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Latitudinal gradients in avian colourfulness

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It has long been suggested that tropical species are generally more colourful than temperate species, but whether latitudinal gradients in organismal colourfulness exist remains controversial. Here we quantify global latitudinal trends in colourfulness (within-individual colour diversity) by collating and analysing a photographic dataset of whole-body plumage reflectance information for >4,500 species of passerine birds. We show that male and female birds of tropical passerine species are generally more colourful than their temperate counterparts, both on average and in the extreme. We also show that these geographic gradients can be explained in part by the effects of several latitude-related factors related to classic hypotheses for climatic and ecological determinants of organismal colourfulness. Taken together, our results reveal that species' colourfulness peaks in the tropics for passerine birds, confirming the existence of a long-suspected yet hitherto elusive trend in the distribution of global biodiversity.

Is life generally more colourful in the tropics? The possible existence of global-scale trends in organismal colourfulness was suggested by nineteenth-century European naturalists such as von Humboldt, Darwin and Wallace, who, upon being afforded the opportunity to travel extensively in the tropics, remarked on the "rich variety" and "mixtures of colors" they encountered during their travels[1–3]. Since then, a variety of explanations focused on latitude-associated gradients in biotic and abiotic factors have been proposed to account for the assumed increases in tropical species' colourfulness, including positive effects of more benign climatic conditions and particular ecological strategies that are more prevalent at low latitudes[2,4–8]. However, in the centuries following these early anecdotal observations, biologists have struggled to conclusively test for the existence of global-scale latitudinal gradients in species colourfulness, calling into question whether this long-assumed biogeographic 'rule' really exists at all[5,7,9,10].

Part of the challenge in resolving this controversy revolves around the difficulty of obtaining accurate, meaningful measurements of organismal colouration, and doing so on a scale that permits a global-scale test of these ideas. Due to practical constraints, previous studies have often addressed this question by using subjective and/or incomplete measures of colourfulness (for example, human scoring) or by studying radiations of species that span only a limited fraction of the Earth's latitudinal gradient[5–12] (Supplementary Table 1). While some of these studies have found patterns consistent with a latitudinal colourfulness gradient in birds and other taxa, other studies have found no such effect, and controversy over the existence of this gradient remains. Fortunately, recent advances in cost-effective imaging technology, combined with the increasing availability of accurate geographic information for many taxa, now make it possible to test for the existence of latitudinal gradients in species' colourfulness on a truly global scale.

Results and discussion

We tested whether a latitudinal gradient in species' colourfulness exists for the global radiation of passerine birds (order Passeriformes)—the largest avian order, comprising ~60% of the ~10,000 bird species. Our approach is centred on a dataset of plumage colouration based on >140,000 calibrated visible (Vis) and ultraviolet (UV) light photographs of male and female museum specimens for 4,527 species (~76% of passerine diversity; Extended Data Fig. 1a,b). For each included specimen, we took photographs from three different angles (dorsal, lateral and ventral), extracted calibrated pixel values from each image using machine learning approaches and mapped these values into avian tetrahedral colour space (Methods). We then sampled 500 points from each view to give a total of 1,500 measurements capturing whole-body plumage reflectance for each specimen (Extended Data Fig. 1c). This process resulted in a dataset consisting of >24,000 photographed specimens and >36 million unique measurements of passerine plumage colouration (Fig. 1a), which together occupy a colour space that is comparable to that estimated for all birds[13].

Quantifying colourfulness. Colourfulness can be considered in multiple ways. Here we follow the sensory ecology literature by defining colourfulness in terms of within-individual colour diversity—that is, the overall colour contrast of a multi-coloured pattern[14]. Defined in this way, colourfulness arises when an organism displays a range of colours (potentially produced by different mechanisms) that are perceptually different from one another, and it can be quantified using metrics that measure the spread of colour traits in colour space[14]. Importantly, this characterization of colourfulness is distinct from other notions of colourfulness that include uniform plumage colouration of a particular (often conspicuous) hue. It also differs from approaches used by other broad-scale bird colouration studies, which have variously quantified plumage colouration in terms of brightness and hue[12] and degree of elaboration (for example, the 'maleness' metric introduced by Dale et al.[11]), rather than colourfulness (that is, colour diversity) per se. Here we use two established metrics of colourfulness: convex hull volume[13,15] and the number of occupied colour loci[16]. The former reliably captures the breadth of colours in a sample but is heavily influenced by extreme values,

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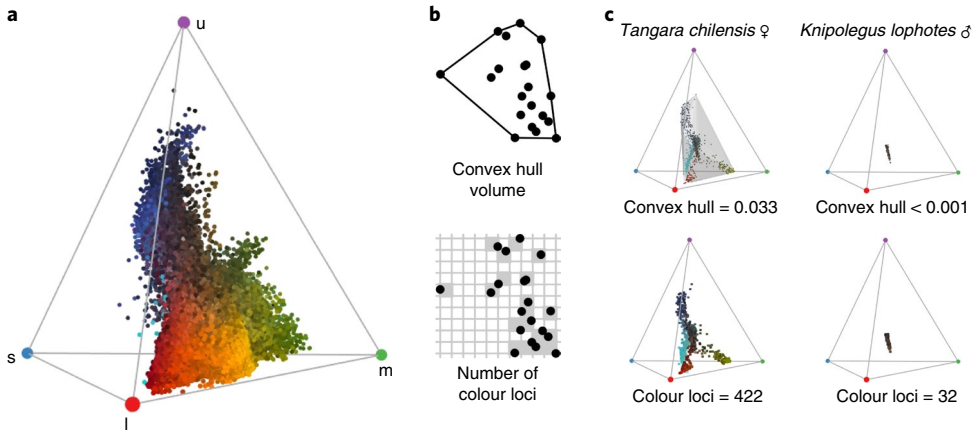

Fig. 1 | The diversity of passerine plumage colours in avian tetrahedral colour space. a, A sample of one million passerine plumage colours analysed in this study, visualized in avian UV-sensitive (UVS) tetrahedral colour space where each vertex represents one of the four colour cone types sensitive to long (l), medium (m), short (s) and UV (u) wavelengths. The measurements are derived from calibrated digital images of male and female museum specimens for 4,527 species. The total number of measurements from which this sample is drawn is >36 million. **b**, An illustration of the two colour diversity metrics used in this study: convex hull volume (top) and number of colour loci (bottom). For simplicity, the example is based on two-dimensional simulated data. **c**, Plots and metric values for the species with the largest (*Tangara chilensis* ♀, left) and smallest (*Knipolegus lophotes* ♂, right) convex hull volume scores. In all plots, the points are coloured according to their approximate appearance as perceived by a human observer by mapping the raw pixel reflectance values to the CIE 1931 XYZ colour space.

whereas the latter reflects that species will generally not occupy all areas of colour space within the extent of occurrence (Fig. 1b). The values of the two metrics are strongly correlated across specimens in our dataset ($r = 0.85$, $P < 0.001$, $n = 24{,}345$; Extended Data Fig. 1d), but because the colour loci metric is generally less sensitive to noise, outliers and large 'gaps' in colour space occupation that can bias estimates of colourfulness[14,16] (Fig. 1b), we focus in the main text on results based on colour loci scores, with colour volume results provided as extended data and Supplementary Information.

Testing for latitudinal colourfulness gradients. We separately mapped mean male and mean female colourfulness scores for grid cell assemblages and found evidence for a strong latitudinal gradient in species' colourfulness in passerine birds (Fig. 2). Analysis of per-cell mean species' colour loci values revealed a pronounced tropical peak in species' colourfulness with respect to latitude that was evident for both male and female birds (Fig. 2a,b). Mean male and mean female colour loci scores for species in tropical cell assemblages are 92 and 86, respectively (<23.5°; $n = 16{,}997$ cells), compared with the corresponding values of 76 and 70 for high-latitude assemblages (>45°; $n = 22{,}412$ cells). Similar patterns were evident when using colour volume scores (Extended Data Fig. 2) and when cell averages were calculated by downweighting the influence of geographically widespread species (Extended Data Fig. 3; for the methods, see 'Statistical analyses'). To formally test the relationship between latitudinal position and species' colourfulness while minimizing the impact of spatial autocorrelation, we calculated mean colourfulness scores across species present in unique terrestrial ecoregions[17] rather than individual grid cells (Fig. 2c) and used spatial simultaneous autoregressive (SAR) models with absolute ecoregion latitude as a predictor[18]. Regardless of how ecoregion colourfulness averages were calculated (Methods), all models had a highly significant effect of latitude on both male and female colourfulness ($P < 0.001$ in all cases; Supplementary Table 2) corresponding to steep declines in the average colourfulness of species within ecoregions moving from the equator towards the poles (Fig. 2c and Extended Data Fig. 2c).

One common assertion is that equatorial regions may be perceived as being more colourful simply because they contain more species overall[2,9,10]. In other words, even if the proportion of colourful species per assemblage is approximately constant across latitudes, tropical communities are regarded as being more colourful simply because they contain a greater absolute number of colourful species. Although our analyses based on average colourfulness scores per assemblage suggest that this is unlikely, we addressed this assertion directly by analysing the geographical distribution of the top 25% most colourful species in our dataset as a proportion of assemblage species richness. These analyses confirm that not only are tropical passerine taxa generally more colourful than temperate-zone taxa, but the tropical zones also harbour a substantially higher-than-expected proportion of the world's most colourful passerine bird species (Extended Data Fig. 4 and Supplementary Table 2).

To corroborate our grid-cell-based results, we also tested the relationship between species' colourfulness and midpoint latitude using species-level phylogenetic comparative analyses (Methods). Consistent with our previous findings, equatorial-zone species (midpoint latitude <23.5°) are generally characterized by higher colourfulness scores than extra-tropical species (Fig. 3a), and as expected, there is a strong relationship between midpoint latitude and colourfulness across species for both sexes (Fig. 3b,c). However, an important consideration is that both midpoint latitude and the degree of male and female colourfulness exhibit considerable phylogenetic conservatism, with mean phylogenetic heritability[19] values of 0.83 (95% credible interval (CI), 0.80, 0.86) for latitude and 0.90 (95% CI, 0.87, 0.91) and 0.88 (95% CI, 0.86, 0.90) for male and female colourfulness, respectively. It is therefore possible that the latitudinal gradient in colourfulness we observe is the result of phylogenetic non-independence between tropical residency and elevated colourfulness—for example, if the ancestors of speciose tropically restricted passerine clades happened to be colourful, and both traits have simply been retained by descendent lineages over evolutionary time[2]. However, testing the relationship between colourfulness and species' absolute latitudinal position while controlling for phylogenetic history, we find significant negative correlations with latitude for both male (standardized slope coefficient, −0.04 (95% CI, −0.07, −0.02)) and female colourfulness scores (−0.12 (95% CI, −0.14, −0.09)) (Supplementary Table 3). This

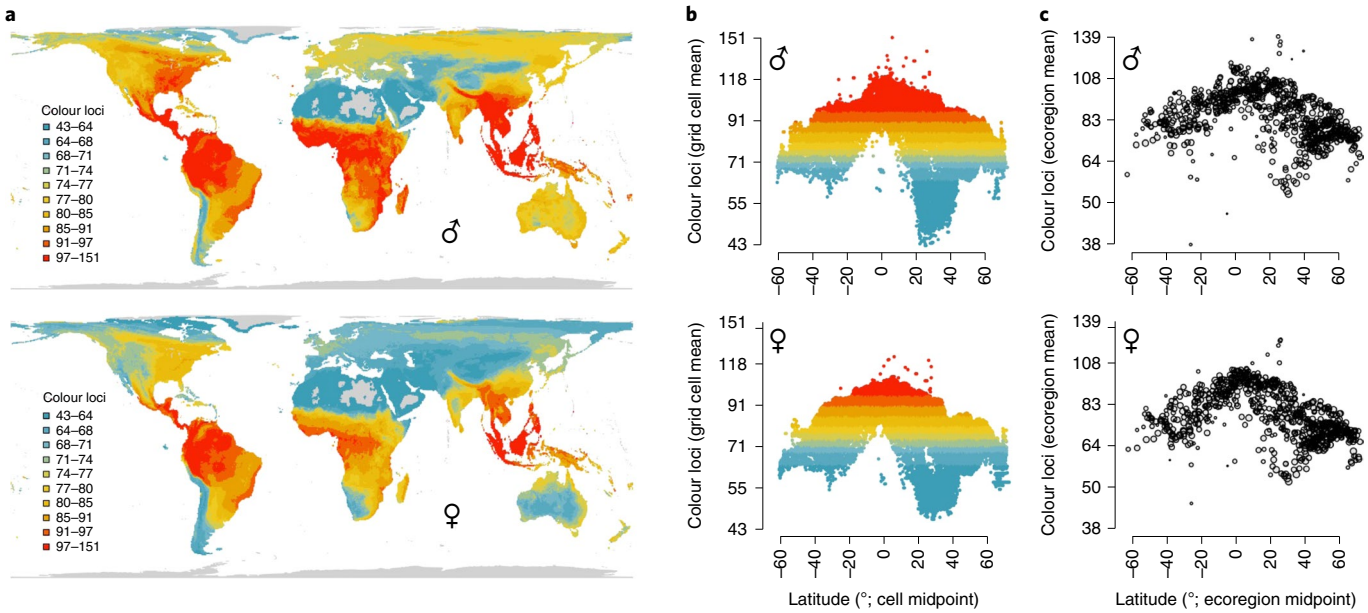

Fig. 2 | Latitudinal gradients in male and female colourfulness in passerine birds. a, Mean colour loci scores for grid cell assemblages, separately for males (top) and females (bottom). **b**,**c**, Distributions of mean species' colour loci scores for grid cells (**b**) and ecoregions (**c**) with respect to latitude, separately for males (top) and females (bottom). The grid cell size is 50 km × 50 km for all panels (Behrman projection), and only cells containing at least five sampled species are plotted. The colour loci scores are based on a UVS visual system.

indicates that the observed gradient in species' colourfulness cannot be explained solely by phylogenetic conservatism of both latitudinal position and degree of colourfulness.

Predictors of colourfulness. Our finding of a clear latitudinal increase in passerine bird colourfulness towards the equator is in line with related findings of other broad-scale studies of avian colouration[11,12], which together support the notion that tropical-zone species tend to be generally more colourful than those in the temperate zone[1–3]. Although unambiguous empirical support for this belief has remained elusive (Supplementary Table 1), several explanations for tropical peaks in species' colourfulness have nonetheless been proposed. These explanations broadly fall into hypotheses focused on latitudinal variation in climatic conditions (for example, energy, temperature, precipitation or productivity), species' behavioural and/or ecological traits, or biotic interactions (particularly interspecific competition and signalling). For example, early explanations focused on "the direct action of heat and light from the sun"[2] in promoting tropical colourfulness, but the importance of climatic factors such as temperature, precipitation and solar radiation have been hotly debated[2,3,5,20]. Another broad class of hypotheses emphasizes the role of species' ecological and behavioural traits in promoting colourfulness. This includes dark, closed habitat types (such as forests) selecting for increased reflectivity[21,22] and the positive effects of particular foraging (for example, frugivorous or nectarivorous) and life-history strategies (for example, sedentary or territorial breeding) that are common in the tropics and may deterministically promote the evolution of colourful plumages[2,11]. Furthermore, the strength of biotic interactions has long been argued to increase towards the equator[23,24], due in part to greater numbers of co-existing species in tropical systems[25]. In theory, elevated levels of colourfulness in tropical taxa may also emerge as a response to increased selection for more distinguishable visual signals for recognizing conspecifics in diverse tropical communities[2,5,6].

To explore the factors promoting passerine colourfulness and to illuminate potential explanations for the latitudinal gradients in colourfulness we observe, we used multi-predictor Bayesian phylogenetic mixed models[26] to assess the relative importance of variables capturing relevant environmental and ecological axes of variation among species ($n = 4{,}415$) (Methods). Importantly, the majority of these predictor variables (11 of 13) were significantly correlated with species' midpoint latitude ($P < 0.001$ in all cases; for the correlation coefficients, see Fig. 4), indicating that they indeed represent viable explanations for the observed latitudinal gradients. The only exceptions to this were species' mean body mass ($P = 0.535$) and degree of sexual dichromatism ($P = 0.802$)—the latter representing a useful proxy for sexual selection acting on visual signalling traits[27,28].

We find that species' colourfulness is significantly predicted by several factors (Fig. 4 and Supplementary Tables 4 and 5). Across all analyses, the strongest correlate of colourfulness that we identified is sexual dichromatism: males of highly dichromatic species are far more colourful on average than males of less dichromatic species. This supports the view that bright male colouration often evolves in response to increases in sexual selection intensity[12,29]. The lack of a similar, or negative, effect in females also implies that dichromatism primarily indexes the intensity of sexual selection acting on males[30] and that variation in female colourfulness across species cannot be explained simply as a correlated response of selection acting on males[12,31].

In addition to dichromatism, we find a strong negative effect of body mass on colourfulness in both sexes, with larger birds being less colourful than smaller birds. Body size has been proposed as an important constraint for the evolution of colourful plumage, due to physiological limits on both the relative number of body feathers and circulating carotenoid levels in larger birds[32]. This hypothesis has received little prior support, particularly considering that other broad-scale bird studies have found positive rather than negative effects of body size on axes of plumage colour elaboration[11,12]. However, these results are difficult to compare due to differences in the taxonomic scope and metrics of colouration used among studies (Supplementary Table 1). Here, focusing only on passerines and using colourfulness metrics that are closely aligned with the concept of 'plumage colour heterogeneity' forming the basis of the original hypothesis[32], we find a strong inverse relationship between body

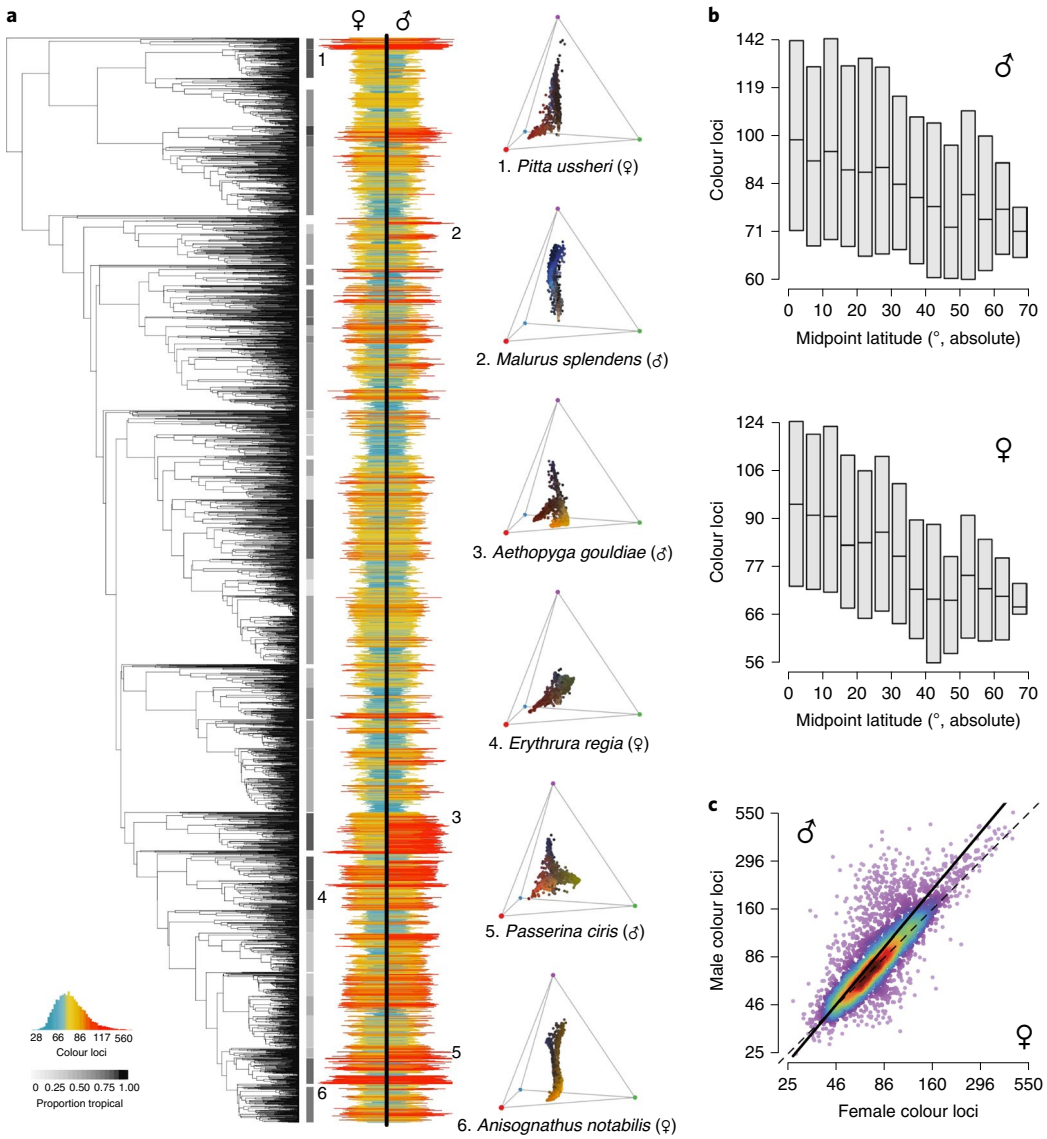

Fig. 3 | The phylogenetic distribution of male and female colourfulness and its relation to species' midpoint latitude in passerine birds. a, The coloured bars indicate male and female colour loci scores for 4,527 passerine species. The grey segments indicate the proportion of tropical species (that is, |midpoint latitude| < 23.5°) within major clades. **b**, Box plots showing the median (horizontal line) and interquartile range (box limits) of the distribution of species' colour loci scores with respect to latitude, separately for males (top) and females (bottom), with species binned into 5° increments. **c**, Scatterplot showing the relationship between male and female colour loci scores across species, with points coloured according to point density in the plot. The solid line indicates the relationship between the variables estimated using phylogenetic reduced major axis regression, which differs significantly ($P < 0.001$) from a one-to-one relationship (dashed line). The colour loci scores are based on a UVS visual system.

size and colourfulness across species. This relationship is therefore consistent with large birds experiencing greater physiological constraints on colourfulness than smaller birds[32], but it could also be explained by size-related differences in visual communication requirements, if individuals of smaller species tend to interact at closer viewing distances and in denser habitats than larger species[33]. Nonetheless, our results argue against the idea that increased predation risks associated with being small strongly constrain the evolution of plumage colourfulness[11].

While these associations provide insight into the factors contributing to variation in passerine colourfulness (Fig. 3a), they are unable to account for a tropical colourfulness peak, as neither dichromatism nor body mass is correlated with latitude. However, our analyses also identified significant effects of several latitude-related climatic and ecological variables that evidently contribute to generating latitudinal gradients in passerine colourfulness (Fig. 4 and Supplementary Tables 4 and 5). First, it has long been suggested that more benign environmental conditions promote elevated colourfulness in the tropics, due to lower evolutionary constraints on elaborate plumage colouration than those imposed by the types of harsh environmental conditions often found towards the poles and in deserts[2]. In support of this, we find that male and female colourfulness scores are consistently and positively associated with precipitation and net primary productivity, such that species are on average more colourful in wetter, more productive areas. Second, we find that species occupying closed (that is, forested) habitat types and foraging niches associated with high degrees of resource defence and carotenoid intake (that is, frugivores and nectarivores) generally have increased levels of colourfulness, supporting hypotheses linking signalling conditions[21,22,34] and dietary factors[2,35]

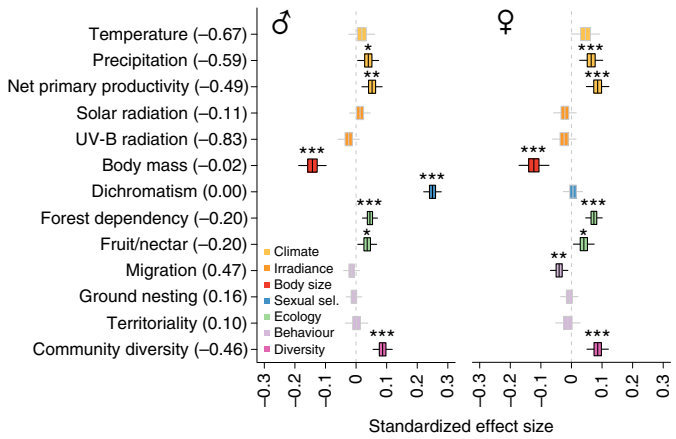

Fig. 4 | Predictors of male and female colourfulness in passerine birds. The box plots summarize the posterior marginal distributions for all fixed effects from Bayesian phylogenetic mixed models applied over a sample of 100 phylogenetic trees predicting male (left) and female (right) colour loci scores. The box widths represent the interquartile range, the median is shown as a vertical line within each box and the whiskers denote the 95% CI of the distribution. The colours indicate the fixed-effect category, with black outlines and asterisks indicating evidence for a non-zero effect of the relevant variable. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. The values in parentheses next to each predictor give the correlation coefficient (Spearman's ρ) for the relationship between the predictor and species' absolute midpoint latitude. The results shown are for colour loci scores calculated assuming a UVS visual system. In all cases, $n = 4{,}415$ species. The full statistical results can be found in Supplementary Table 4.

to interspecific differences in colourfulness. Third, a strong and consistent positive association between colourfulness and community diversity (that is, the average number of co-occurring passerine species) supports the suggestion that latitudinal gradients in species' colourfulness emerge at least in part due to selection on both sexes for accurate conspecific recognition in species-rich tropical communities[2,5,6,9]. Finally, for female birds, we find a strong negative effect of migration on colourfulness that is absent in males. An association between migration and reduced female colourfulness across passerines generalizes earlier findings[36] (though see ref. [12]) and reinforces the idea that in migratory passerine taxa at least, changes in selection acting on females may play an important role in generating sex differences in colouration (see above)[2,35]. As many high-latitude breeding passerines are migratory, this female-specific reduction in colourfulness in migratory taxa may also help explain a general pattern emerging from our analysis: that latitudinal gradients in colourfulness tend to be more pronounced in females than in males (Fig. 3b and Supplementary Table 6).

Conclusions

Together, our results support the existence of a strong latitudinal gradient in species' colourfulness for passerine birds. This gradient exists for both male and female colouration and is consistent across major tropical realms. We demonstrate that this pronounced tropical-zone peak in colourfulness can be explained, in part, by latitude-associated gradients in climatic conditions and species' ecological traits that facilitate the evolution of increased colour diversity of tropical passerine species. However, we note that many potentially important factors remain to be investigated, including latitudinal gradients in predation pressure[24] and the intensity of social selection[31], particularly acting on females. More broadly, we note that conceptions of the latitudinal colourfulness gradient are not limited to the plumages of birds, with early naturalists such as Alexander von Humboldt remarking on the apparent colourfulness of many tropical taxa, including plants, insects, fish and "even crayfish"[37]. Thus, while our results provide clear support for broad-scale latitudinal gradients in colourfulness for passerine birds, the extent to which other global radiations follow the 'rule' that life in the tropics is generally more colourful than in the temperate zones remains to be seen.

Methods

Specimen selection. We based our data collection on the taxonomic framework of Jetz et al.[38], which currently represents the only integrated species-level taxonomic and phylogenetic dataset for all (passerine) birds. We collected data on plumage colouration using study skins housed at the Natural History Museum, Tring, UK. We focused on species with representatives of both sexes and for which geographic range data were available (see below). Where possible, we sampled specimens of three males and three females, taking care to select only mature individuals in breeding plumage with no obvious signs of moult. On the basis of these criteria, we were able to sample specimens of both sexes for 4,527 (76%) of the 5,966 taxa represented in the Jetz et al. taxonomy, with a mean sampling of 2.77 male and 2.61 female specimens per species and 24,345 specimens in total.

Digital photography. Whole-specimen plumage colouration was measured using calibrated UV and Vis light photography[27]. To do this, we used a modified Nikon D7000 digital single-lens reflex camera with a Nikon 105 mm f/4.5 UV Nikkor lens combined with two Baader photographic lens filters: one permitting human Vis wavelengths (400–680 nm; Baader UV/IR Cut filter / L filter) and another permitting UV wavelengths (320–380 nm; Baader U-Venus-Filter). The specimens were illuminated using two Broncolor Pulso G 1600 J lamps (with UV filters removed) connected to a single Broncolor Scoro 1600 S Power Pack. The same camera settings were used for all photographs (1/250 sec, f/16.0, ISO 100, 'Daylight' white balance, RAW photo format), except that a higher ISO sensitivity (2,000) was used for the UV images to achieve the correct exposure. Each image also contained five Labsphere Spectralon Diffuse Reflectance standards of known relative reflectance (2%, 40%, 60%, 80% and 99%). All specimens were photographed through each filter (UV and Vis) from three different angles (dorsal, lateral and ventral), resulting in six images per specimen. Our digital photography dataset therefore consisted of $6 \times 24{,}345 = 146{,}070$ images.

Image segmentation using deep learning. To facilitate the extraction of pixel information from our photography dataset, we applied an automated image segmentation protocol based on convolutional neural networks. The full details of this approach and a comprehensive analysis of its performance, particularly in relation to other methods, can be found in He et al.[39]. A brief account is also provided below.

We used DeepLabv3+, which is a deep convolutional neural network architecture based on fully convolutional networks[40], to build a pixel-wise semantic segmentation network capable of accurately identifying specimen pixels in each of our images. DeepLabv3+ has been shown to outperform both classical computer vision techniques (such as thresholding) and other neural network architectures for sematic segmentation on benchmark tasks[40]. It has also previously been shown to perform well when applied to a task similar to ours, involving the segmentation of biological specimens from photographic images of herbarium specimens[41].

To generate a dataset of expert-labelled images for use in network training and evaluation, we placed polygons on a diverse sample of bird specimen images using Project Plumage (www.projectplumage.org), an online citizen science project with bespoke image-labelling protocols. These polygons were used to manually identify plumage areas and to exclude non-plumage areas obscuring the specimen, such as eye holes, feet, specimen labels and string. The images labelled as part of developing this protocol form part of a broader effort to measure avian colouration. As such, across the three views (dorsal, lateral and ventral), a total of 5,094 images were labelled for 1,698 species distributed across the entire avian radiation (that is, passerines and non-passerines), encompassing representatives of more than 81% of all bird genera and 27 bird orders.

We used this 5,094-image dataset to train and validate the network and then to generate specimen segmentation predictions for each of the >140,000 images in our dataset[39], which took ~72 hours to complete on a desktop computer. Finally, each of the resulting image masks was individually checked by eye and manually refined where necessary using bespoke software (https://github.com/EchanHe/PhenoLearn).

Image processing. All raw (.NEF) images of specimens were linearized and exported as linear TIFF files using DCRAW (https://www.dechifro.org/dcraw/). The pixel values were then normalized using mean pixel intensity values from the five grey standards included in each image to control for variation in lighting conditions, following established approaches[27,42]. Finally, the image was segmented using the image masks described above to leave only pixel values corresponding to the specimen in each image. As individual pixel measurements can be noisy—and

because different specimens were represented by different numbers of pixels in our raw dataset—we downsampled each specimen image to a comparable resolution (Extended Data Fig. 1c), prior to calculating cone catch values and colourfulness metrics (see below). To do this, we treated each specimen image as a raster and, using the aggregate() function in the R package raster (version 3.4–5)[43], we found the smallest aggregation factor in the range 100 to 1 that resulted in at least 500 aggregated cells (pixels) being returned, with aggregated cell values calculated as the mean of relevant neighbouring values. We then randomly sampled 500 measurements from this aggregated dataset to represent the plumage colouration of that specimen view in all further analyses. Samples from the each of the three specimen views (dorsal, lateral and ventral) were pooled to give a final set of 1,500 whole-body plumage colour measurements per specimen.

As well as helping reduce the impact of measurement noise on our colour measurements, another benefit of this procedure of downsampling each image to a comparable resolution is that it ensures that a comparable proportion of the surface of each specimen view is sampled when taking a sample of a set number of measurements. For example, taking a random sample of 500 pixels from raw specimen datasets represented by 1,000 and 5,000 pixel values would result in 50% coverage of the former and only 10% coverage of the latter. However, when pixel values are first aggregated to an approximately equal resolution—in our case, to a resolution resulting in approximately, but no less than, 500 points per view—subsequent random sampling of 500 values for each specimen view results in approximately equal coverage (~100%) in each case.

Visual modelling. We used established methods[42] to generate mapping functions to convert sampled specimen RGB pixel values into avian cone catch values. This approach works by first estimating camera responses and visual system cone catch values to a library of natural spectra under a specific illuminate, and then using multiple regression to create mapping functions for each receptor channel from the camera's responses. Using tools available in the IMAGEJ Multispectral Image Calibration and Analysis Toolbox (version 2.2)[42], we generated mapping functions for each photoreceptor using equations containing second-order polynomial terms and three-way interactions between channels. Note that this approach does not incorporate information on camera responses in the UV G channel due to typically low sensitivities of the G channel in the UV range[42]. We fit these equations to our data incorporating information on the estimated spectral sensitivities of our camera set-up and the irradiance spectrum of our illuminant (that is, flash units), both of which had been estimated previously[27]. For modelling receptor responses, we assumed idealized illumination conditions[13,15] and receptor sensitivities corresponding either to an 'average' violet-sensitive or an 'average' UVS avian visual system, both extracted from the R package pavo (version 2.6.1)[44]. We used this information to generate mapping functions for each cone class, and the resulting models were all characterized by a high degree of mapping accuracy ($R^2 > 0.99$). These mapping functions were then used to convert linearized and normalized image RGB values into cone catch values (u/v, s, m and l) for use in downstream analyses. We have previously shown that cone catch values generated by this photography-based approach are highly correlated ($r > 0.92$) with corresponding values calculated from spectrophotometric measurements[27].

Following previous studies, we represented chromatic (that is, colour) variation among measurements using a standard avian colour space model in which raw cone catch values are converted to relative cone catch values and projected in a tetrahedron[13,15]. This tetrahedron—in which the luminance (that is, achromatic) dimension is removed and each vertex represents one of the four cones characterizing avian colour vision (that is, u/v, s, m and l)—is the sensory equivalent of a morphospace, where similar colours fall in close proximity in the colour space and disparate colours are far apart[13,15,45]. As quantifying the colour of patches with very low overall reflectance can be problematic[46], pixels exhibiting a mean normalized reflectance value of <1% across all channels (uR, uB, vR, vG and vB) were re-cited to the achromatic centre.

Colourfulness metrics. We quantified colourfulness using two simple and intuitive metrics for quantifying variation in organismal colourfulness[14] (Fig. 1b). First, we calculated the volume of the minimum convex polygon containing all colour measurements for a given specimen, which represents the standard and most widely used metric of (avian) colourfulness employed in the literature[13,15]. However, convex hull polygon volume can strongly depend on extreme values[14] and can generate overinflated volume estimates when highly disparate colours are separated by large areas of unoccupied colour space[47]. We therefore also employed a second metric of colour space occupation that is less sensitive to these issues. This approach[16] is based on subdividing (rasterizing) tetrahedral colour space into a series of equally sized three-dimensional cells termed 'colour loci'. This is done by defining two two-dimensional grid systems in the XY and YZ axes of colour space that, when intersected, define a three-dimensional grid system covering the entirety of colour space. Each three-dimensional cell (dimensions: $0.022 \times 0.022 \times 0.022$) therefore represents a 'chromatic locus' and provides a way of partitioning the continuous variation in colour space into discrete units. The strength of this approach is that the colour diversity (that is, colourfulness) of a particular set of measurements can then be assessed by simply counting the number of colour loci occupied[16], with these estimates being less impacted by outlier values and intermediate areas of unoccupied colour space.

We calculated estimates of convex hull volume and number of colour loci occupied for each specimen separately, and then calculated species-level values for each sex as the mean of $\log_{10}$-transformed specimen-level values.

Phylogenetic framework. To provide a phylogenetic framework for the species included in our analysis ($n = 4{,}527$), we downloaded 100 trees from the posterior distribution of complete trees produced by Jetz et al.[38] from http://www.birdtree.org, which were then pruned to generate a distribution of trees containing only the focal species set. All of our analyses incorporating phylogenetic information were run over this distribution of 100 trees to incorporate phylogenetic uncertainty into our parameter estimates. For plotting purposes, we identified a maximum clade credibility tree from this posterior distribution of trees using the maxCladeCred() function in the R package phangorn (version 2.5.5)[48].

Geographic data. We based our geographic analyses on the comprehensive dataset of bird species' geographic range maps produced by BirdLife International (http://datazone.birdlife.org/). We resolved taxonomic differences between the BirdLife and Jetz et al. datasets as far as possible, manually editing (that is, combining or splitting) range maps for BirdLife taxa where necessary. We focused on species' breeding geographic ranges only (seasonality, 1 or 2) and regions where species are known to be native or reintroduced (origin, 1 or 2) and extant or probably extant (presence, 1 or 2). To map and test the predictors of species' colourfulness, we extracted polygon range maps onto an equal-area grid (Behrmann projection) at 0.5° resolution (~50 km at the equator). Species' latitudinal midpoints were calculated as the mean latitude of occupied grid cells. The same projection and grid system were also used to extract range-wide values for species' environmental variables (see below).

Predictor variables. To test the role of factors hypothesized to influence passerine species' colourfulness and its possible covariation with latitude, we collected data for 13 key environmental and ecological variables.

Global spatial information on temperature, precipitation, solar radiation, UV-B radiation and net primary productivity were extracted from various sources and then reprojected and resampled to match the resolution of our range dataset. Annual mean temperature (bio1) and annual precipitation (bio12) data were downloaded from the WorldClim (version 2.1) database[49] (https://worldclim.org/) at 2.5-arc-minute resolution. Monthly information on solar radiation was downloaded at 30-arc-second resolution, and monthly totals were summed to give a measure of total annual solar radiation. Information on annual mean UV-B radiation was extracted from Beckmann et al.[50] at 15-arc-minute resolution. Information on net primary productivity at 1 km resolution was extracted from datasets produced by Running et al.[51]. In all cases, species' values represent averages across their geographic range.

Information on species-level ecological and behavioural traits was extracted from two sources: BirdLife International's Data Zone (http://www.datazone.birdlife.org) (forest dependency) and Tobias and Pigot[52] (foraging niche, migration, nest placement, territoriality and body mass). To reduce the complexity of the categorical variables included in these datasets and to facilitate effect size comparison in our multipredictor models, we recoded variation in forest dependency, foraging niche, migration, nest placement and territoriality as binary variables that aligned with our hypotheses (see the main text). Specifically, species were coded as forest dependent ('low', 'medium' or 'high' dependency) or not ('does not usually occur in forest'), frugivorous/nectarivorous or not (all other dietary niches), migratory ('migratory' or 'partially migratory') or not ('sedentary'), ground nesting ('exposed ground') or not ('cavity' or 'exposed elevated'), and territorial ('strong' or 'weak') or not ('none'). Sexual dichromatism was scored from handbook plates as the mean value of plumage dimorphism estimated from five body regions (head, back, belly, wings and tail) using the following scheme: −2, the female was substantially brighter and/or more patterned than the male; −1, the female was brighter and/or more patterned than the male; 0, there was no sex difference in the body region, or there was a difference but neither could be considered brighter than the other; 1, the male was brighter and/or more patterned than the female; 2, the male was substantially brighter and/or more patterned than the female. These scores are thus independent of the data used in this study to quantify colourfulness, and positive values represent male-biased ornamentation, zero represents unbiased ornamentation and negative values represent female-biased ornamentation. To assess the effect of variation in community diversity on species' colourfulness, we generated a variable capturing the average richness of passerine species co-occurring with each species in our dataset. To do this, we used range data for all passerine species (that is, not just those sampled in our dataset) to calculate for each grid cell the number of co-occurring passerine species. We then calculated the mean value of this variable across species' geographic ranges to provide a measure of average community diversity for each species, analogous to the community diversity metric generated by Dalrymple et al.[5]. Overall, we were able to collect complete data on these variables for 4,415 of the 4,527 species in our dataset.

Finally, social mating system has been shown to correlate with various aspects of avian colouration, including dichromatism, brightness/hue and extent of elaboration[11,12,53]. To assess the importance of social mating system relative to the factors outlined above, we used available data from Dunn et al.[12] ($n = 608$ species)

to run a parallel set of models including mating system as a factor alongside the other predictors. As above, mating system variation was recoded as a binary variable contrasting mating systems associated with relatively low social polygyny rates ('monogamy' ($n=469$), 'cooperative' ($n=79$) or 'polyandry' ($n=1$)) versus those with higher rates ('mostly polygyny' ($n=31$) or 'lekking or promiscuous' ($n=28$)). On the basis of this dataset, we found no evidence that variation in social mating system correlates with male or female colourfulness (Supplementary Table 7). We explored the sensitivity of these findings using alternative classification strategies (for example, monogamy yes/no and cooperative yes/no), but the results were similar in all cases; therefore, only results based on the classification scheme outlined above (and on UVS colour scores) are presented. The lack of a clear effect of social mating system on colourfulness using this dataset suggests that mating system variation across species cannot account for any of the patterns we report in our main analysis, particularly the effect of dichromatism, which remained significant even in this reduced dataset (Supplementary Table 7).

Statistical analyses. *Grid-cell-based analyses.* We calculated mean sex-specific colourfulness scores (volume and loci) for local assemblages of passerine species that are presumed to occur together at the scale of 50 km × 50 km grid cells. We calculated the mean colourfulness score for individual grid cells in two different ways. First, we simply calculated the mean ($\log_{10}$-transformed) colourfulness score for all species present in a particular cell (Fig. 2). Next, to reduce the impact of spatial and taxonomic pseudoreplication across cells, we followed previous studies[18,38] by calculating weighted (arithmetic) means of colourfulness scores to reduce the contribution of geographically widespread taxa to the overall mean of a given cell. Weights for each species were calculated as the inverse of the number of grid cells in which the species was found (that is, their range size)[18,38].

To formally assess the relationship between latitude and assemblage-level colourfulness, we followed the approach of Rabosky et al.[18] by testing this relationship at the scale of ecoregions rather than individual grid cells. We chose to do this to reduce the computation burden of analysing the full 59,102-grid-cell dataset and, more importantly, to minimize levels of autocorrelation between assemblages, which is far higher between adjacent grid cells than between adjacent ecoregions[18]. We therefore calculated mean colourfulness scores for all cells within terrestrial ecoregions of the world[17] containing passerine species in our dataset ($n=800$) and related this to the absolute latitude of ecoregions' centroid position. To account for spatial autocorrelation between ecoregions, we used SAR models implemented using the function spautolm() in the R package spdep (version 1.1–5)[54]. For these models, neighbours were defined as those ecoregions with contiguous boundaries. We then selected the appropriate weighting style using Akaike information criterion model selection based on code provided by Rabosky et al.[18]. We used Moran's *I* to test for spatial autocorrelation in the residuals of SAR regressions to determine the extent to which SAR models successfully accounted for spatial non-independence in the data. These results showed that all models retained some evidence of residual spatial autocorrelation, but to a lesser degree in models based on richness-corrected ecoregion colourfulness scores (see below) than in those based on raw ecoregion scores (Supplementary Table 1).

An important consideration when analysing aggregated species-level variables in a spatial context is that underlying species richness gradients can generate strong spatial patterns in aggregated data[55]. To address the extent to which the latitudinal colourfulness gradients we observe in our spatial analyses are independent of underlying species richness differences, we used a randomization approach to calculate colourfulness standardized effect size values for each ecoregion, which corrects for the effect of species richness differences on aggregated trait scores[55]. To do this, we generated 200 null communities for each ecoregion by randomizing species' colourfulness scores with respect to species' identity across our dataset. These null communities were then used to generate a null distribution of mean colourfulness scores for each ecoregion, against which the observed colourfulness scores were compared. The resulting standardized effect size scores, in which the effects of species richness on mean colourfulness values have been factored out, were then analysed using the same SAR modelling approach described above.

Species-level analyses. To test the relationship between species' absolute midpoint latitude and colourfulness, and between species' colourfulness scores and variation in the 13 predictor variables described above, we used multipredictor Bayesian phylogenetic mixed models implemented in the R package MCMCglmm (version 2.32)[26,56]. All models included a phylogenetic random effects term and were run over a posterior distribution of 100 trees to incorporate phylogenetic uncertainty, and posterior distributions of parameter estimates associated with different trees were pooled to give model estimates that incorporate phylogenetic error[57]. In all cases, the models were run for 55,000 iterations (sampled every 25th iteration) with a 5,000 iteration burn-in, and we used standard non-informative priors (that is, list(R = list(V = 1, nu = 0.002), G = list(G1 = list(V = 1, nu = 0.002)))). All variables were standardized (mean, 0; standard deviation, 1) prior to model fitting to facilitate effect size comparison. Before running the models, we also checked for evidence of multi-collinearity among predictors in our multipredictor models using variance inflation factors (VIFs) and found no evidence of severe (VIF > 10) or even moderate (VIF > 4) multi-collinearity in our models (median VIF, 1.60; range, 1.05–3.89).

Finally, phylogenetic heritability (H^2) values[19] were estimated by fitting intercept-only models for each variable of interest and then calculating the proportion of the total variance explained by phylogenetic effects across the posterior distribution of parameter estimates.

All statistical analyses were conducted in R (version 4.1.0)[58].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All analysis data are available in Supplementary Data 1. In addition, the phylogenetic trees were downloaded from http://www.birdtree.org, the geographic and ecological data were accessed via BirdLife International's Data Zone (http://www.datazone.birdlife.org), and the global climate data were downloaded from WorldClim (https://worldclim.org/).

Code availability

The R code is available at https://github.com/christophercooney/Avian-colourfulness.

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Author contributions

C.R.C. and G.H.T. designed the research. C.R.C., Z.K.V., L.O.N., C.J.A.M., M.D.J., A.L. and T.S. collected the data. C.R.C. and Y.H. conducted the analyses. C.R.C. wrote the manuscript, with input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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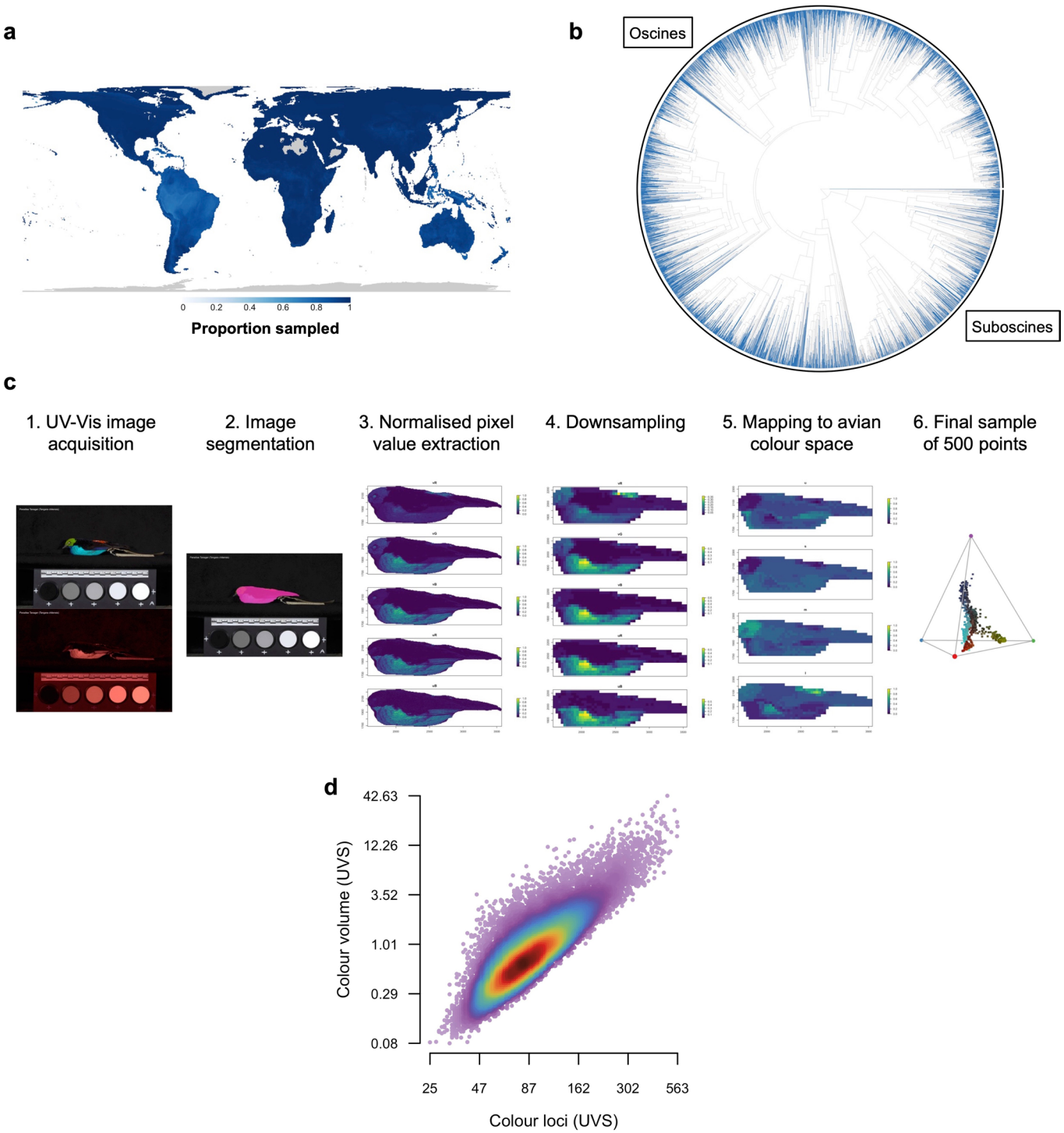
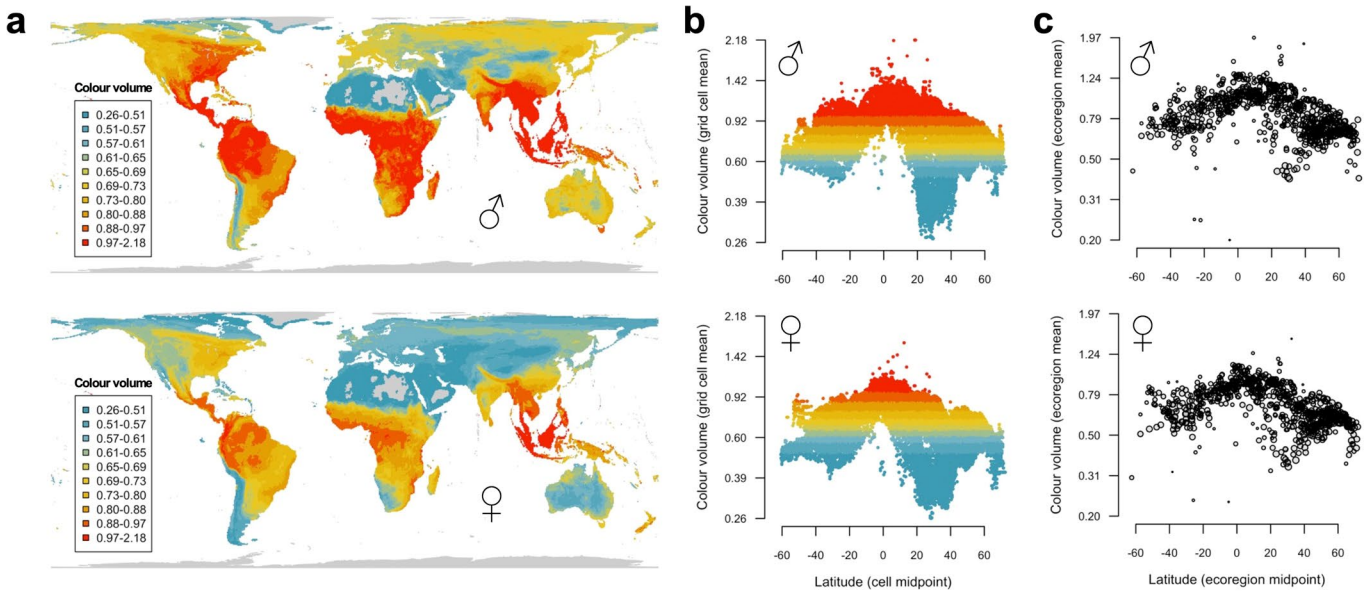
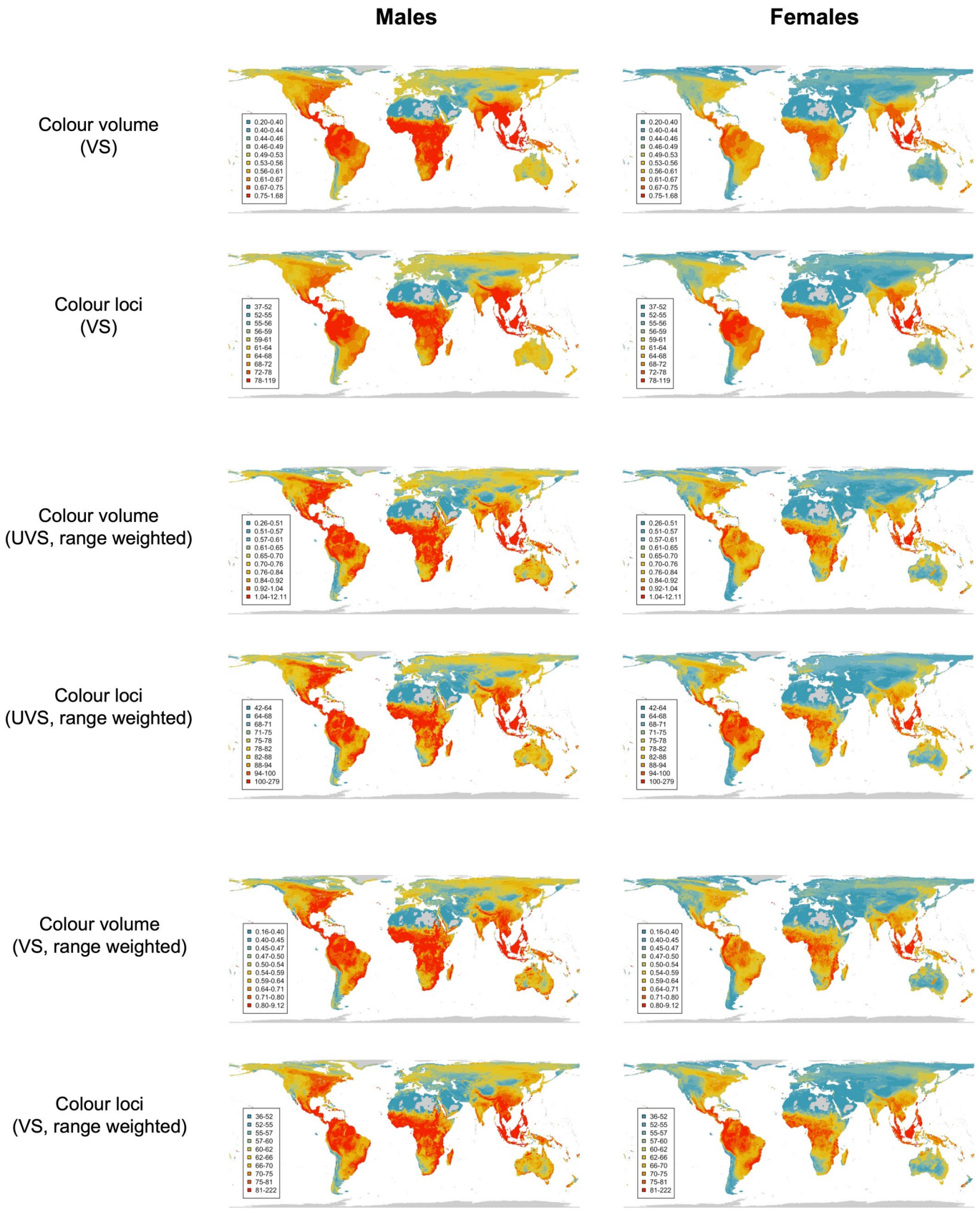


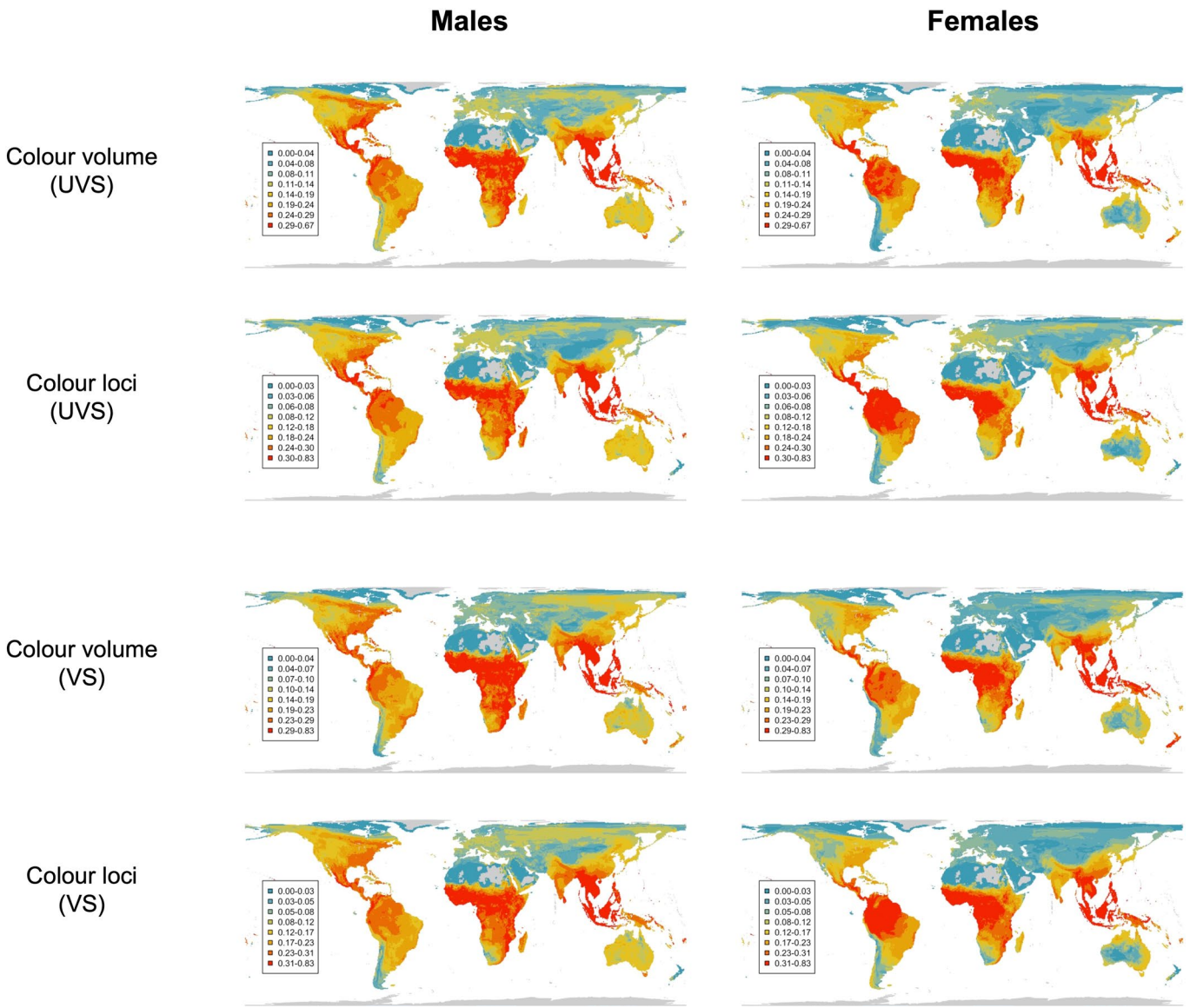
Extended Data Fig. 1 | The distribution of sampled species and illustrations of the colouration data workflow and colour diversity metrics used in this study. a, The proportion of passerine species sampled per grid cell. Grid cell size is 50 × 50 km (Behrman projection) and only cells containing at least 5 passerine species are plotted. **b**, The phylogenetic distribution of sampled species (blue, $n = 4{,}527$) relative to the whole passerine radiation ($n = 5{,}966$). **c**, An example showing the workflow used to extract whole-body reflectance data from specimen images, as applied to lateral (side) view images. An analogous workflow is applied to the other two views of the specimen (dorsal and ventral). The resulting sets of measurements for each view are then combined into a final dataset of 1,500 measurements for each specimen, capturing whole-body plumage colouration. **d**, The relationship between specimen-level scores of colour loci and colour volume based on a ultraviolet-sensitive (UVS) visual system.



Extended Data Fig. 2 | Latitudinal gradients in male and female colourfulness in passerine birds using colour volume. a, Mean colour volume scores for grid cell assemblages, separately for males (top) and females (bottom). **b**, **c**, Distributions of mean species' colour volume scores for grid cells (**b**) and ecoregions (**c**) with respect to latitude, separately for males (top) and females (bottom). Grid cell size is 50 × 50 km for all panels (Behrman projection) and only cells containing at least 5 sampled species are plotted. Colour volumes are based on an ultraviolet- sensitive (UVS) visual system. Note: colour volume values are multiplied by 1000.



Extended Data Fig. 3 | Geographic distributions of male and female colourfulness in passerine birds using different datasets. Grid cell size is 50 × 50 km for all panels (Behrman projection) and only cells containing at least 5 sampled species are plotted. UVS, ultraviolet sensitive; VS, violet sensitive. Note: colour volume values are multiplied by 1000.



Extended Data Fig. 4 | Geographic distribution of the proportion of species in passerine assemblages in the top colour diversity quartile using different datasets. Grid cell size is 50 × 50 km for all panels (Behrman projection) and only cells containing at least 5 sampled species are plotted. UVS, ultraviolet sensitive; VS, violet sensitive.

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Software and code

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Data collection	No custom software used for data collection.
Data analysis	Data were analysed in R (version 4.1.0) using the open source R packages cited in the text: raster (version 3.4-5), pavo (version 2.6.1), phangorn (version 2.5.5), spdep (version 1.1-5), MCMCglmm (version 2.32). We also used DeepLabV3+ accurately identifying specimen pixels in each of our images, DCRAW (version 9.27) to linearise the digital image data and the IMAGEJ Multispectral Image Calibration and Analysis Toolbox (version 2.2) to generate cone catch mapping functions. All are open source and available from the sources listed in the text.

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All analysis data is available in Supplementary Data 1.xlsx. In addition, phylogenetic trees were downloaded from http://www.birdtree.org, geographic and ecological data were accessed via BirdLife International's Data Zone (http://www.datazone.birdlife.org), and global climate data were downloaded from WorldClim (https://worldclim.org/). R code is available at https://github.com/christophercooney/Avian-colourfulness.

Field-specific reporting

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☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The manuscript addresses global latitudinal trends in colourfulness and their underlying causes in passerine birds.
Research sample	Our research sample consisted of individual museum specimens (males and females) of 4,527 passerine bird species. We aimed to sample as many species as possible. The final total was determined by specimen availability within the museum's collection. For each specimen, we took calibrated digital UV-vis photographs from three orientations (dorsal, lateral, ventral).
Sampling strategy	We collected plumage colouration data for up to three males and three female of all passerine bird species housed at the NHM, Tring. Final sample size was determined by specimen availability.
Data collection	Digital images of individual specimens were taken using a modified Nikon D7000 digital single-lens reflex camera with a Nikon 105mm f/4.5 UV Nikkor lens combined with two Baader photographic lens filters: one permitting human visible wavelengths (400–680 nm; Baader UV/IR Cut filter / L filter) and another permitting UV wavelengths (320–380 nm; Baader U-Venus-Filter). Specimens were illuminated using two Bronocolor Pulso G 1600 J lamps (with UV filters removed) connected to a single Broncolor Scoro 1600 S Power Pack. Photographs were taken by C.C., Z.K.V., L.O.N., C.J.A.M. and M.D.J. Data for predictor variables were sourced from the literature.
Timing and spatial scale	Plumage colouration data were sampled from the collections at NHM Tring during the period 2016-2019. The dataset is global in spatial scale.
Data exclusions	No data were excluded from the analyses.
Reproducibility	Ours is a non-experimental study.
Randomization	Randomisation was not used in sample selection. Sample selection was determined by the availability of museum specimens.
Blinding	Blinding was not relevant to this study as species sampling was as exhaustive as possible and species were sampled without regard to their phenotypes.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging