Environmental drivers of structural colour in bees (Hymenoptera: Anthophila)

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Running title: Environmental drivers of bee struct. colour

Abstract

Aim: Environmental drivers frequently predict global patterns of colour diversity, but whether such patterns depend on the underlying colour mechanisms – pigments or microscopic structures – has scarcely been considered. Structural colour may have different functional properties that result in different associations with environmental variables. Here we test whether the presence of structural colour is linked with environmental variables that reflect potential thermoregulatory and water repellent properties.

Location: Global.

Major taxa studied: Bees (Hymenoptera: Anthophila).

Methods: We scored the presence of structural colour and extracted climate data for 1,784 bee species. We used phylogenetic generalised linear mixed models to control for phylogenetic relatedness and tested whether environmental variables, related to temperature and humidity, explain the presence of structural colour.

Results: A higher proportion of tropical species had structural colour, despite the higher species richness of bees at higher latitudes. Structural colouration was more likely to occur in cool, sunny environments, in which it is expected to provide the greatest thermal benefit. Structural colour was also more prevalent in environments with higher annual precipitation. These ecogeographic patterns were independent of body size.

Main conclusions: Our study reveals global ecogeographic patterns of structural colouration in bees, consistent with thermoregulatory and potentially water repellence functions. In addition, our findings highlight that structural colours probably have multiple coexisting functions, including both visual and non-visual functions, that need to be disentangled to understand global patterns of colour diversity.

Keywords
Bees, ecogeographical patterns, Hymenoptera, structural colour, thermoregulation, hydrophobicity

Introduction

At a macroecological scale, there is extensive evidence that environmental drivers can explain patterns of colour diversity. For example, some taxa are more colourful in the tropics (Cooney *et al.*, 2022), and darker colours are more frequent in humid (Gloger's rule; Delhey, 2019) and cold environments (Bogert's rule; Bogert, 1949). However, colours can be produced by different mechanisms – pigments or microstructures – that could affect their adaptive function and global distribution. When microscopic structures that interact with light are periodic and ordered, they create vivid structural colours that cannot be produced by pigments alone, including highly reflective, iridescent and/or metallic appearances (Johnsen, 2012). These same structures can have non-visual functions, such as water repellence (Zheng *et al.*, 2007) and thermal management (Shi *et al.*, 2015a), which may influence their relationship with climate. In birds, for example, structurally coloured plumage is more frequent in tropical species, with ordered-structural colour more prevalent in cool and dry climates, and quasi-ordered structural colours more prevalent in warm, humid climates (Eliason *et al.*, 2024). However, with the exception of birds (Eliason *et al.*, 2024), the specific environmental drivers of structural colour remain scarcely studied. Additionally, it is not known whether the prevalence of structural colour in the tropics applies to other taxa with different and more diverse structural colour mechanisms. Understanding the environmental factors driving the evolution of structural colour could have significant implications for explaining the diversity and distribution of colouration across the tree of life.

An important adaptive function of animal colour is to help regulate body temperature. Colour arises from visible wavelengths of the solar spectrum, whereas heat gain depends on absorption of sunlight across the full solar spectrum (i.e., solar radiation), including ultraviolet, human-visible and near-infrared (NIR) wavelengths (Stuart-Fox *et al.*, 2017). In addition, heating rates depend on body size, with greater body size often predicting lower heating rates likely due to higher thermal inertia (Wang *et al.*, 2021). Thus, body size could interact with the absorption of sunlight and affect thermal costs and benefits. The thermal effects of structural colours depend on the optical properties of the structures involved (Dou *et al.*, 2021). For example, the tiny hairs of Saharan silver ants (*Cataglyphis bombycina*) enhance broadband reflection, and help these insects reduce heat load by reflecting a large portion of both visible and NIR solar radiation (Shi *et al.*, 2015b). In contrast, in some taxa structural colour increases heat load due to lower reflectance of NIR wavelengths. Examples of lower NIR reflectance can be found in

the iridescent elytra of tiger beetles *Cicindela* (Coleoptera: Carabidae), bodies of some species of Christmas beetles (Coleoptera: Scarabidae: Rutelinae), and the feathers of Nectariniidae birds, which reflect a narrow range of the solar spectrum (i.e., “narrow-band” reflectance) (Schultz & Hadley, 1987; Shawkey *et al.*, 2017; Ospina-Rozo *et al.*, 2022b). These examples suggest that structural colour is often linked to narrow-band reflectance and lower reflectivity, thus increasing heat gain. For ectotherms, low reflectivity enables them to more rapidly reach active temperatures, at which they can forage, fly, mate and thermoregulate behaviourally (Xing *et al.*, 2016). The thermal advantages of low reflectivity are greatest in cool, sunny environments or environments with high daily temperature variation (Kingsolver *et al.*, 1991; Britton & Davidowitz, 2023). We may therefore predict that structural colour is more prevalent in cooler environments with high solar radiation or environments with large diel temperature changes (cool mornings, warm days).

Water repellence (hydrophobicity) is another important non-visual function attributed to structural colour. Water repellence in insects depends on the surface microstructures and the outer chemical composition of the cuticle (Sun *et al.*, 2012). The organized pattern of some structural colour mechanisms that are present on the surface of living organisms reduce the adhesion of water droplets (Zheng *et al.*, 2007; Wei *et al.*, 2019). Photonic crystals, such as those present in the wing scales of some butterfly species, play a significant role in water repellence as the ordered nature of these structures also create air pockets that reduce the contact area of water with the surface of the wing (Zheng *et al.*, 2007). In some beetle species with diffraction gratings (e.g., Scarabaeidae), certain arrangements of the gratings produce air pockets that enhances hydrophobicity (Wei *et al.*, 2019). On the other hand, colour displays produced by multilayer reflectors located in the integument of insects (Seago *et al.*, 2009), are often enhanced by specular reflectance that is the result of smooth surfaces (Franklin & Ospina-Rozo, 2021). Smooth surfaces can also be hydrophobic depending on the chemical composition of the cuticle (Holdgate, 1955; Sun *et al.*, 2012). Water repellence in turn prevents weight increase through water accumulation, and reduces adhesion of foreign particles and pathogens – i.e. self-cleaning (Schroeder *et al.*, 2018). If structural colouration is linked with water repellence, we predict a higher prevalence of structural colour in more humid environments.

Bees (Hymenoptera: Anthophila) are a globally distributed group of insects that display a variety of colour patterns (Michener, 2007) produced by different colour mechanisms (Saranathan *et al.*, 2015; Polidori *et al.*, 2017; Garduño-Medina *et al.*, 2021). Ordered and quasi-ordered structural colour in bees probably involves mechanisms that reflect a narrow band of wavelengths. This is because pure gold or silver mirror-like appearances, which suggest broadband reflectance (Seago *et al.*, 2009), have not been described in this group of insects. The ecology and evolution of bees have been extensively investigated, since they are important pollinators. Nevertheless, few studies investigate the diversity of colouration in bees because their colour patterns are widely assumed to function primarily as warning signals (Chatelain *et al.*, 2023). While there is some experimental evidence for an antipredator function of colour in bumblebees (Brower *et al.*, 1960; Evans & Waldbauer, 1982), it is unlikely that it is the sole or even the most important function of colouration in bees, as the efficacy of bees' warning colouration has been questioned (Linsley, 1960; Cane, 1986; Stelzer *et al.*, 2010). Sexual signalling, another primary function of structural colour, is also unlikely to be important in bees. Although sexual dichromatism exists in some bee species (Leys & Hogendoorn, 2008), mate recognition seems to rely primarily on olfaction (Galvani *et al.*, 2012, 2017). Instead, structural colour in bees may have non-visual functions, suggesting that environmental drivers may predict its distribution.

In this study, we tested whether environmental factors related to temperature and humidity predict the presence of structural colour in bees. We collected information on the presence of structural colour and the climatic niche characteristics of bees present in the publicly available bee phylogeny (Henríquez-Piskulich et al., 2024), and investigated the potential link between the presence of structural colour and environmental factors while controlling for phylogenetic relatedness. We specifically address two hypotheses: i. if structural colour plays a role in thermoregulation, then we predict a prevalence of structural colouration in cooler environments with high solar radiation or environments with greater daily temperature variation; and ii. if structural colour plays a role in water repellence, we predict it will be more prevalent in environments with higher humidity. In addition, we expect that the link between temperature and structural colour could be mediated by body size.

Methods

Structural colour scoring

Although studies on the colour-production mechanism in bees are scarce (Saranathan *et al.*, 2015; Hines *et al.*, 2017; Polidori *et al.*, 2017), previous studies on invertebrate structural colour have made possible (Sun *et al.*, 2013; Vukusic & Chittka, 2013), with reasonable confidence, the visual classification of colours consistent with those produced by structures. In birds, similar visual assessments of structural colour have been demonstrated to be reliable (Owens & Hartley, 1998; Delhey, 2016; Eliason *et al.*, 2024). The colours produced within the visible spectrum when these structures are present, either alone or in combination with pigments, can produce dull green or blue (Prum *et al.*, 2004, 2006), or vivid and intense hues which sometimes appear iridescent (Kroiss *et al.*, 2009; Stavenga *et al.*, 2014), pearlescent (Stavenga, 2021; Ospina-Rozo *et al.*, 2022a), or metallic-like, spanning blue, bluish-green, greenish-gold, gold, silver and occasionally purple or red (8, 28, 77, 94–96).

Because accessing collection specimens of the 4,586 bee species in our phylogeny (Henríquez-Piskulich *et al.*, 2024) was not logistically possible, we searched for high-resolution images of both males and female from reliable sources to ensure accurate identification (e.g., Atlas Hymenoptera, BugGuide, Discover Life, PaDIL, USGS Bee Inventory and Monitoring Lab, PCYU digital galleries). P.H.-P. then scored the inferred presence of structural colour as a binary variable (yes/no) for each bee species, as to avoid inter-observer variation. Wing colour was not considered because the structure of transparent wing membranes generally produce interference patterns (Shevtsova *et al.*, 2011), although some species display more distinct appearances (Stavenga *et al.*, 2022). Therefore, if either the male or the female exhibited dull green, dull blue, iridescent, pearlescent, and/or a metallic-like colours on the cuticle or setae in any part of the body, structural colour was scored as present for that species. Additionally, we included structural colour information for species without reliable pictures by using descriptions from published taxonomic studies for bee genera and species (Table S1). Structural colour was scored as present if the species descriptions included descriptions of colour that matched the criteria described above.

Geographical data

For the species we found information on presence/absence of structural colour (n = 3,499), we used geographical records previously obtained from iDigBio (iDB), Global Biodiversity Information Facility (GBIF), Symbiota Collections of Arthropods Network (SCAN), and Atlas of Living Australia (ALA) (see Henríquez-Piskulich *et al.*, (2024) Supplementary file 4 for a description of the methods). We excluded geographical coordinates that reflected anthropogenic introduction such as all records for *Apis mellifera* (Apidae) that were outside of Europe, Africa and Western Asia. The mean number of geographical records per species was 50.16 (95% CI: 46.76-53.77) of 1,948,983 records. To improve reliability, we excluded species with fewer than 47 geographic records, reflecting the lower limit of the 95% confidence interval.

Climatic variables

We used the geographical records in our dataset to extract the climatic variables at a 30 arc-seconds resolution (1-km spatial resolution; data from 1970-2000) from WorldClim (Fick & Hijmans, 2017). We then averaged values for all records for a given species to obtain a single value for each climate variable per species. We selected five climate variables that best represented our temperature and humidity predictions: mean annual temperature, mean solar irradiance, isothermality, water vapour pressure and mean annual precipitation. Details of the justification and process for selecting these five climate variables are provided in Supplementary Information. Additionally, we included the absolute median latitude in our analyses because our dataset includes globally distributed bee species, and structural colour may be affected by other unmeasured environmental variables associated with the geographical location of species.

Data analyses

All analyses were conducted in R (version 4.3.0, R Core Team 2023 R Core Team, 2023). We explored the selected climatic variables (i.e., mean annual temperature, mean solar irradiance, isothermality, water vapour pressure and mean annual precipitation) for the presence of collinearity with the package performance (Lüdecke *et al.*, 2021), to remove variables that may confound relationships or inflate parameter uncertainty. Mean annual temperature, mean annual precipitation and water vapour pressure had moderate to high variance inflation factor (VIF; Figure S3A). Because of this, we designed and compared models that explored independent effects of mean annual precipitation and water vapour

pressure by including them in separate PGLMM models, while keeping mean solar irradiance and isothermality constant. Mean annual temperature was not included in these models given its high VIF (Figure S3A). Mean annual precipitation was a better predictor and had a stronger effect on the presence of structural colour ($\beta = 0.619 \pm 0.096$, z-score = 6.442, p = <0.001; AIC = 1573) than water vapour pressure ($\beta = 0.446 \pm 0.110$, z-score = 4.053, p = <0.001; AIC = 1603; Table S3), when included in a model with mean solar irradiance and isothermality. Therefore, our final models included the interaction between mean annual temperature and mean solar irradiance, and isothermality representing the temperature hypothesis, and mean annual precipitation representing the humidity hypothesis. We produced three final models because isothermality was highly correlated to mean annual temperature and mean solar irradiance (Spearman's rho > 0.8; Figure S1), and because median latitude had high VIF when included in the model with all selected predictors from our thermoregulation hypotheses (Figure S3B): i. the interaction between mean annual temperature and mean solar irradiance, and mean annual precipitation; ii. isothermality and mean annual precipitation; and iii. mean annual precipitation and median latitude. We then explored our final models with PGLMMs for all bee species included in our dataset. We chose the model that best explained the presence of structural colour based on its Akaike information criteria (AIC) and predicted R-squared (R^2), which indicates how well each model predicts the presence of structural for new observations.

We also explored the potential role of body size, measured as female body length (i.e., total length from the head to end of the final tergite) in millimetres. We tested whether body size could predict the presence of structural colour separately and when interacting with temperature. Female body size was obtained from available and previously published datasets and species descriptions. We obtained body size data for 738 species for which we had data on presence/absence of structural colour. Of these species, we had climatic data available for 521. Thus, we explored the relationship between female body size and the presence of structural colour for the subset of 738 species, and the interaction of mean annual temperature and female body size for the subset of 521 species. Variables were z-score standardised to be able to compare the relative effect size of the predictors (Agresti, 2012). In addition, to control for phylogenetic uncertainty, we ran the final models and body size models on a sample of 100 randomly selected bootstrap sample trees.

Results

Geographic and phylogenetic distribution of structural colour

We obtained geographical data for 1,784 species, of which 383 had structural colour (367 in the cuticle and 16 in the setae; Figure 1). Bee species distributed at lower latitudes have a higher probability of being structurally coloured ($\beta = -0.487 \pm 0.088$, z-score = -5.533, $p = <0.001$; Figures 2A, 3C, and Table 1). Of the 283 bee species distributed in tropical regions (i.e., absolute median latitude below or equal to 25 degrees), 29% (83 species) had structural colour, whereas of the 1,501 species in temperate regions (i.e., absolute median latitude above 25 degrees), 20% (300 species) had structural colour. Tropical species with structural colour belonged to Apidae (61 of 83 species; 74%) and Halictidae (20 species; 24%), with only one colletid and one andrenid bee species. Temperate species belonged primarily to the families Halictidae (137 of 300 species; 46%) and Megachilidae (88 species; 29%), followed by smaller numbers of Andrenidae (34 species; 11%), Apidae (32 species; 11%), and Colletidae (9 species; 3%).

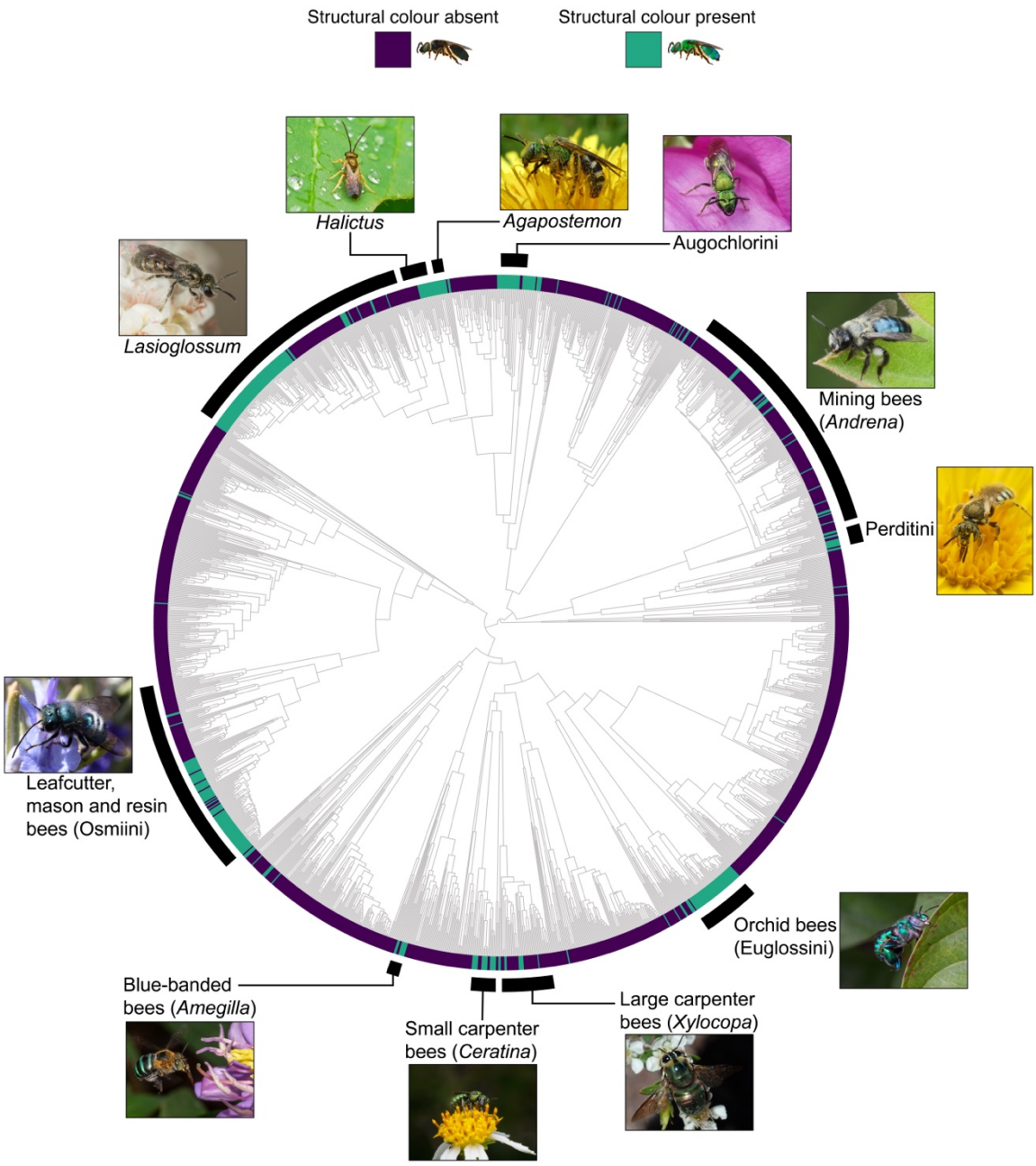

Figure 1. Phylogenetic relationships and distribution of structural colour of bees included in the study. Colour tips represent the presence or absence of structural colour. Images of bees with structural colour include *Lasioglossum* sp. (Halictidae; original photo: Jesse Rorabaugh), *Halictus aerarius* (Halictidae; original photo: Hitoshi Watanabe), *Agapostemon virescens* (Halictidae; original photo: Bruce Cook), *Augochlora pura* (Halictidae; original photo: Bruce Cook), *Andrena cerasifolii* (Andrenidae; original photo: Garth Harwood), *Perdita bruneri* (Andrenidae; original photo: Thilina Hettiarachchi), *Euglossa dilemma* (Apidae; original photo: Eridan Xharahi), *Xylocopa* sp. (Apidae; original photo: Thomas Mesaglio), *Ceratina smaragdula* (Apidae; original photo: Wildan Ardani), *Amegilla andrewsi* (Apidae; original photo: Lee Ismail), and *Osmia ribifloris* (Megachilidae; original photo: Catherine Galley).

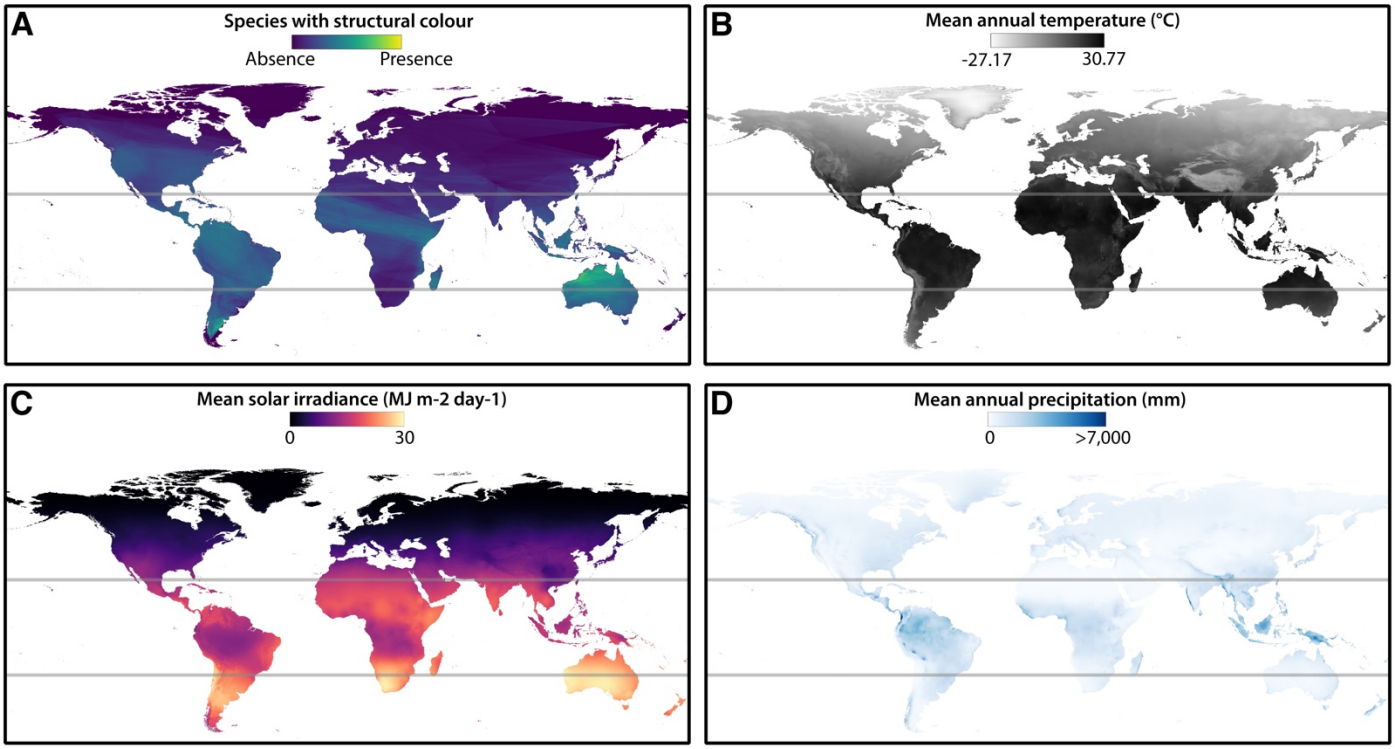

Figure 2. (A) Distribution of bees with structural colour from our dataset. Heat map was produced from distribution polygons for each species with structural colour included in the study. (B) Mean annual temperature (°C). (C) Mean solar irradiance (MJ m^{-2} day^{-1}). (D) Mean annual precipitation (mm). Grey lines mark the boundaries of the tropics. Raster files and the shapefile of the world map were exported to QGIS to plot the heat maps which were later edited in Adobe Illustrator. Maps of climatic variables display means, which were obtained by averaging monthly climate data from WorldClim.

We found no relationship between structural colour and female body size, either separately (β = 0.159 ± 0.289, z-score = 0.551, p = 0.582; 95% highest posterior density interval (HPD) of 100 random trees: β = 0.149 to 0.178, p-value > 0.05) or in interaction with temperature (β = 0.414 ± 0.331, z-score = 1.250, p = 0.211; 95% highest posterior density interval (HPD) of 100 random trees: β = 0.395 to 0.428, p-value > 0.05; Figure S4). For this reason, and because we only had female body size data for a subset of 521 species, we did not include female body size in subsequent models with climatic predictors.

Climatic predictors of structural colour

The model that included the interaction between mean solar irradiance and mean annual temperature was a better predictor of the presence of structural colour (AIC = 1556.4; R^2pred = 0.384; Table 1) than the model including isothermality (AIC = 1630.7; R^2pred = 0.347; Table S4). Bee species in cooler environments with higher solar irradiance (β = -0.473 ± 0.101, z-score = -4.665, p = <0.001; 95% highest posterior density interval (HPD) of 100 random trees: β = -0.498 to -0.432, p-value = <0.001) and higher

annual precipitation ($\beta = 0.565 \pm 0.098$, z-score = 5.742, p = <0.001; 95%HPD 100 trees: $\beta = 0.536$ to 0.610, p-value = <0.001) were more likely to be structurally coloured (Figures 2, 3, and Table 1). In warmer environments, bees with and without structural colours were found in locations with similar or lower radiation levels. The effect of annual precipitation disappeared ($\beta = 0.072 \pm 0.080$, z-score = 0.902, p = 0.367; 95%HPD 100 trees: $\beta = 0.059$ to 0.109, p-value > 0.05) in the model with median latitude rather than the model that included the interaction between mean solar irradiance and mean annual temperature. This suggests that latitude has an overall strong association with the presence of structural colour which might obscure the effect of climatic variables.

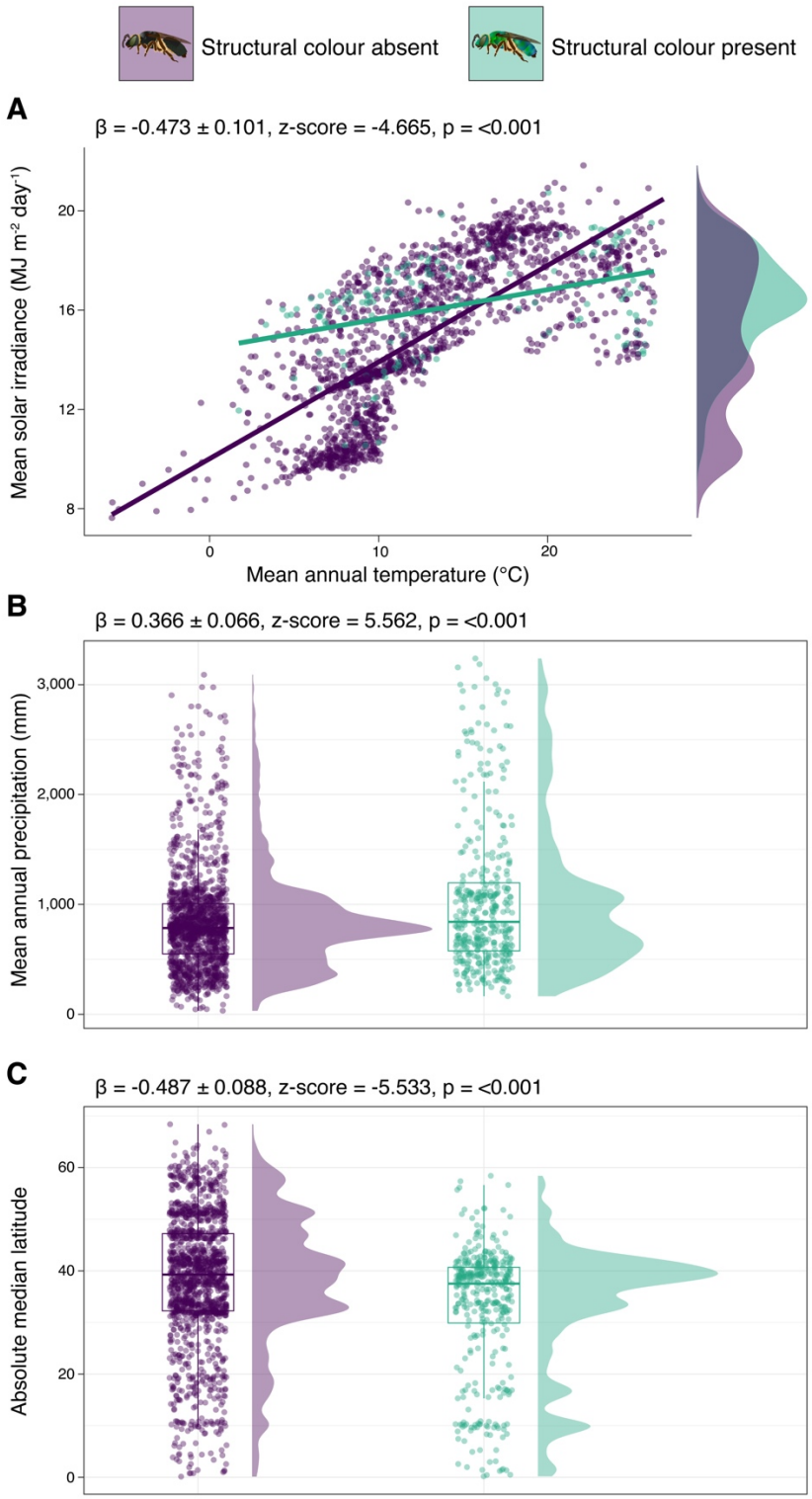

Figure 3. Association between environmental variables and structural colour for all bees included in the analyses (n = 1,784 species without structural colour; n = 383 species with structural colour). (A) Association between mean solar irradiance (MJ m^{-2} day^{-1}) and mean annual temperature for bees with and without structural colour. Lines represent prediction from model presented in Table 1. (B) Distribution of mean annual precipitation, results from the model that included the interaction between mean solar irradiance and mean annual temperature. (C) Distribution of absolute median latitude. For (B) and (C), lines within each box represent the median, and the upper and lower lines of the box indicate the minimum and maximum quantiles.

Table 1. Results of final PGLMM models predicting structural colour and how much of the variation is explained by climatic variables. Each cell includes the estimate, the standard error of the estimate, the z-score and p-value for each predictor included in the model. AIC = Akaike information criterion; R^2lik = coefficient of determination, values are between 0 and 1, denoting the proportion of the variation explained by the model; R^2pred = predictive R^2, indicates how well the model predicts responses for new observations.

	Model with mean solar irradiance * mean annual temperature	**Model with median latitude**
(Intercept)	−1.734***	−1.994***
	s.e = 0.452	s.e = 0.451
	z = −3.832	z = −4.427
	p = <0.001	p = <0.001
Solar irradiance	0.758***	
	s.e = 0.135	
	z = 5.624	
	p = <0.001	
Mean annual precipitation	0.565***	0.072
	s.e = 0.098	s.e = 0.080
	z = 5.742	z = 0.902
	p = <0.001	p = 0.367
Mean annual temperature	−0.231	
	s.e = 0.143	
	z = −1.614	
	p = 0.106	
Mean solar irradiance * mean annual temperature	−0.473***	
	s.e = 0.101	
	z = −4.665	
	p = <0.001	
Median latitude		−0.487***
		s.e = 0.088
		z = −5.533
		p = <0.001
Num.Obs.	1784	1784
AIC	1556.4	1607.9
R^2lik	0.161	0.135
R^2pred	0.384	0.364

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Discussion

In this work, we explored whether the presence of structural colour in bees exhibits ecogeographical patterns that may arise from potential non-visual functions of structural colouration, namely thermoregulation and water repellence. The majority of bee species are found at higher latitudes, but tropical species were more likely to have structural colour. We found strong support for the main prediction of the thermoregulation hypothesis, that structural colouration should be more prevalent in cool, sunny environments, in which low reflectivity provides the greatest thermal benefit (Kingsolver *et al.*, 1991; Britton & Davidowitz, 2023). Consistent with the water repellence hypothesis, structural colour was also more prevalent in more humid environments (higher annual precipitation), but this pattern could arise from the association of structural colour with latitude. The link between structural colour and climate appear to be independent of body size. These results provide novel evidence for large scale ecogeographic patterns of structural colouration in insects.

We found that structural colouration was more likely to occur in environments that are cool and sunny and less prevalent in hot and sunny environments. Structural colours tend to have lower reflectivity (proportion of sunlight reflected by a surface; Ospina-Rozo *et al.* (2022b)) than pigment-based colours (Schultz & Hadley, 1987; Shawkey *et al.*, 2017; Ospina-Rozo *et al.*, 2022b). This is because structural colours often reflect a narrow range of visible wavelengths (narrow-band), enhanced by absorption of remaining wavelengths, including the near-infrared, which accounts for more than 50% of the energy in sunlight (Campbell & Norman, 2000). By contrast, pigments absorb specific wavelengths, with non-absorbed wavelengths often reflected by a disordered matrix in which the pigments are embedded (Stuart-Fox *et al.*, 2025). This results in an overall higher proportion of solar radiation that is absorbed by most structural colours compared to pigment-based colours. The amount of solar radiation that is reflected or absorbed by an insect's surface has direct thermal consequences (Amore *et al.*, 2017; Kang *et al.*, 2021), with the greatest effect on heat gain in cool, sunny conditions (Kingsolver *et al.*, 1991; Gates, 2012; Munro *et al.*, 2019). Like other insects, bees are ectotherms most of the time and thus, thermal properties of their environment restrict their activity. Although, some bees can produce their own heat by using their thoracic flight muscles, they first need to reach a minimum muscle temperature to warm-up endothermically which is constrained by environmental temperature (Willmer & Stone, 2004). Structural colours could allow bees to warm-up and reach their optimal active temperature faster

in environments with high solar radiation and cool air temperatures, which would allow bees to be active early in the day and/or early in the season. Conversely, structural colouration could be a disadvantage in hot, sunny environments. Although, we found a higher prevalence of structural colouration in the tropics, these species tend to be in montane or forested environments, rather than hot, exposed environments.

Bees with structural colouration are also more prevalent in environments that have higher precipitation, consistent with a potential function for structural colouration in water repellence. These results agree in part with the distribution patterns found in birds with structural colours. Eliason et al. (2024) recently showed that birds with ordered structural colours are more prevalent in cool and dry environments while species with quasi-ordered structural colours are more prevalent in warm and humid environments. The reason for correlations between different types of structural colour and climate variables in birds is unclear, but is unlikely to be associated with water repellence. Although one of the key features of bird feathers is water repellence, which is a direct function of macro and microstructural feather properties (Muzio & Rubega, 2024), feathers with structural colours seem to have reduced water repellence when compared with feathers that do not have structural colour (Eliason & Shawkey, 2011). By contrast, in insects, structures that produce structural colour are often linked with enhanced water repellence (Holdgate, 1955; Zheng *et al.*, 2007; Sun *et al.*, 2012; Wei *et al.*, 2019), indicating that non-visual functions of structural colour - and hence correlations with climate - may be lineage specific. Most studies examining the correlation between colour and precipitation test for Gloger's rule (i.e., darker colours are more frequent in humid environments; Delhey, 2019), but future work should examine the relationship between structural mechanisms and hydrophobicity.

We found a strong latitudinal gradient in the prevalence of structural colour, similar to what has recently been found in birds, where structurally coloured plumage is more frequent in tropical species (Eliason *et al.*, 2024). It has long been suggested that organisms are more colourful closer to the tropics - with studies that support this pattern (Adams *et al.*, 2014; Cooney *et al.*, 2022), and others that do not (Dalrymple *et al.*, 2015, 2020; Lopez *et al.*, 2021). Although we did not measure colourfulness (i.e., how much of the colour space is occupied by a taxon), structural colour often provides access to a wider colour palette than pigments alone (Maia *et al.*, 2013). Amongst the reasons suggested as promoters

of colourfulness in the tropics are relaxed evolutionary constraints on elaborate colours due to less extreme environmental conditions in the tropics (Cooney *et al.*, 2022); and warning colouration and/or accurate conspecific recognition driven by a greater number of co-occurring species (Adams *et al.*, 2014). Bees however, have higher species richness in xeric and temperate regions (Orr *et al.*, 2020). We found that bees distributed in tropical regions were more likely to have structural colour, suggesting that bees might be more colourful in the tropics despite their lower diversity in these regions.

Perhaps the most iconic tropical bees that display vivid structural colours are orchid bees (Apidae: Euglossini) (Michener, 2007). Orchid bees are found mostly in the tropical regions of the Neotropics, from Mexico to central Argentina (Roubik, 1992), and seem to be more diverse in cloud forests than lowland forests (Roubik & Ackerman, 1987). In cloudy, montane environments, higher solar absorptivity due to structural colouration may enable orchid bees to maximise heat gain during brief sunny periods. However, thermal benefits are unlikely to be the only (or even primary) function of vivid structural colours in orchid bees, or other bees. There are likely several, and possibly competing, selective pressures affecting the evolution of structural colour, which could also vary geographically. These other selective pressures could explain some of the variation we observed that was not explained by our climate variables. For example, iridescence and gloss produced by structural colours can have an anti-predator function (Kjernsmo *et al.*, 2022; Henríquez-Piskulich *et al.*, 2023; Franklin *et al.*, 2024) and lower latitudes are often linked to higher predation (Tomas Roslin *et al.*, 2017; Hargreaves, 2024). One of the mechanisms proposed for this link is that warmer environments increase feeding rates of living organisms (Brown *et al.*, 2004; Rall *et al.*, 2012). The prevalence of structural colour at lower latitudes in bees, such as orchid bees, could therefore be a response to higher predation pressure selecting for antipredator strategies, as suggested for butterflies (Adams *et al.*, 2014).

Our findings reveal that environmental drivers could have shaped the evolution of structural colour in bees, potentially linked to thermoregulatory and water repellence benefits. In addition, we also show that body size does not predict the presence of structural colour. We only considered colours likely to be produced by ordered or quasi-ordered structures that likely produce narrow-band reflectance and therefore low reflectivity. However, in bees, white setae probably have underlying structures that produce broadband scattering (Polidori *et al.*, 2017), just as silver hairs produce high solar reflectivity

in Saharan silver ants (Shi *et al.*, 2015a). In the Sonoran Desert, pale (grey/white) and large male morphs of the species *Centris pallida* (Apidae: Centridini) have been found to have higher reflectance of solar radiation (UV-visible-NIR), when compared with brown and small morphs (Barrett & O'Donnell, 2023). These differences might be linked to behaviour and microclimate: large-morph males are fully exposed to the sun because they patrol near the ground attempting to locate females in underground nests, while small-morph males chase after flying females and typically hover one metre or more above the ground near vegetation (Alcock *et al.*, 1977). Understanding a broader range of structural colours, how this relates to the underlying mechanisms, and linking this to the natural history of bees, could expand our understanding of the role of photonic structures in nature beyond the vivid colours they produce.

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Supporting information

Environmental drivers of structural colour in bees (Hymenoptera: Anthophila)

Supplementary Methods

Selection of climate variables

We initially selected five niche variables that best represented our temperature prediction and four for our humidity prediction. For the temperature prediction, we obtained the mean, minimum, and maximum annual temperature (°C), solar irradiance (kJ m^{-2} day^{-1}) and isothermality. Although there may be temporal variation in the activity levels among bee species in the dataset, mean annual temperatures are highly correlated with mean temperature values of the activity periods of seasonal species (Kang *et al.*, 2021). Thus, mean annual temperatures can reliably capture climatic variation for a global scale analysis. In addition, the temperature variables were chosen to capture variation in mean temperatures as well as temperature variability, reflected by isothermality. For humidity we included water vapour pressure (kPa), mean annual precipitation (mm), precipitation seasonality from WorldClim (Fick & Hijmans, 2017), and aridity index (Zomer *et al.*, 2022). We included precipitation seasonality because mean precipitation and water vapor pressure can hide important seasonal variation. In addition, humidity depends on the ratio of precipitation to evaporation, which is captured by the aridity index. A higher aridity index represents more humid conditions, while low values represent higher aridity (Zomer *et al.*, 2022).

Climatic variables tend to be highly correlated and while this can be accommodated by principal components analysis (PCA), if used as input variables in a comparative framework, PCs can produce incorrect inferences as the principal components represent a biased sample of a multivariate pattern (Uyeda *et al.*, 2015). Thus, we first used non-parametric Spearman correlations to identify and discard variables that were highly correlated for each hypothesis (Spearman's rho ≥ 0.8). We selected mean annual temperature, mean solar irradiance and isothermality for our thermoregulation hypothesis because temperature variables considered for this hypothesis were highly correlated (Spearman's rho = 0.88 – 0.98; Figure S1), and thus, were well captured by mean annual temperature. The climatic predictors for our water repellence hypothesis were correlated to each other in different directions (minimum Spearman's rho = -0.56, maximum Spearman's rho = 0.65). Median latitude was correlated with most climatic variables except mean annual precipitation (Spearman's rho = -0.13), with the direction being negative for most variables except for aridity index (Spearman's rho = 0.51).

Because the variables from our water repellence hypothesis were not highly correlated, we selected variables for this hypothesis by fitting single predictor models for all variables and assessing the importance of each of them on the presence of structural colour. The importance of variables was defined by a drop in support values (i.e., ΔAIC) when comparing the single predictor model to a reduced model (intercept only), with larger ΔAIC indicating greater statistical support for the importance of a variable (Burnham & Anderson, 2004; Cooney *et al.*, 2020). To do this, we ran phylogenetic generalized linear mixed models (PGLMMs; Ives et al., 2010), as implemented in the package phyr to account for phylogenetic relatedness (Li *et al.*, 2020). In addition, climatic variables were z-score standardised to be able to compare the relative effect size of each predictor for all models (Agresti, 2012). From the water repellence hypothesis, we selected water vapour pressure (ΔAIC = 25.135; Figure S2 and Table S2) and mean annual precipitation (ΔAIC = 23.755), because they had the highest statistical support when ran in individual models and did not have a very strong correlation with each other (Spearman's rho = 0.61). We did not do this for our thermoregulation hypothesis, as removing any of the remaining variables would have affected our ability to test our specific predictions. Thus, our final climate variables were mean annual temperature, mean solar irradiance, isothermality, water vapour pressure and mean annual precipitation.

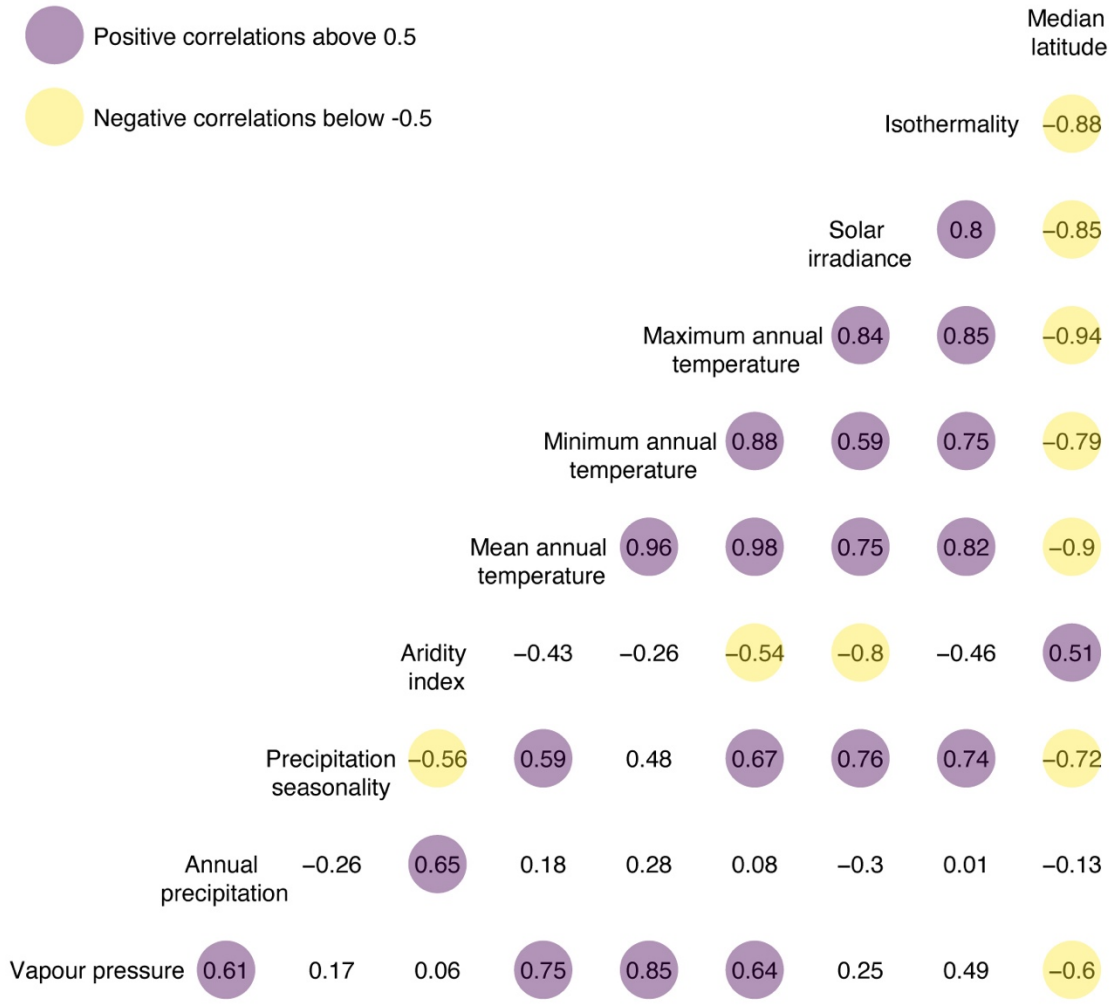

Figure S1. Spearman rank-order correlation coefficient for the climatic variables included in this work. Highlighted are all correlation coefficients superior to 0.5 (colour purple) and inferior to -0.5 (colour yellow).

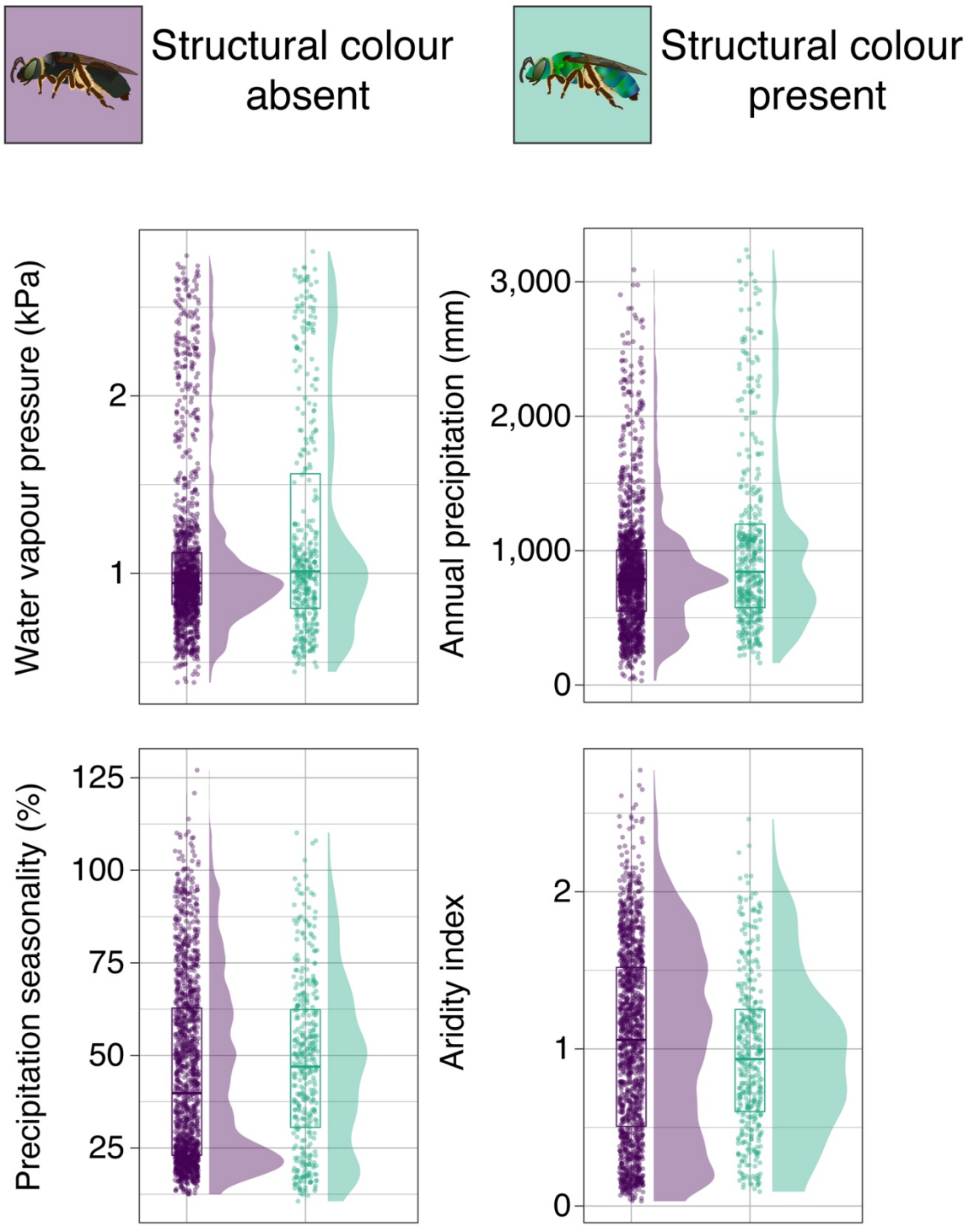

Figure S2. Relationships between the presence of structural colour and individual predictor variables for the water repellence hypothesis. (n = 1,784 species without structural colour; n = 383 species with structural colour). Lines within each box represent the median, and the upper and lower lines of the box indicate the minimum and maximum quantiles. Plots highlighted in grey are variables considered for the thermoregulation hypothesis and, plots not highlighted are variables considered for the water repellence hypothesis.

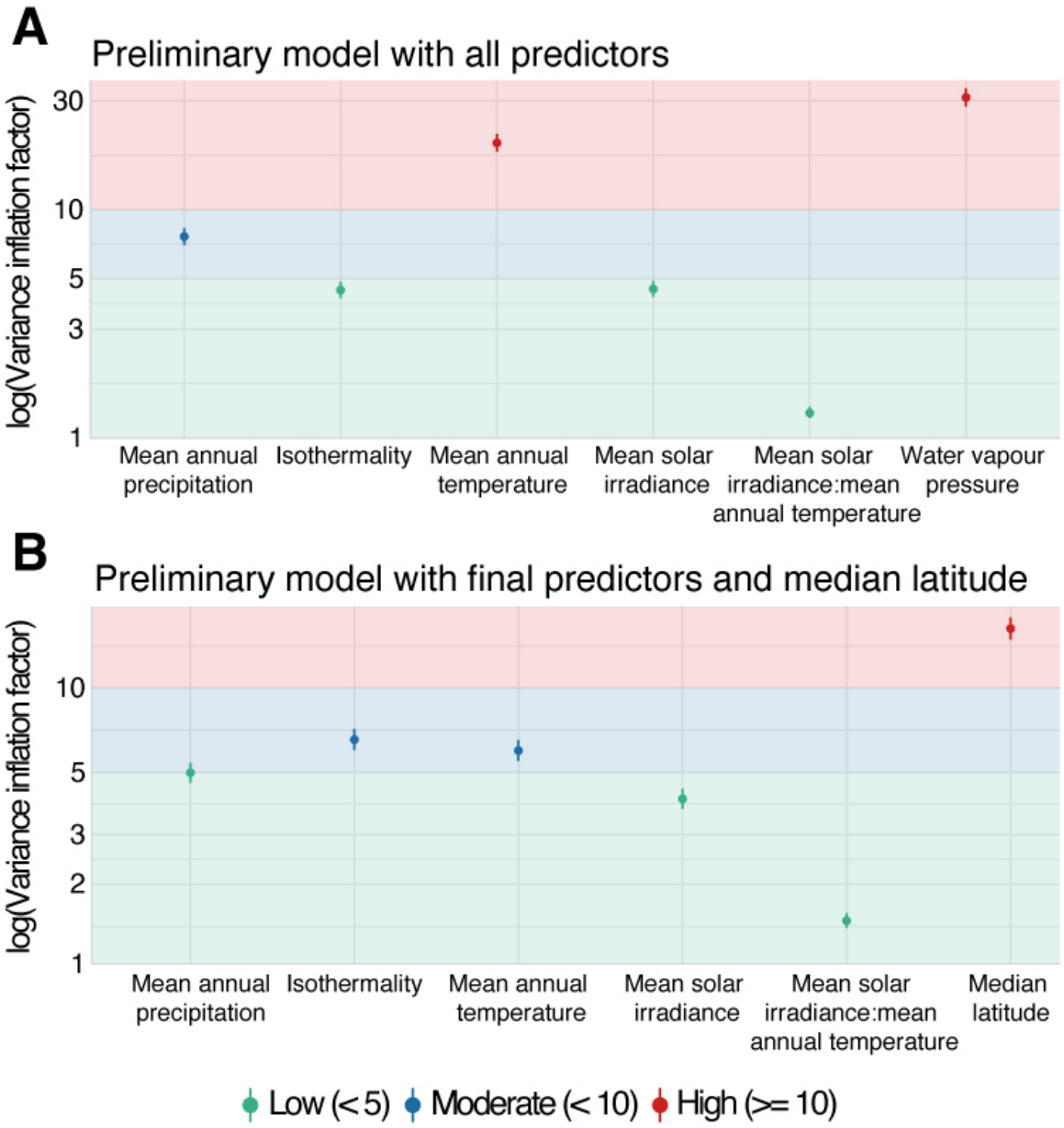

Figure S3. Collinearity plot of all climatic predictors considered in the preliminary PGLMM models.

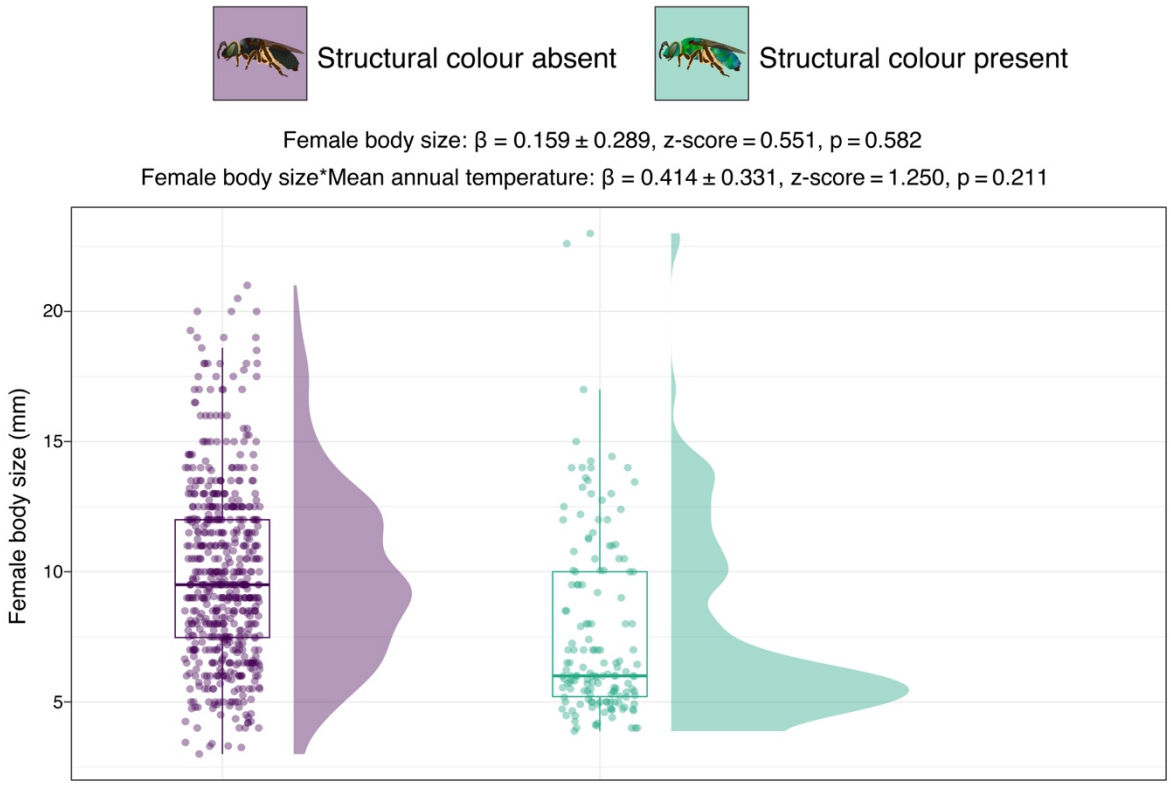

Figure S4. Distribution of female body size (total length from the head to end of the final tergite in millimetres) for species with and without structural colour (n = 587 species without structural colour; n = 151 species with structural colour). Lines within each box represent the median, and the upper and lower lines of the box indicate the minimum and maximum quantiles.

Table S1. Literature used to score structural colour for bee species without available and reliable images.

Study
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Table S2. Results of preliminary single predictor PGLMM models testing the association in isolation of climatic variables with structural colour for the water repellence hypothesis. Variables were z-score standardised to be able to compare the relative strength of each predictor on the presence of structural colour. ∆AIC = difference in Akaike information criterion score between single predictor model and the reduced model (intercept only).

Variable	Estimate	Standard error	z-score	p-value	∆AIC
Water vapour pressure	0.350	0.067	5.263	<0.001	25.135
Mean annual precipitation	0.336	0.066	5.089	<0.001	23.755
Precipitation seasonality	0.196	0.069	2.854	0.004	7.215
Aridity index	-0.232	0.070	-3.300	0.001	11.618

Table S3. Results of preliminary PGLMM models testing the association of climatic variables with structural colour that had moderate VIF while keeping mean solar irradiance and isothermality constant. Each cell includes the estimate, the standard error of the estimate, the z-score and p-value for each predictor included in the model. AIC = Akaike information criterion; R^2lik = coefficient of determination, values are between 0 and 1, denoting the proportion of the variation explained by the model; R^2pred = predictive R^2, indicates how well the model predicts responses for new observations.

	Model with water vapour pressure	**Model with mean annual precipitation**
(Intercept)	−2.057***	−2.045***
	s.e = 0.459	s.e = 0.451
	z = −4.484	z = −4.531
	p = <0.001	p = <0.001
Mean solar irradiance	0.598***	0.894***
	s.e = 0.107	s.e = 0.126
	z = 5.590	z = 7.079
	p = <0.001	p = <0.001
Isothermality	−0.330*	−0.485***
	s.e = 0.145	s.e = 0.132
	z = −2.271	z = −3.674
	p = 0.023	p = <0.001
Water vapour pressure	0.446***	
	s.e = 0.110	
	z = 4.053	
	p = <0.001	
Mean annual precipitation		0.619***
		s.e = 0.096
		z = 6.442
		p = <0.001
Num.Obs.	1784	1784
AIC	1602.7	1573.3
R^2lik	0.138	0.152
R^2pred	0.373	0.38
+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001		

Table S4. Results of PGLMM model predicting structural colour and how much of the variation is explained by isothermality. Each cell includes the estimate, the standard error of the estimate, the z-score and p-value for each predictor included in the model. AIC = Akaike information criterion; R^2lik = coefficient of determination, values are between 0 and 1, denoting the proportion of the variation explained by the model; R^2pred = predictive R^2, indicates how well the model predicts responses for new observations.

	Model with isothermality (95%HPD 100 trees)
(Intercept)	−1.932*** (-1.988 to -1.720)
	s.e = 0.437 (0.382 to 0.465)
	z = −4.420 (-4.766 to -3.967)
	p = <0.001 (<0.001)
Isothermality	0.250** (0.207 to 0.266)
	s.e = 0.081 (0.080 to 0.083)
	z = 3.106 (2.463 to 3.257)
	p = 0.002 (0.001 to 0.013)
Annual precipitation	0.209** (0.195 to 0.246)
	s.e = 0.077 (0.076 to 0.079)
	z = 2.718 (2.578 to 3.189)
	p = 0.007 (0.001 to 0.010)
Num.Obs.	1784
AIC	1630.7
R^2lik	0.123
R^2pred	0.347

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001