*Global Ecology and Biogeography*

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

# Structural Colour in Bees (Hymenoptera: Anthophila) Is Linked to Climate and Latitude

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**Received:** 19 November 2025 | **Revised:** 23 June 2026 | **Accepted:** 17 August 2026

**Handling Editor:** Adam C. Algar

**Keywords:** bees | ecogeographical patterns | hydrophobicity | Hymenoptera | structural colour | thermoregulation

## 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 1784 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.

## 1 | 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; Gloger 1833; Rensch 1929) 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. 2015), 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. 2015). 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 and 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 and 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 organised 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 and 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—that is, self-cleaning (Schroeder et al. 2018). To test associations between water repellence and species traits, climatic variables such as annual precipitation (Attard et al. 2021), and discrete categories such as habitat type (e.g., terrestrial, riparian, aquatic), have previously been used as proxies (Shu-hui et al. 2006; Pap et al. 2017; Osváth et al. 2018). Therefore, 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). Although there is some experimental evidence for an anti-predator function of colour in bumblebees (Brower et al. 1960; Evans and 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 and Hogendoorn 2008), mate recognition seems to rely primarily on olfaction as it has been shown that males and females produce sex pheromones that are recognised by conspecifics (Ayasse et al. 2001). In addition, sex pheromones seem to drive the configuration of male chemosensory systems in bees (Brockmann and Brückner 2001; Sandoz et al. 2007), with some groups having males with a higher proportion of likely olfactory antennal sensilla compared to females (Galvani et al. 2012; but see Galvani et al. 2017). This suggests that structural colour

in bees might not be relevant for sexual signalling. Instead, these colour-producing structures could have non-visual functions, suggesting that environmental drivers may predict their 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 body size to have an effect on the association between temperature and structural colour, with structural colour being more prevalent in larger species. Radiative heat transfer is expected to play a relatively more important role in thermoregulation for large than small insects, which are more strongly coupled to convection due to their low thermal inertia (May 1979; Lahondère 2023).

## 2 | Methods

### 2.1 | Structural Colour Scoring

Although research on colour-production mechanisms in bees is limited (Saranathan et al. 2015; Hines et al. 2017; Polidori et al. 2017), studies on invertebrate structural colour have enabled the visual classification of these colours with reasonable confidence (Sun et al. 2013; Vukusic and Chittka 2013). In birds, similar visual assessments of structural colour have been demonstrated to be reliable (Owens and 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 (Lenau and Barfoed 2008; Seago et al. 2009; Schenk et al. 2013; Shi et al. 2015; Kilchoer et al. 2018; Cai et al. 2020). These visual effects cannot be explained by the presence of pigments only (Sun et al. 2013). In bees, multilayers are behind the metallic green appearance of *Euglossa* orchid bees (Garduño-Medina et al. 2021), whereas dull blue and green in blue-banded bees (genus *Amegilla*) and cuckoo bees (genus *Thyreus*) arise from quasi-ordered structures within their setae (Saranathan et al. 2015). Although pigments such as tetrapyrroles, carotenoids, quinones and flavonoids can contribute to dull blue and green colouration in some insects (Futahashi and Osanai-Futahashi 2021), these colours are more commonly produced by structures, and no pigments responsible for such colouration have been identified in bees or other hymenopterans (Vukusic and Chittka 2013; Futahashi and Osanai-Futahashi 2021). Furthermore, species with dull blue and green colours included in our dataset from the genera *Amegilla* and *Thyreus* have been shown to be structural (Saranathan et al. 2015). Although pigments may contribute to the dull blue colouration observed in the setae of *Xylocopa* species (Stavenga 2023), only a single dull blue species from this genus is present in our data. Thus, any misclassification of structural colouration is likely limited to very few species in our dataset and would have little impact on our analyses. White arises from disordered structures (Seago et al. 2009; Vukusic and Chittka 2013), and may underlie the white setae observed in some bee species (Polidori et al. 2017). However, our study focused on colours produced by ordered or quasi-ordered structures, whose presence can be assessed visually with reasonable confidence.

Because accessing collection specimens of the 4586 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 for all species included in the phylogeny, using reliable sources to ensure accurate identification (e.g., Atlas Hymenoptera, BugGuide, Discover Life, PaDIL, USGS Bee Inventory and Monitoring Lab, PCYU digital galleries). When possible, and for each species and sex, we collected head, dorsal and lateral view photographs (i.e., three pictures per sex and six per species). In total, we viewed 15,193 photographs of bees. 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 the male and 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. Our classification of structural colour from images was consistent with all published studies in which colour-producing structures have been found in bees (Table S1). To further assess the reliability of scoring structural colour from a single image, we selected a subset of five species from our dataset and obtained images of five individuals per species. The presence or absence of structural colour was consistent across all individuals examined within each species (Table S2). Additionally, we included structural colour information for species without reliable pictures by using descriptions from published taxonomic studies for bee genera and species (Appendix). Structural colour was scored as present if the species descriptions included descriptions of colour that matched the criteria described above. For the species with structural colour, only 13 species were scored based on one of the sexes, either because data were not publicly available or because the male or female for that species had not been described. However, the presence of structural colour rarely differs between sexes as we identified only one species with sexual dimorphism for this trait (*Megachile pruina*), for which we scored structural colour as present.

To check the robustness of our statistical inferences to potential misclassification of structural colouration, we reran our

statistical models (see Section 2.4) using different classification error rates (details in Supporting Information).

## 2.2 | Geographical Data

Of the 4586 bee species in the phylogeny, we found information on presence/absence of structural colour for 3499. For the species with structural colour data, 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 data 5 for a detailed description of the methods used to obtain and clean the geographical records used in this work). We excluded geographical coordinates that reflected anthropogenic introduction by manually checking the native distribution of each bee species included in this work. Species that had geographical coordinates outside of their native range and the areas that were removed from the distribution data are detailed in Table S3. The mean number of geographical records per species was 50.16 (95% CI: 46.76–53.77) of 1,948,983 records (Figure S1). To improve reliability and reduce bias caused by including species with an extremely low number of geographical records, we calculated the mean number of records for the species in this clade and its 95% confidence interval (CI) (Salgado-Roa et al. 2024) for the number of geographical records available for all species and removed species with an extremely low number of records within our dataset (i.e., $<47$ records), reflecting the lower limit of the 95% CI. Of the initial 3499 species with phylogenetic and structural colour data, we obtained reliable geographical records for 1784 species to test our hypotheses.

## 2.3 | 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 to 2000) from WorldClim (Fick and Hijmans 2017). We initially considered nine climatic variables: five relevant to 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 mean diurnal range. 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 and solar radiation, reflected by mean diurnal range and solar irradiance, respectively. For humidity we considered water vapour pressure (kPa), mean annual precipitation (mm), precipitation seasonality from WorldClim (Fick and Hijmans 2017) and aridity index (Zomer et al. 2022). We included precipitation seasonality because mean annual precipitation and water vapour 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, whereas low values represent higher aridity (Zomer et al. 2022). We averaged values for all records for a given species to obtain a single value for each climate variable per species.

After extracting nine relevant climate variables, we reduced the number of variables to five based on two complementary approaches. First, we used non-parametric Spearman correlations to identify variables that were highly correlated (Spearman's rho $\geq 0.8$). Second, we assessed the importance of variables by fitting single predictor phylogenetic generalised linear mixed models (PGLMMs; Ives and Garland 2010) and evaluating the drop in support values (i.e., $\Delta$AIC) compared to an intercept only model (Burnham and Anderson 2004; Cooney et al. 2020). Based on these evaluations, we selected five climate variables that best represented our temperature and humidity predictions: mean annual temperature, mean solar irradiance, mean diurnal range, water vapour pressure and mean annual precipitation. Details of the climate variables that were initially extracted, and justification and process for selecting these five variables are provided in Supporting Information (Figure S2 and Table S4). 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.

## 2.4 | Data Analyses

All analyses were conducted in R (version 4.3.0; R Core Team 2023). We first explored the five selected climatic variables (i.e., mean annual temperature, mean solar irradiance, mean diurnal range, 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. We found that mean annual temperature, mean annual precipitation and water vapour pressure had moderate to high variance inflation factor (VIF; Figure S3A), indicating that these variables should not be included in the same model. To choose the variable that best represented our humidity hypothesis (mean annual precipitation or water vapour pressure), we compared the effect of each of these variables in separate preliminary PGLMM models with mean solar irradiance and mean diurnal range. Mean annual temperature was not included in these models given its high VIF (Figure S3A). We found that mean annual precipitation was a better predictor and had a stronger effect on the presence of structural colour ($\beta = 0.590 \pm 0.089$, $z$-score $= 6.666$, $p = < 0.001$; AIC $= 1569$) than water vapour pressure ($\beta = 0.438 \pm 0.096$, $z$-score $= 4.544$, $p = < 0.001$; AIC $= 1597$; Table S5). Therefore, our final model included mean annual precipitation representing the humidity hypothesis and mean diurnal range and the interaction between mean annual temperature and mean solar irradiance representing the thermoregulation hypothesis. The interaction term between mean annual temperature and solar irradiance was included in our final model to test the specific prediction that structural colour should be more prevalent in cooler environments with high solar radiation. Median latitude was highly correlated to mean annual temperature and mean solar irradiance (Spearman's rho $> 0.8$; Figure S4), and

had high VIF when included in the model with all selected predictors from our thermoregulation hypotheses (Figures S3B, S3C, and S3D): Therefore, to explore the effect of latitude, we ran a second model with mean annual precipitation and median latitude.

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. Body size was obtained from available and previously published datasets and species descriptions. We obtained female and male body size data for 738 and 674 species, respectively, for which we had data on presence/absence of structural colour. Of these species, we were able to obtain climatic data for 521 species for which we had female body size and 488 species for which we had male body size. Given that sex differences in the presence of structural colour are rare in bees and we had more body size data for females than males, we chose the former to explore the effect of body size. 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). Additionally, to control for phylogenetic uncertainty, we ran the models on a sample of 100 randomly selected bootstrap sample trees. We found no relationship between structural colour and female body size, either separately ($\beta = 0.157 \pm 0.293$, $z$-score $= 0.538$, $p = 0.591$; 95% highest posterior density interval (HPD) of 100 random trees: $\beta = 0.146–0.176$, $p$-value $> 0.05$) or in interaction with temperature ($\beta = 0.462 \pm 0.341$, $z$-score $= 1.356$, $p = 0.175$; 95% HPD of 100 random trees: $\beta = 0.443–0.476$, $p$-value $> 0.05$; Figure S5). Using data subsets of different sizes can affect model estimates; however, these results suggest that the effect of body size on structural colour, either separately or in interaction with temperature, is unlikely to be strong. For this reason, and because we only had female body size and climate data for a subset of 521 species, we did not include female body size in subsequent models with climatic predictors.

## 3 | Results

### 3.1 | Geographic and Phylogenetic Distribution of Structural Colour

Of the 1784 species included in our work, 382 had structural colour (366 in the cuticle and 16 in the setae; Figure 1). Bee species distributed at lower latitudes have a higher probability of being structurally coloured ($\beta = -0.484 \pm 0.088$, $z$-score $= -5.484$, $p = < 0.001$; 95% HPD of 100 random trees: $\beta = -0.506$ to $-0.449$, $p$-value $= < 0.001$; Figures 2A and 3C and Table 1). Of the 283 bee species distributed in tropical regions (i.e., absolute median latitude below or equal to 25°), 29% (83 species) had structural colour, whereas of the 1501 species in temperate regions (i.e., absolute median latitude above 25°), 20% (299 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 299 species; 46%) and Megachilidae (88 species; 29%), followed by smaller numbers of Andrenidae (33 species; 11%), Apidae (32 species; 11%) and Colletidae (9 species; 3%).

### 3.2 | Climatic Predictors of Structural Colour

Bee species in cool environments that have higher solar irradiance ($\beta = -0.393 \pm 0.108$, $z$-score $= -3.653$, $p = < 0.001$; 95% HPD of 100 random trees: $\beta = -0.417$ to $-0.356$, $p$-value $= < 0.001$) and higher annual precipitation ($\beta = 0.635 \pm 0.108$, $z$-score $= 5.866$, $p = < 0.001$; 95% HPD 100 trees: $\beta = 0.609–0.687$, $p$-value $= < 0.001$) were more likely to be structurally coloured (Figures 2 and 3 and Table 1). In warmer environments, bees with and without structural colours were found in locations with similar or lower radiation levels. In addition, environments with high daily temperature variation seem to host bees with and without structural colour ($\beta = 0.256 \pm 0.145$, $z$-score $= 1.760$, $p = 0.078$; 95% HPD 100 trees: $\beta = 0.201–0.302$, $p$-value $= 0.031–0.149$). The effect of annual precipitation disappeared ($\beta = 0.074 \pm 0.080$, $z$-score $= 0.926$, $p = 0.355$; 95% HPD 100 trees: $\beta = 0.061–0.112$, $p$-value $> 0.1$) 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. Alternatively, it could also mean that the apparent relationship between structural colour and mean annual precipitation could be due to its correlation with latitude. The robustness tests of the statistical models indicated that even with some classification error the statistical results remained consistent, and the statistical tendency was only lost when a classification error rate of 10% or above was imposed, a scenario we consider unlikely given the visual distinctiveness of structural colour (Figure S6).

## 4 | 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 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 and Davidowitz 2023). Consistent with the water repellence hypothesis, structural colour was 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 appears 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

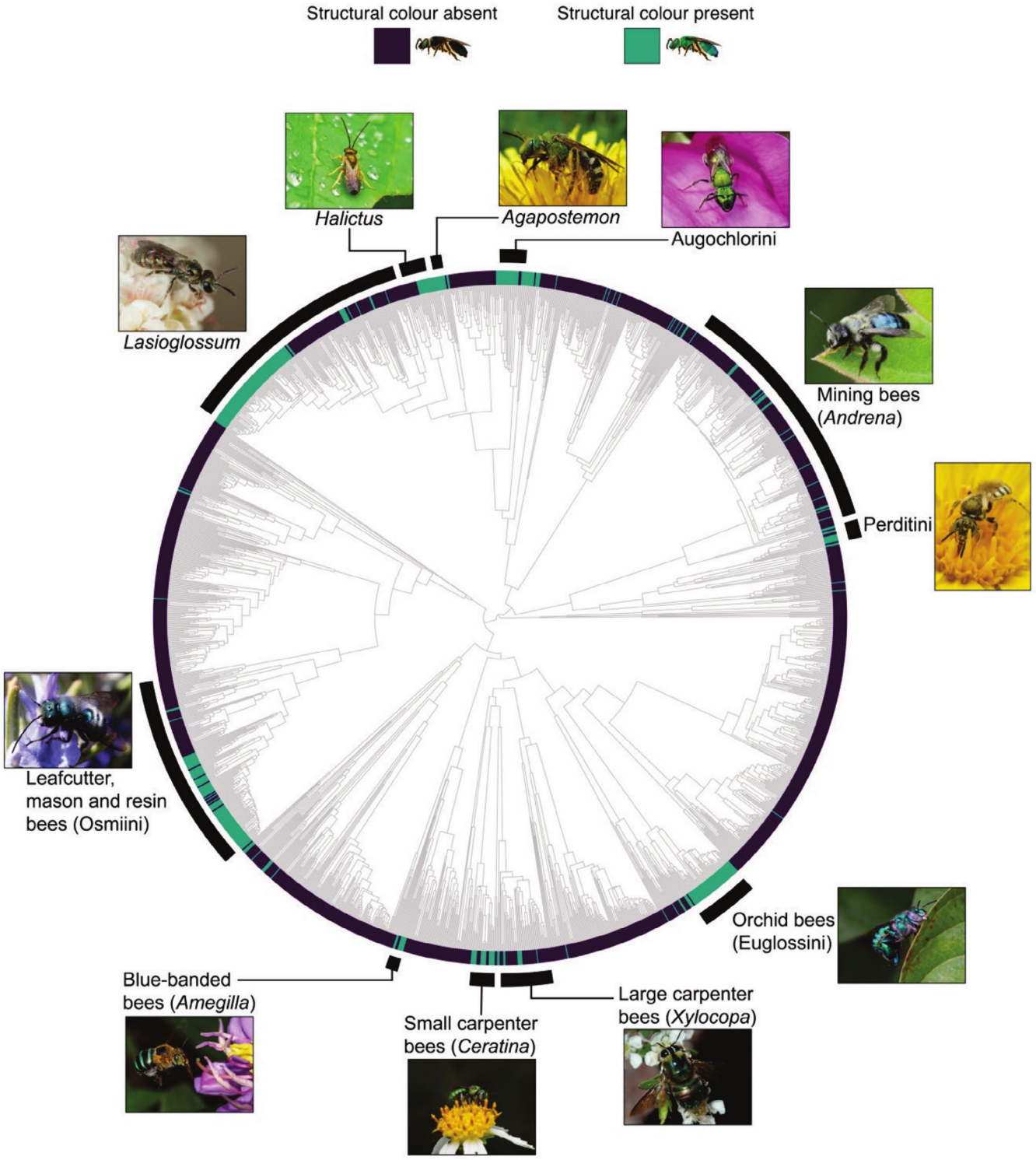


**FIGURE 1** | Phylogenetic relationships and distribution of structural colour of bees included in the study ($n = 1784$). Colour tips represent the presence or absence of structural colour. Images of bees with structural colour include *Lasioglossum* sp. (Halictidae; original photo: Jesse Rorabaugh), *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).

lower reflectivity (proportion of sunlight reflected by a surface; Ospina-Rozo et al. 2022b) than pigment-based colours (Schultz and 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

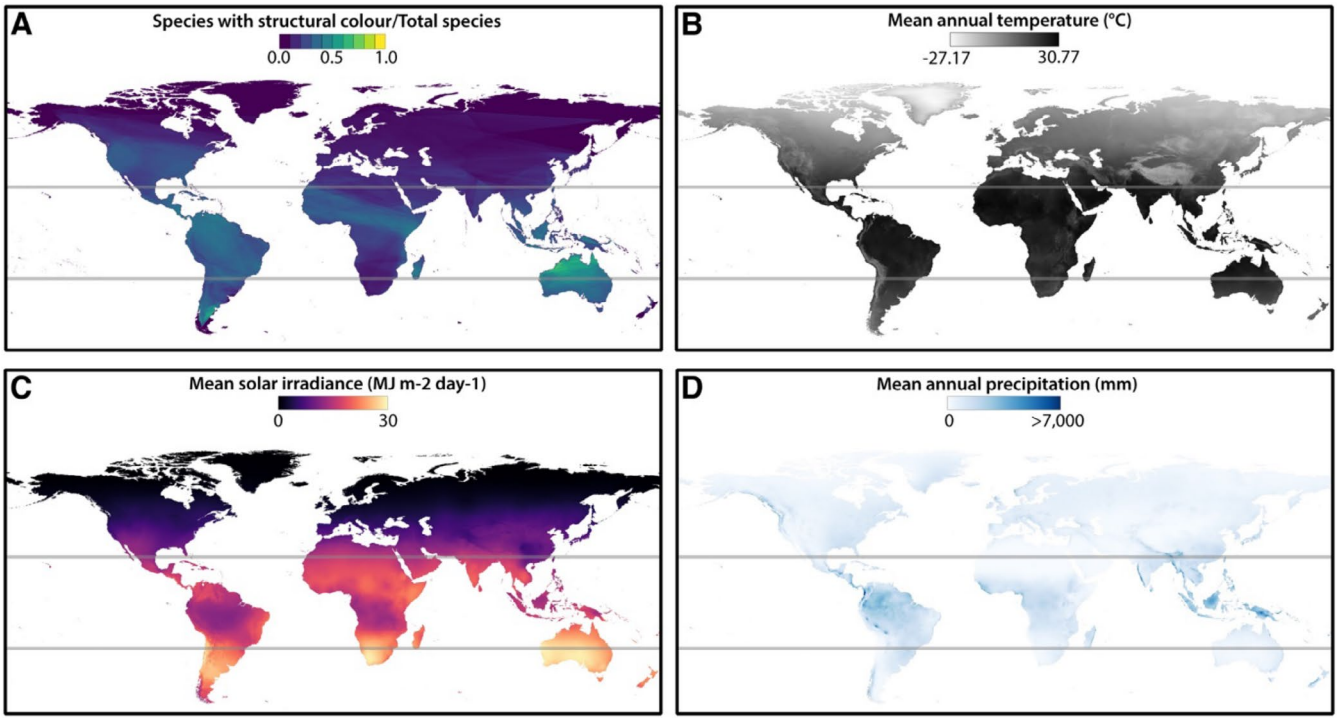


**FIGURE 2** | (A) Proportional richness of bees with structural colour out of the total number of species in our dataset. Heat map was produced from distribution polygons for each species included in the study with minimum convex polygons made directly around the species occurrence points. Raster of species with structural colour was then divided by the raster of total number of species to obtain proportional richness. (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.

accounts for more than 50% of the energy in sunlight (Campbell and 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, the 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 and Stone 2004). Structural colours could potentially 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 possibly 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 (Roubik and Ackerman 1987).

Bees with structural colouration are also more prevalent in environments that have higher precipitation, which suggests 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 and Rubega 2024), feathers with structural colours seem to have reduced water repellence when compared with feathers that do not have structural colour (Eliason and 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

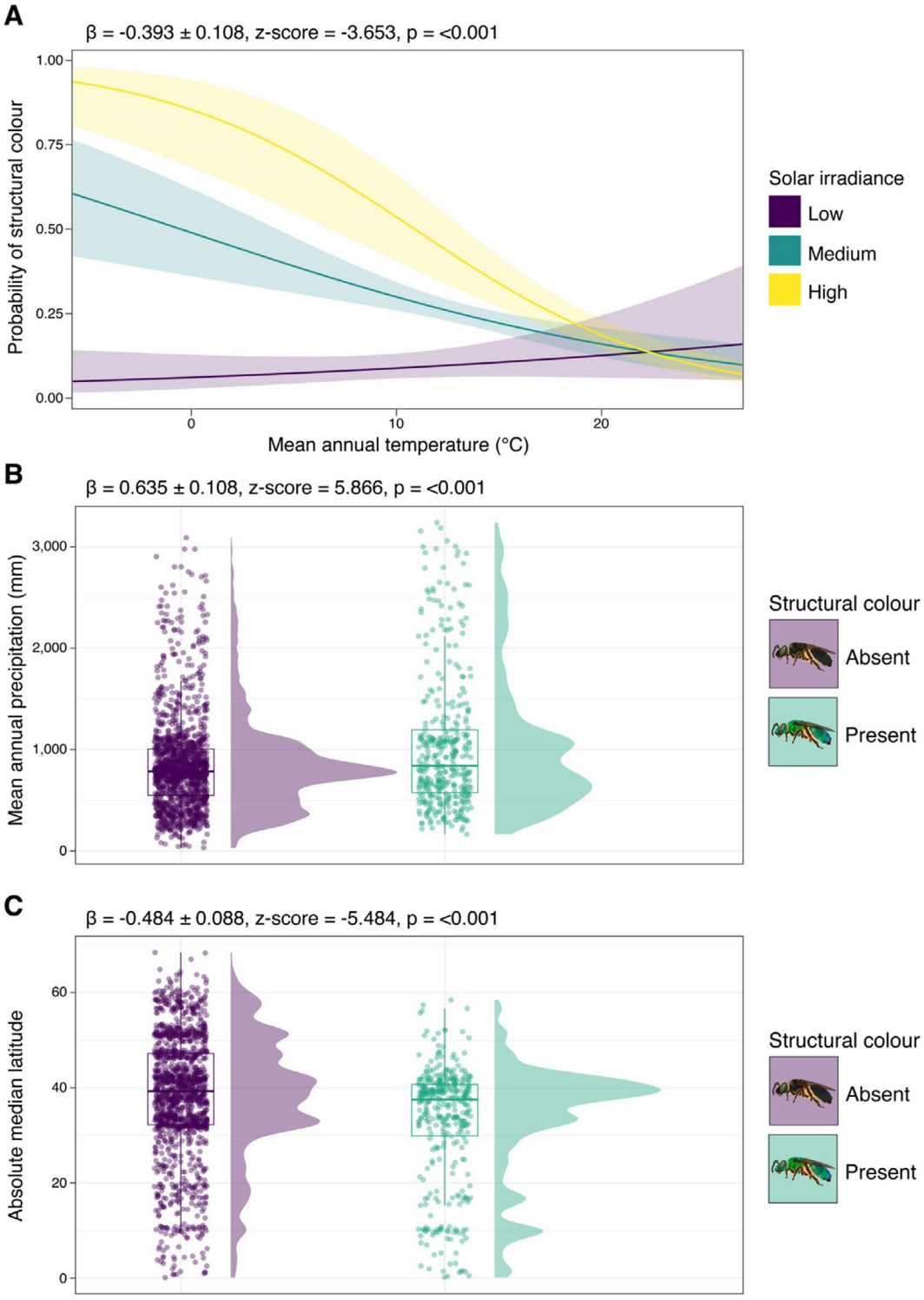


**FIGURE 3** | Association between environmental variables and structural colour for all bees included in the analyses ($n = 1402$ species without structural colour; $n = 382$ species with structural colour). (A) Predicted probability of structural colour presence as a function of the interaction between mean annual temperature and solar irradiance. Lines show fitted model values with solar irradiance grouped in low (10th percentile), medium (50th percentile) and high (90th percentile) values of the observed distribution. Shaded areas indicate 95% confidence intervals. (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, C), lines within each box represent the median, and the upper and lower lines of the box indicate the maximum and minimum quantiles, respectively.

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

**TABLE 1** | Results of final PGLMM models predicting structural colour and how much of the variation is explained by climatic variables ($n = 1784$).

| | Model with mean solar irradiance * mean annual temperature + mean diurnal range (95% HPD 100 trees) | Model with median latitude (95% HPD 100 trees) |
|---|---|---|
| (Intercept) | −1.795*** (−1.83 to −1.64) | −2.000*** (−2.07 to −1.78) |
| | SE = 0.457 (0.391 to 0.492) | SE = 0.453 (0.394 to 0.479) |
| | $z = -3.926$ (−4.37 to −3.52) | $z = -4.412$ (−4.76 to −4.01) |
| | $p = < 0.001$ (< 0.001) | $p = < 0.001$ (< 0.001) |
| Solar irradiance | 0.548** (0.504 to 0.613) | |
| | SE = 0.176 (0.174 to 0.180) | |
| | $z = 3.113$ (2.87 to 3.49) | |
| | $p = 0.002$ (< 0.001 to 0.004) | |
| Mean annual temperature | −0.186 (−0.253 to −0.150) | |
| | SE = 0.145 (0.143 to 0.149) | |
| | $z = -1.288$ (−1.75 to −1.03) | |
| | $p = 0.198$ (0.066 to 0.282) | |
| Mean diurnal range | 0.256+ (0.201 to 0.302) | |
| | SE = 0.145 (0.144 to 0.149) | |
| | $z = 1.760$ (1.36 to 2.02) | |
| | $p = 0.078$ (0.031 to 0.149) | |
| Mean annual precipitation | 0.635*** (0.609 to 0.687) | 0.074 (0.061 to 0.112) |
| | SE = 0.108 (0.107 to 0.111) | SE = 0.080 (0.079 to 0.082) |
| | $z = 5.866$ (5.55 to 6.28) | $z = 0.926$ (0.752 to 1.40) |
| | $p = < 0.001$ (< 0.001) | $p = 0.355$ (> 0.1) |
| Mean solar irradiance * mean annual temperature | −0.393*** (−0.417 to −0.356) | |
| | SE = 0.108 (0.106 to 0.110) | |
| | $z = -3.653$ (−3.86 to −3.26) | |
| | $p = < 0.001$ (< 0.001) | |
| Median latitude | | −0.484*** (−0.506 to −0.449) |
| | | SE = 0.088 (0.087 to 0.091) |
| | | $z = -5.484$ (−5.63 to −4.97) |
| | | $p = < 0.001$ (< 0.001) |
| Num. obs. | 1784 | 1784 |
| AIC | 1553.5 | 1604.5 |
| $R^2$lik | 0.162 | 0.135 |
| $R^2$pred | 0.39 | 0.366 |

*Note:* Each cell includes the estimate, the standard error of the estimate, the $z$-score and $p$-value for each predictor included in the model.
Abbreviations: 95% HPD, 95% highest posterior density interval (HPD); AIC, Akaike information criterion; $R^2$lik, coefficient of determination, values are between 0 and 1, denoting the proportion of the variation explained by the model; $R^2$pred, predictive $R^2$, indicates how well the model predicts responses for new observations.
$^+p < 0.1$, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

pigments alone (Maia et al. 2013). Among 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 and 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 (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).

This study scored ordered and quasi-ordered structural colour as a binary variable (i.e., presence/absence), but there are multiple structural mechanisms underlying these colours (Sun et al. 2013). These mechanisms can sometimes have opposing effects, such as the silver hairs of ant *C. bombycina* that reduce heat load and the elytra of tiger beetles from the genus *Cicindela* that increase it (Schultz and Hadley 1987; Shi et al. 2015). Thus, simplifying structural colour to a binary category could potentially hide climate associations that are mechanism specific. However, ordered and quasi-ordered structural colour in bees probably involves mechanisms that reflect narrow band of wavelengths which has been found to increase heat load (Schultz and Hadley 1987; Shawkey et al. 2017; Ospina-Rozo, et al. 2022b). Pure gold or silver mirror-like displays, which suggest broadband reflectance (Seago et al. 2009) and thus, a potential function in reducing heat load, have not been described in this group of insects. This suggests that the mechanisms behind structural colours in bees could have similar thermal consequences.

Our findings suggest 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. 2015). 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 and 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, whereas small-morph males chase after flying females and typically hover 1 m or more above the ground near vegetation (Alcock et al. 1977). *C. pallida* is probably not the only desert bee species with white setae that have higher reflectance of solar radiation. Desert bee species frequently display higher pilosity and lightness, traits that are also positively correlated, suggesting these structures are involved in thermoregulation across taxa (Ostwald et al. 2025). 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.

### Author Contributions

P.H.-P., I.M. and D.S.-F. designed research; K.J.R. contributed data; P.H.-P. performed research; P.H.-P. analysed the data; P.H.-P., I.M., F.C.S.-R., A.F.H., M.E. and D.S.-F. analysed the results; P.H.-P., I.M., F.C.S.-R., A.F.H., K.J.R., M.E. and D.S.-F. revised and edited the paper; and P.H.-P. wrote the paper.


### Acknowledgements

P.H.-P. was supported by funding awarded from the Agencia Nacional de Investigación y Desarrollo de Chile (Scholarship ID 72210037) and by the Dr. Albert Shimmins Fund. Open access publishing facilitated by The University of Melbourne, as part of the Wiley - The University of Melbourne agreement via the Council of Australasian University Librarians.

### Funding

This work was supported by Agencia Nacional de Investigación y Desarrollo (72210037) and The Dr. Albert Shimmins Fund.


### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The dataset and R code are available from Dryad Digital Repository (https://doi.org/10.5061/dryad.h70rxwdwq).

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Distribution of geographical records of bee species included in this study ($n = 1784$). Majority of species had less than 1000 records (1488; 83.41%). Only 23 species (1.29%) including *Apis mellifera*, had more than 10000 records. **Figure S2:** Relationships between the presence of structural colour and individual predictor variables for the water repellence hypothesis ($n = 1402$ species without structural colour; $n = 382$ 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. **Figure S3:** Collinearity plots of all climatic predictors considered in the preliminary and final PGLMM models. **Figure S4:** 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 S5:** 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 ($n = 588$ species without structural colour; $n = 150$ 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. **Figure S6:** Robustness of statistical models to classification error in colour type. Results of sensitivity analyses in which images were randomly reassigned to the opposite colour category (pigment or structural) at error rates of 5%, 10%, 15% and 40%, repeated 100 times per error rate. (A) Mean estimates (± SE) and (B) mean *p*-values (± SE) for each predictor variable across error rates, shown separately for Model 1 (Predictors: interaction between mean annual temperature and mean solar irradiance, mean diurnal range and mean annual precipitation) and Model 2 (Predictors: mean annual precipitation and median latitude). The dashed line in (B) indicates the significance threshold ($p = 0.05$). **Table S1:** Published studies on structural colour mechanism present in bees. **Table S2:** Presence of structural colour across individuals of the same bee species. **Table S3:** Species with geographical records outside of their native distribution and areas that were removed from the distribution data. **Table S4:** 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. ΔAIC = difference in Akaike information criterion score between single predictor model and the reduced model (intercept only). **Table S5:** Results of preliminary PGLMM models testing the association of climatic variables with structural colour that had moderate VIF while keeping mean solar irradiance and mean diurnal range in the models. 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; $R^2$lik = coefficient of determination, values are between 0 and 1, denoting the proportion of the variation explained by the model; $R^2$pred = predictive $R^2$, indicates how well the model predicts responses for new observations.

## Appendix : Literature Used to Score Structural Colour for Bee Species Without Available and Reliable Images

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