morphs: pathogen protection could drive the prevalence of black individuals, and camouflage could favour orange individuals in each environment.

Our data also showed that the black-and-white morph is the most successful colour variant. This morph was the most abundant in all our sources of collection records, exhibited the highest frequency in nearly all sampled locations (minimum 43.5%), and was the only colour variant found in isolation. Since we did not find a thermal advantage provided by the presence of white patches in this morph, nor a clear macroclimatic pattern, we hypothesise that the abundance of the black-and-white morph over the other morphs could be due to a camouflage advantage via disruptive colouration (Cuthill, 2019; Endler, 2006). It is likely that colour polymorphism in this species is maintained through the interplay of multiple selective processes. If selection pressures act in opposing directions, different colour variants may be favoured within a single population (Endler, 1983; Nokelainen et al., 2011; Poloni et al., 2024). This phenomenon has been documented in various arthropods, where positive frequency-dependent selection favouring one morph is counterbalanced by negative frequency-dependent selection favouring another phenotype (Chouteau et al., 2017; Poloni et al., 2024; Takahashi et al., 2011). Another possibility is that the coexistence of multiple colour morphs is a consequence of highly heterogeneous environments that impose different forms of spatially and temporally varying selection at a small geographical scale (Nosil et al., 2024). To test these hypotheses, further research is needed to identify the functions of body colourations in *A. minax*, given that we currently do not know whether colour in this species acts as a warning signal, camouflage or improves prey capture.

Taken together, our work reveals a strong link between precipitation and the presence of multiple colour variants in the Christmas spider, with little evidence that ambient temperature plays a similar role. This level of understanding was possible only through the combination of broad scale, field, and laboratory approaches, providing important evidence for the role of the environment in driving the evolution of colour morphs in spiders. The patterns described here should be explored in depth to elucidate the proximate and ultimate factors maintaining both within- and between-population colour variation in this species. Based on our findings, we propose that background matching may drive frequencies of the black and orange morphs, while aposematism or prey attraction could maintain the high frequency of the black-and-white morph. Understanding how these multiple selective pressures interact offers the opportunity to explore key questions: Does the trade-off between multiple selective pressures facilitate the presence of phenotypically variable populations across space and time? Do the same selective pressures promote variation in geographically distant locations? Beyond this system, it is also important to test the prevalence of the links found here in other polymorphic species, especially in those with dark or melanic morphs.

AUTHOR CONTRIBUTIONS

Fabian C. Salgado-Roa, Devi Stuart-Fox and Iliana Medina conceived the ideas and designed the methodology; Fabian C. Salgado-Roa and

Iliana Medina acquired funding; Fabian C. Salgado-Roa collected and analysed the data, produced the visualisations and led the writing of the manuscript; Devi Stuart-Fox and Iliana Medina supervised the study. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We declare that there are no competing interests in the publication of this work.

DATA AVAILABILITY STATEMENT

Data, which this study is based, are available through Zenodo: <https://zenodo.org/records/14027791> (Salgado-Roa, Stuart-Fox, & Medina, 2024). Some updated versions of the scripts are also available here: https://github.com/fcsalgado/christmas_spider_climate.

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SUPPORTING INFORMATION

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

Table S1. Parameter estimation, their standard error (SE) and ANOVA significant test results (sum of squares, *F* statistic and *p*-value) from the linear models per side (dorsal or ventral). These models used as response variable the total temperature differences between the initial and final measurements after 5 min (ΔT). The colour morph variable used 'black' as reference, and 'black-and-white' as comparison.

Table S2. Parameter estimation, their standard error (SE) and ANOVA significant test results (sum of squares, *F* statistic and *p*-value) from the linear models per side (dorsal or ventral). These models used as response variable the maximum change in temperature in 20-s

intervals ($\max HR = \Delta T/s$). The colour morph variable used 'black' as reference, and 'black-and-white' as comparison.

Table S3. Parameter estimation, their standard error (SE) and ANOVA significant test results (sum of squares, F statistic and p -value) from the linear models per side (dorsal or ventral). These models used as response variable the average temperature in the field ($^{\circ}C$). The colour morph variable used 'black' as reference, and 'black-and-white' as comparison.

Table S4. Tukey HSD test comparing the mean values between colour morphs of the Christmas spider across six climatic variables. Values in bold are statistically significant.

Table S5. Results of the pairwise comparison of the climatic niche of the colour morphs of *Austracantha minax* using COUE (Centroid shift, Overlap, Unfilling and Expansion) scheme. The comparisons were made based on the second morph's niche using the first morph's niche as reference.

Table S6. Results of the multiple matrix regression models (MMR) using change in colour morph frequency (including all the colour morphs) as response variable. For each variable, we reported their partial correlation coefficient (r_{partial}) and p -value. Variables with a significant effect are in bold.

Table S7. Results of the pairwise multiple matrix regression models (MMR) with the variables with a significant effect on the change in colour morph frequency. MMR models incorporated only two morphs at a time, to examine if certain variables strongly influenced frequency changes in specific morphs. For each variable, we reported their partial correlation coefficient (r_{partial}). Variables with a significant effect are in bold.

Figure S1. Heating rates experimental set-up. We used a solar simulator as the light source coupled to if the black-and-white and black differ in their heating rates. The samples were inside a thermal chamber that minimizes the effect convection or conduction due to its cooling system that kept a stable air temperature.

Figure S2. Principal component dimensionality and contribution per variable. We summarized the climatic variation in two principal components (PC) which explained 95.4% of the climatic variation.

Figure S3. Realized climatic niche density plots per variable of the CHELSA v2.1 dataset. Colour morphs are coded as in Figure 3.

Figure S4. Realized climatic niche density plots per variable of the AGCD/AWAP v2.1 dataset. Colour morphs are coded as in Figure 3.

Figure S5. Relative frequency with each morph per soil brightness category. Chi-square test of independence result is $X^2 = 35.86$, $df = 2$, $p < 0.001$.

Figure S6. Pearson's correlation heatmap of the values of climatic variables at the field locations. The left panel displays the pairwise correlation values from the AGCD/AWAP dataset, while the right panel exhibits the pairwise correlation values from the CHELSA v2.1 dataset.

Figure S7. Hierarchical clustering analysis using Pearson correlation values resulting from all possible pairwise comparisons between the climatic variables per dataset. We considered a pair of variables as independent if they had a pairwise distance > 0.5 . Left panel corresponds to the AGCD/AWAP dataset and right panel corresponds to the CHELSA v2.1.

Figure S8. Probability density function of the brightness values of the geographical records in our dataset. This graph clearly shows that the variable is not continue and evenly distributed.

Figure S9. Reflectance spectra of colour morphs across different body regions. Each panel shows reflectance (%) as a function of wavelength (nm) for three colour morphs: orange (orange line), black-and-white (grey line), and black (black line). Red dots on the illustrated morphs indicate the measurement location for each panel. Top-left panel illustrates the results of the ventral side, and the other panel correspond to the dorsal side.

Figure S10. Multispectral photographs of three colour morphs of *Austracantha minax* under different illumination conditions. Each row represents a different colour morph: black-and-white (top row), orange (middle row), and black (bottom row). Each column shows the same specimens photographed under different light sources: VIS (visible light, left column), UV (ultraviolet light, middle column) and NIR (near-infrared light, right column). The left panel corresponds to the dorsal side of the specimens and the left panel to the ventral side.

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