eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

Title: Latitudinal gradients in avian colourfulness

Author list: Christopher R. Cooney[1]*, Yichen He[1], Zoë K. Varley[1,6], Lara O. Nouri[1], Christopher J. A. Moody[1], Michael D. Jardine[1], András Liker[2,3], Tamás Székely[4,5], Gavin H. Thomas[1,6]

Affiliations:

[1] Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield; Alfred Denny Building, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

[2] MTA-PE Evolutionary Ecology Research Group, University of Pannonia, Veszprém H-8210, Hungary

[3] Behavioral Ecology Research Group, Center for Natural Sciences, University of Pannonia, Veszprém H-8210, Hungary

[4] Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom

[5] *Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen H-4032, Hungary*

[6] Bird Group, Department of Life Sciences, The Natural History Museum at Tring; Akeman Street, Tring, HP23 6AP, UK.

*Corresponding author. Email: c.cooney@sheffield.ac.uk

Abstract

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 effect 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.

Main text

Introduction

Is life generally more colourful in the tropics? The possible existence of global-scale trends in organismal colourfulness was suggested by 19th 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 using subjective and/or incomplete measures of colourfulness (e.g. human scoring) or by studying radiations of species that span only a limited fraction of the Earth's latitudinal gradient[5-12] (see 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

73 geographic information for many taxa, now make it possible to test for the existence of
74 latitudinal gradients in species' colourfulness on a truly global scale.

Results and Discussion

76 We tested whether a latitudinal gradient in species' colourfulness exists for the global
77 radiation of passerine birds (Order: Passeriformes)—the largest avian order comprising
78 ~60% of the ~10,000 bird species. Our approach is centred around a novel dataset of
79 plumage colouration based on >140,000 calibrated visible and ultraviolet light
80 photographs of male and female museum specimens for 4,527 species (~76% of
81 passerine diversity; Extended Data Fig. 1a,b). For each included specimen, we took
82 photographs from three different angles (dorsal, lateral, ventral), extracted calibrated pixel
83 values from each image using machine learning approaches, and mapped these into
84 avian tetrahedral colour space (see Methods). We then sampled 500 points from each
85 view to give a total of 1,500 measurements capturing whole-body plumage reflectance
86 for each specimen (Extended Data Fig. 1c). This process resulted in a dataset consisting
87 of >24,000 photographed specimens and >36 million unique measurements of passerine
88 plumage colouration (Fig. 1a), which together occupy a colour space that is comparable
89 to that estimated for all birds[13].

90 **Quantifying colourfulness.** Colourfulness can be considered in multiple ways. Here we
91 follow the sensory ecology literature by defining colourfulness in terms of within-individual
92 colour diversity; that is, the overall colour contrast of a multi-coloured pattern[14]. Defined
93 in this way, colourfulness arises when an organism displays a range of colours (potentially
94 produced by different colour producing mechanisms) that are perceptually different from
95 one another, and can be quantified using metrics that measure the spread of colour traits
96 in colour space[14]. Importantly, this characterisation of colourfulness is distinct from other
97 notions of colourfulness that include uniform plumage colouration of a particular (often
98 conspicuous) hue and also differs from approaches used by other broad-scale bird
99 colouration studies, which have variously quantified plumage colouration in terms of
100 brightness and hue[12] and degree of elaboration (e.g. the 'maleness' metric introduced by
101 Dale et al.)[11], rather than colourfulness (i.e. colour diversity) *per se*. Here we use two
102 established metrics of colourfulness: convex hull volume[13,15] and the number of occupied
103 colour loci[16]. The former reliably captures the breadth of colours in a sample but is heavily
104 influenced by extreme values, whereas the latter reflects that species will generally not
105 occupy all areas of colour space within the extent of occurrence (Fig. 1b). Values of the
106 two metrics are strongly correlated across specimens in our dataset ($r = 0.85$, $P < 0.001$,
107 $n = 24,345$; Extended Data Fig. 1d) but because the colour loci metric is generally less
108 sensitive to noise, outliers and large 'gaps' in colour space occupation that can bias
109 estimates of colourfulness[14,16] (Fig. 1b), we focus in the main text on results based on
110 colour loci scores, with colour volume results provided as Extended Data and
111 Supplementary Information.

112

Testing for latitudinal colourfulness gradients. We separately mapped mean male and mean female colourfulness scores for grid cell assemblages and find 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). For example, 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 to 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 are calculated by downweighting the influence of geographically widespread species (Extended Data Fig. 3; for methods see 'Statistical analyses'). To formally test the relationship between latitudinal position and species' colourfulness while minimising 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 are calculated (see 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 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 that 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 (see Methods). Consistent with our previous findings, equatorial-zone species (midpoint latitude <23.5°) are generally characterised 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

154 (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)
155 for male and female colourfulness, respectively. It is therefore possible that the latitudinal
156 gradient in colourfulness we observe is the result of phylogenetic non-independence
157 between tropical residency and elevated colourfulness—for example, if the ancestors of
158 speciose tropically-restricted passerine clades happened to be colourful, and both traits
159 have simply been retained by descendent lineages over evolutionary time[2]. However,
160 testing the relationship between colourfulness and species' absolute latitudinal position
161 while controlling for phylogenetic history, we find significant negative correlations with
162 latitude for both male [standardised slope coefficient: -0.04 (95% CI: -0.07, -0.02)] and
163 female colourfulness scores [-0.12 (95% CI: -0.14, -0.09)] (Supplementary Table 3). This
164 indicates that the observed gradient in species' colourfulness cannot be explained solely
165 by phylogenetic conservatism of both latitudinal position and degree of colourfulness.

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

189 To explore the factors promoting passerine colourfulness and to illuminate potential
190 explanations for the latitudinal gradients in colourfulness we observe, we used multi-
191 predictor Bayesian phylogenetic mixed models[26] to assess the relative importance of
192 variables capturing relevant environmental and ecological axes of variation among
193 species (n = 4,415) (see Methods). Importantly, the majority of these predictor variables
194 (11 of 13) were significantly correlated with species' midpoint latitude (P < 0.001 in all

cases; for 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 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 also 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 (see 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 size and colourfulness across species. This relationship is therefore consistent with large birds experiencing greater physiological constraints on colourfulness than smaller birds[32], but 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 in the factors contributing to variation in passerine colourfulness (i.e. 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

235 colouration imposed by the types of harsh environmental conditions often found towards
236 the poles and in deserts[2]. In support of this, we find that male and female colourfulness
237 scores are consistently and positively associated with precipitation and net primary
238 productivity (NPP), such that species are on average more colourful in wetter, more
239 productive areas. Second, we also find that species' occupying closed (i.e. forested)
240 habitat types and foraging niches associated with a high degree of resource defence and
241 carotenoid intake (i.e. frugivores and nectarivores) generally have increased levels of
242 colourfulness, supporting hypotheses linking signalling conditions[21,22,34] and dietary
243 factors[2,35] to interspecific differences in colourfulness. Third, a strong and consistent
244 positive association between colourfulness and community diversity (i.e. the average
245 number of co-occurring passerine species) supports the suggestion that latitudinal
246 gradients in species' colourfulness emerge at least in part due to selection on both sexes
247 for accurate conspecific recognition in species-rich tropical communities[2,5,6,9]. Finally, for
248 female birds we find a strong negative effect of migration on colourfulness that is absent
249 in males. An association between migration and reduced female colourfulness across
250 passerines generalises earlier findings[36] (though see [12]) and reinforces the idea that in
251 migratory passerine taxa at least, changes in selection acting on females may play an
252 important role in generating sex-differences in colouration (cf. above)[2,35]. As many high-
253 latitude breeding passerines are migratory, this female-specific reduction in colourfulness
254 in migratory taxa may also help to explain a general pattern emerging from our analysis:
255 that latitudinal gradients in colourfulness tend to be more pronounced in females than in
256 males (e.g. Fig. 3b; Supplementary Table 6).

257 **Conclusions**

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

273 **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. Based on 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 ultraviolet (UV) and visible (Vis) light photography[27]. To do this we used 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. The same camera settings were used for all photographs (1/250 sec, f/16.0, ISO 100, 'Daylight' white balance, RAW photo format), with the exception that a higher ISO sensitivity (2000) was used for UV images to achieve 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, Vis) from three different angles (dorsal, lateral, ventral), resulting in six images per specimen. Therefore our digital photography dataset of consisted of 6 x 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. 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 (e.g. 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 similar task as 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 ventral) a total of 5,094 images were labelled for 1,698 species distributed across the entire avian radiation (i.e. 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 linearised and exported as linear TIFF files using DCRAW (https://www.dechifro.org/dcraw/). Pixel values were then normalised using mean pixel intensity values from the five grey standards included in each image in order 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 (see 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), 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, ventral) were pooled to give a final set of 1,500 whole-body plumage colour measurements per specimen.

As well as helping to 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, respectively, would result in 50% coverage of the former and only 10% coverage of the latter. However, by first aggregating pixel

353 values to an approximately equal resolution—in our case, to a resolution resulting in
354 approximately, but no less than, 500 points per view—then subsequent random sampling
355 of 500 values for each specimen view results in approximately equal coverage (~100%)
356 in each case.

357 **Visual modelling.** We used established methods[42] to generate mapping functions to
358 convert sampled specimen RGB pixel values into avian cone-catch values. This approach
359 works by first estimating camera responses and visual system cone-catch values to a
360 library of natural spectra under a specific illuminate, and then uses multiple regression to
361 create mapping functions for each receptor channel from the camera's responses. Using
362 tools available in the IMAGEJ Multispectral Image Calibration and Analysis Toolbox
363 (version 2.2)[42], we generated mapping functions for each photoreceptor using equations
364 containing second-order polynomial terms and three-way interactions between channels.
365 Note that this approach does not incorporate information on camera responses in the UV
366 G channel due to typically low sensitivities of the G channel in the UV range[42]. We fit
367 these equations to our data incorporating information on the estimated spectral
368 sensitivities of our camera set up and the irradiance spectrum of our illuminant (i.e. flash
369 units), both of which had estimated previously[27]. For modelling receptor responses, we
370 assumed idealised illumination conditions[13,15] and receptor sensitivities corresponding
371 either to an 'average' violet-sensitive (VS) or 'average' ultraviolet-sensitive (UVS) avian
372 visual system, both extracted from the R package pavo (version 2.6.1)[43]. We used this
373 information to generate mapping functions for each cone class, and the resulting models
374 were all characterised by a high degree of mapping accuracy (R^2 values > 0.99). These
375 mapping functions were then used to convert linearised and normalised image RGB
376 values into cone catch values (u/v, s, m, l) for use in downstream analyses. We have
377 previously shown that cone catch values generated by this photography-based approach
378 are highly correlated (r > 0.92) with corresponding values calculated from
379 spectrophotometric measurements[27].

380 Following previous studies, we represented chromatic (i.e. colour) variation among
381 measurements using a standard avian colour space model in which raw cone catch
382 values are converted to relative cone catch values and projected in a tetrahedron[13,15].
383 This tetrahedron—in which the luminance (i.e. achromatic) dimension is removed and
384 each vertex represents one of the four cones characterising avian colour vision (i.e. u/v,
385 s, m, l)—is the sensory equivalent of a morphospace, where similar colours fall in close
386 proximity in the colour space and disparate colours are far apart[13,15,44]. As quantifying the
387 colour of patches with very low overall reflectance can be problematic[45], pixels exhibiting
388 a mean normalised reflectance value of <1% across all channels (uR, uB, vR, vG, vB)
389 were re-cited to the achromatic centre.

390 **Colourfulness metrics.** We quantified colourfulness using two simple and intuitive
391 metrics for quantifying variation in organismal colourfulness[14] (Fig. 1b). First, we
392 calculated the volume of the minimum convex polygon containing all colour

393   measurements for a given specimen, which represents the standard and most widely-
394   used metric of (avian) colourfulness employed in the literature[13,15]. However, convex hull
395   polygon volume can strongly depend on extreme values[14] and can generate overinflated
396   volume estimates when highly disparate colours are separated by large areas of
397   unoccupied colour space[46]. Therefore we also employed a second metric of colour space
398   occupation that is less sensitive to these issues. This approach[16] is based on sub-dividing
399   (rasterising) tetrahedral colour space into a series of equally-sized 3D cells termed 'colour
400   loci'. This is done by defining two 2D grid systems in the XY and YZ axes of colour space
401   that, when intersected, define a 3D grid system covering the entirety of colour space.
402   Each 3D cell (dimensions: 0.022 × 0.022 × 0.022) therefore represents a 'chromatic locus'
403   and provides a way of partitioning the continuous variation in colour space into discrete
404   units. The strength of this approach is that the colour diversity (i.e. colourfulness) of a
405   particular set of measurements can then be assessed by simply counting the number of
406   colour loci occupied [16], with these estimates being less impacted by outlier values and
407   intermediate areas of unoccupied colour space.

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

411   **Phylogenetic framework.** To provide a phylogenetic framework for the species included
412   in our analysis ($n = 4,527$), we downloaded 100 trees from the posterior distribution of
413   complete trees produced by Jetz *et al.* [38] from http://www.birdtree.org, which were then
414   pruned to generate a distribution of trees containing only the focal species set. All of our
415   analyses incorporating phylogenetic information were run over this distribution of 100
416   trees to incorporate phylogenetic uncertainty into our parameter estimates. For plotting
417   purposes, we identified a maximum clade credibility (MCC) tree from this posterior
418   distribution of trees using the maxCladeCred() function in the R package phangorn
419   (version 2.5.5)[47].

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

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

Global spatial information on temperature, precipitation, solar radiation, ultraviolet-B (UV-B) radiation and net primary productivity (NPP) 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[48] (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.* [49] at 15 arc-minute resolution. Information on NPP at 1 km was extracted from datasets produced by Running *et al.* [50]. In all cases, species' values represent averages across their geographic range.

Information on species-level ecological and behavioural traits were extracted from several sources, specifically BirdLife International's Data Zone (http://www.datazone.birdlife.org) (forest dependency) and Tobias and Pigot [51] (foraging niche, migration, nest placement, territoriality, 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 re-coded variation in forest dependency, foraging niche, migration, nest placement, and territoriality as binary variables that aligned with our hypotheses (see 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. Thus these scores are independent of the data used in this study to quantify colourfulness and positive values represent male-biased ornamentation, zero represent 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 (i.e. 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

473   generated by Dalrymple et al. [5]. Overall, we were able to collect complete data on these
474   variables for 4,415 of the 4,527 species in our dataset.

475   Finally, social mating system has been shown to correlate with various aspects of avian
476   colouration, including dichromatism, brightness/hue and extent of elaboration[11,12,52]. To
477   assess the importance of social mating system relative to the factors outlined above, we
478   used available data from Dunn et al. [12] (n = 608 species) to run a parallel set of models
479   including mating system as a factor alongside the other predictors. As above, mating
480   system variation was re-coded as a binary variable contrasting mating systems
481   associated with relatively low social polygyny rates ['monogamy' (n = 469), 'cooperative'
482   (n = 79), 'polyandry' (n = 1)] versus those with higher rates ['mostly polygyny' (n = 31),
483   'lekking or promiscuous' (n = 28)]. Based on this dataset, we found no evidence that
484   variation in social mating system correlates with male or female colourfulness
485   (Supplementary Table 7). We explored the sensitivity of these findings using alternative
486   classification strategies (e.g. monogamy yes/no, cooperative yes/no) but results were
487   similar in all cases and so only results based on the classification scheme outlined above
488   (and on UVS colour scores) are presented. The lack of a clear effect of social mating
489   system on colourfulness using this dataset suggests that mating system variation across
490   species cannot account for any of the patterns we report in our main analysis, particularly
491   the effect of dichromatism, which remained significant even in this reduced dataset
492   (Supplementary Table 7).

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

504   To formally assess the relationship between latitude and assemblage-level colourfulness,
505   we followed the approach of Rabosky et al. [18] by testing this relationship at the scale of
506   ecoregions rather than individual grid cells. We chose to do this to reduce the computation
507   burden of analysing the full 59,102 grid cell dataset and, more importantly, to minimise
508   levels of autocorrelation between assemblages, which is far higher between adjacent grid
509   cells than between adjacent ecoregions[18]. We therefore calculated mean colourfulness
510   scores for all cells within terrestrial ecoregions of the world[17] containing passerine species
511   in our dataset (n = 800) and related this to the absolute latitude of ecoregions' centroid
512   position. To account for spatial autocorrelation between ecoregions, we used

simultaneous autoregressive error (SAR) models implemented using the function spautolm() in the R package spdep (version 1.1-5). For these models, neighbours were defined as those ecoregions with contiguous boundaries and we then selected the appropriate weighting style using Akaike information criterion (AIC) 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 lesser degree in models based on richness-corrected ecoregion colourfulness scores (see below) than 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[53]. 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 randomisation approach to calculate colourfulness standardised effect size (SES) values for each ecoregion, which corrects for the effect of species richness differences on aggregated trait scores[53]. To do this we generated 200 null communities for each ecoregion by randomising 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 observed colourfulness scores were compared. The resulting SES 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 multi-predictor Bayesian phylogenetic mixed models implemented in the R package MCMCglmm (version 2.32)[26,54]. 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[55]. In all cases, 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 [i.e. list(R=list(V=1, nu=0.002), G=list(G1=list(V=1, nu=0.002)))]. All variables were standardised (mean = 0, standard deviation = 1) prior to model fitting to facilitate effect size comparison. Before running models we also checked for evidence of multi-collinearity among predictors in our multi-predictor 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).

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

556 All statistical analyses were conducted in R (version 4.1.0).

Authors contributions statement: 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 data; C.R.C. and Y.H. conducted the analyses. C.R.C. wrote the manuscript, with input from all authors.

Competing interests statement: The authors have no competing interests.

Figure 1. The diversity of passerine plumage colours in avian tetrahedral colourspace. a, A sample of one million passerine plumage colours analysed in this study, visualised in avian ultraviolet-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 ultraviolet (*u*) wavelengths. 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. The vertices of the colourspace **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 2-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 score, respectively. In all plots, points are coloured according to their approximate appearance as perceived by a human observer by mapping raw pixel reflectance values to CIE 1931 XYZ colour space.

Figure 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). Grid cell size is 50 x 50 km for all panels (Behrman projection) and only cells containing at least 5 sampled species are plotted. Colour loci scores are based on an ultraviolet-sensitive (UVS) visual system.

Figure 3. The phylogenetic distribution of male and female colourfulness and its relation to species' midpoint latitude in passerine birds. a, Coloured bars indicate male and female colour loci scores for 4,527 passerine species. Grey segments indicate the proportion of tropical species (i.e. |midpoint latitude| < 23.5°) within major clades. **b**, Box plots showing the median and interquartile range 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 variables estimated using phylogenetic reduced major axis (pRMA) regression, which differs significantly ($P < 0.001$) from a one-to-one relationship (dashed line). Colour loci scores are based on an ultraviolet- sensitive (UVS) visual system.

Figure 4. Predictors of male and female colourfulness in passerine birds. Box plots summarise 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. Box widths represent the interquartile range, the median is shown as a vertical line within each box, and whiskers denote the 95% credibility interval of the distribution. Colours indicate the fixed-effect category, with

black outlines and asterisks indicating evidence for a non-zero effect of the relevant variable. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values in parentheses next to each predictor give the correlation coefficient (Spearman's *rho*) for the relationship between each predictor and species' absolute midpoint latitude. Results shown are for colour loci scores calculated assuming an ultraviolet-sensitive (UVS) visual system. In all cases, *n* = 4,415 species. Full statistical results can be found in Supplementary Table 4.

References

1   Darwin, C. R. *On the origin of species, or the preservation of favoured races in the struggle for life.* (John Murray, 1859).

2   Wallace, A. R. *Natural selection and tropical nature: essays on descriptive and theoretical biology. 2nd edition.* (Macmillan, 1895).

3   Darwin, C. R. *A naturalist's voyage round the world.* (John Murray, 1913).

4   Wallace, A. R. Colour in nature. *Nature* **19**, 580-581 (1879).

5   Dalrymple, R. L. *et al.* Abiotic and biotic predictors of macroecological patterns in bird and butterfly coloration. *Ecol. Monogr.* **88**, 204-224 (2018).

6   Adams, J. M., Kang, C. & June-Wells, M. Are tropical butterflies more colorful? *Ecol. Res.* **29**, 685-691, doi:10.1007/s11284-014-1154-1 (2014).

7   Bailey, S. F. Latitudinal gradients in colors and patterns of passerine birds. *Condor* **80**, 372-381 (1978).

8   Wilson, M. F. & Von Neaumann, R. A. Why are Neotropical birds more colourful than North American birds? *Avicultural Magazine* **78**, 141-147 (1972).

9   Dalrymple, R. L. *et al.* Birds, butterflies and flowers in the tropics are not more colourful than those at higher latitudes. *Global Ecol. Biogeogr.* **24**, 1424-1432, doi:10.1111/geb.12368 (2015).

10   Friedman, N. R. & Remeš, V. Ecogeographical gradients in plumage coloration among Australasian songbird clades. *Global Ecol. Biogeogr.* **26**, 261-274, doi:10.1111/geb.12522 (2017).

11   Dale, J., Dey, C. J., Delhey, K., Kempenaers, B. & Valcu, M. The effects of life history and sexual selection on male and female plumage colouration. *Nature* **527**, 367-370, doi:10.1038/nature15509 (2015).

12   Dunn, P. O., Armenta, J. K. & Whittingham, L. A. Natural and sexual selection act on different axes of variation in avian plumage color. *Science Advances* **1**, e1400155 (2015).

13   Stoddard, M. C. & Prum, R. O. How colorful are birds? Evolution of the avian plumage color gamut. *Behav. Ecol.* **22**, 1042-1052, doi:10.1093/beheco/arr088 (2011).

14   Renoult, J. P., Kelber, A. & Schaefer, H. M. Colour spaces in ecology and evolutionary biology. *Biological Reviews* **92**, 292-315, doi:10.1111/brv.12230 (2017).

15   Stoddard, M. C. & Prum, R. O. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *Am. Nat.* **171**, 755-776, doi:10.1086/587526 (2008).

16   Delhey, K. The colour of an avifauna: a quantitative analysis of the colour of Australian birds. *Scientific Reports* **5**, 18514, doi:10.1038/srep18514 (2015).

17   Olson, D. M. *et al.* Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience* **51**, 933-938 (2001).

669　18　Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes.
670　　　　*Nature* **559**, 392-395, doi:10.1038/s41586-018-0273-1 (2018).
671　19　Lynch, M. Methods for the analysis of comparative data in evolutionary biology.
672　　　　*Evolution* **45**, 1065-1080 (1991).
673　20　Delhey, K. A review of Gloger's rule, an ecogeographical rule of colour: definitions,
674　　　　interpretations and evidence. *Biol. Rev. Camb. Philos. Soc.* **94**, 1294-1316,
675　　　　doi:10.1111/brv.12503 (2019).
676　21　Marchetti, K. Dark habitats and bright birds illustrate the role of the environment in
677　　　　species divergence. *Nature* **362**, 149-152 (1993).
678　22　Endler, J. A. The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1-27
679　　　　(1993).
680　23　Schemske, D. W. in *Speciation and Patterns of Diversity* (eds R. Butlin, J. Bridle, & D.
681　　　　Schluter) Ch. 12, 219-239 (2001).
682　24　Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. & Roy, K. Is there a
683　　　　latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.*
684　　　　**40**, 245-269, doi:10.1146/annurev.ecolsys.39.110707.173430 (2009).
685　25　MacArthur, R. H. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* **1**, 19-30
686　　　　(1969).
687　26　Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative
688　　　　biology: phylogenies, taxonomies and multi-trait models for continuous and categorical
689　　　　characters. *J. Evol. Biol.* **23**, 494-508, doi:10.1111/j.1420-9101.2009.01915.x (2010).
690　27　Cooney, C. R. *et al.* Sexual selection predicts the rate and direction of colour divergence
691　　　　in a large avian radiation. *Nature communications* **10**, 1773, doi:10.1038/s41467-019-
692　　　　09859-7 (2019).
693　28　Cooney, C. R., MacGregor, H. E. A., Seddon, N. & Tobias, J. A. Multi-modal signal
694　　　　evolution in birds: re-assessing a standard proxy for sexual selection. *Proc. R. Soc.*
695　　　　*London Ser. B* **285**, 20181557, doi:10.1098/rspb.2018.1557 (2018).
696　29　van der Bijl, W. *et al.* Butterfly dichromatism primarily evolved via Darwin's, not
697　　　　Wallace's, model. *Evolution Letters* **4**, 545-555, doi:10.1002/evl3.199 (2020).
698　30　Darwin, C. R. *The descent of man, and selection in relation to sex.* (John Murray, 1871).
699　31　Tobias, J. A., Montgomerie, R. & Lyon, B. E. The evolution of female ornaments and
700　　　　weaponry: social selection, sexual selection and ecological competition. *Philos. Trans. R.*
701　　　　*Soc. London Ser. B* **367**, 2274-2293, doi:10.1098/rstb.2011.0280 (2012).
702　32　Galván, I., Negro, J. J., Rodríguez, A. & Carrascal, L. M. On showy dwarfs and sober
703　　　　giants: body size as a constraint for the evolution of bird plumage colouration. *Acta*
704　　　　*Ornithologica* **48**, 65-80, doi:10.3161/000164513x670007 (2013).
705　33　Kiltie, R. A. Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.*
706　　　　**14**, 226-234 (2000).
707　34　Zahavi, A. & Zahavi, A. *The Handicap Principle.* (Oxford University Press, 1997).
708　35　Badyaev, A. V. & Hill, G. E. Avian sexual dichromatism in relation to phylogeny and
709　　　　ecology. *Annu. Rev. Ecol. Evol. Syst.* **34**, 27-49,
710　　　　doi:10.1146/annurev.ecolsys.34.011802.132441 (2003).
711　36　Simpson, R. K., Johnson, M. A. & Murphy, T. G. Migration and the evolution of sexual
712　　　　dichromatism: evolutionary loss of female coloration with migration among wood-
713　　　　warblers. *Proc. R. Soc. London Ser. B* **282**, 20150375, doi:10.1098/rspb.2015.0375
714　　　　(2015).
715　37　Helferich, G. *Humboldt's Cosmos.* (Tantor eBooks, 2011).

716 38 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity
717   of birds in space and time. *Nature* **491**, 444-448, doi:10.1038/nature11631 (2012).
718 39 He, Y. *et al.* Segmenting biological specimens from photos to understand the evolution of
719   UV plumage in passerine birds. *bioRxiv*, doi:https://doi.org/10.1101/2021.07.22.453339
720   (2021).
721 40 Chen, L. C., Zhu, Y., Papandreou, G., Schroff, F. & Adam, H. Encoder-decoder with
722   atrous separable convolution for semantic image segmentation. *arXiv* **1802**, 02611
723   (2018).
724 41 Hussein, B. R., Malik, O. A., Ong, W.-H. & Slik, J. W. F. in *Computational Science and
725   Technology Lecture Notes in Electrical Engineering* Ch. Chapter 31, 321-330 (2020).
726 42 Troscianko, J. & Stevens, M. Image calibration and analysis toolbox – a free software
727   suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and
728   Evolution* **6**, 1320-1331, doi:10.1111/2041-210x.12439 (2015).
729 43 Maia, R., Gruson, H., Endler, J. A., White, T. E. & O'Hara, R. B. pavo 2: new tools for
730   the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* **10**,
731   1097-1107, doi:10.1111/2041-210x.13174 (2019).
732 44 Stoddard, M. C. *et al.* Wild hummingbirds discriminate nonspectral colors. *Proc. Natl.
733   Acad. Sci. U.S.A.* **117**, 15112-15122, doi:10.1073/pnas.1919377117 (2020).
734 45 Gomez, D. & Théry, M. Simultaneous crypsis and conspicuousness in color patterns:
735   comparative analysis of a Neotropical rainforest bird community. *Am. Nat.* **169**, S42-S61
736   (2007).
737 46 Blonder, B. Do hypervolumes have holes? *Am. Nat.* **187**, E93-E105, doi:10.1086/685444
738   (2016).
739 47 Schliep, K. P. phangorn: phylogenetic analysis in R. *Bioinformatics* **27**, 592-593 (2011).
740 48 Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces
741   for global land areas. *International Journal of Climatology* **37**, 4302-4315,
742   doi:10.1002/joc.5086 (2017).
743 49 Beckmann, M. *et al.* glUV: a global UV-B radiation data set for macroecological studies.
744   *Methods in Ecology and Evolution* **5**, 372-383, doi:10.1111/2041-210x.12168 (2014).
745 50 Running, S. W. *et al.* A continuous satellite-derived measure of global terrestrial primary
746   production. *Bioscience* **54**, 547-560 (2004).
747 51 Tobias, J. A. & Pigot, A. L. Integrating behaviour and ecology into global biodiversity
748   conservation strategies. *Philos. Trans. R. Soc. London Ser. B* **374**, 20190012,
749   doi:10.1098/rstb.2019.0012 (2019).
750 52 Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. Mating systems, sperm competition,
751   and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161-175 (2001).
752 53 Hawkins, B. A. *et al.* Structural bias in aggregated species-level variables driven by
753   repeated species co-occurrences: a pervasive problem in community and assemblage
754   data. *J. Biogeogr.* **44**, 1199-1211, doi:10.1111/jbi.12953 (2017).
755 54 Hadfield, J. D. MCMC methods for multi-response generalised linear mixed models: the
756   MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22 (2010).
757 55 Healy, K. *et al.* Ecology and mode-of-life explain lifespan variation in birds and
758   mammals. *Proc. R. Soc. London Ser. B* **281**, 20140298, doi:10.1098/rspb.2014.0298
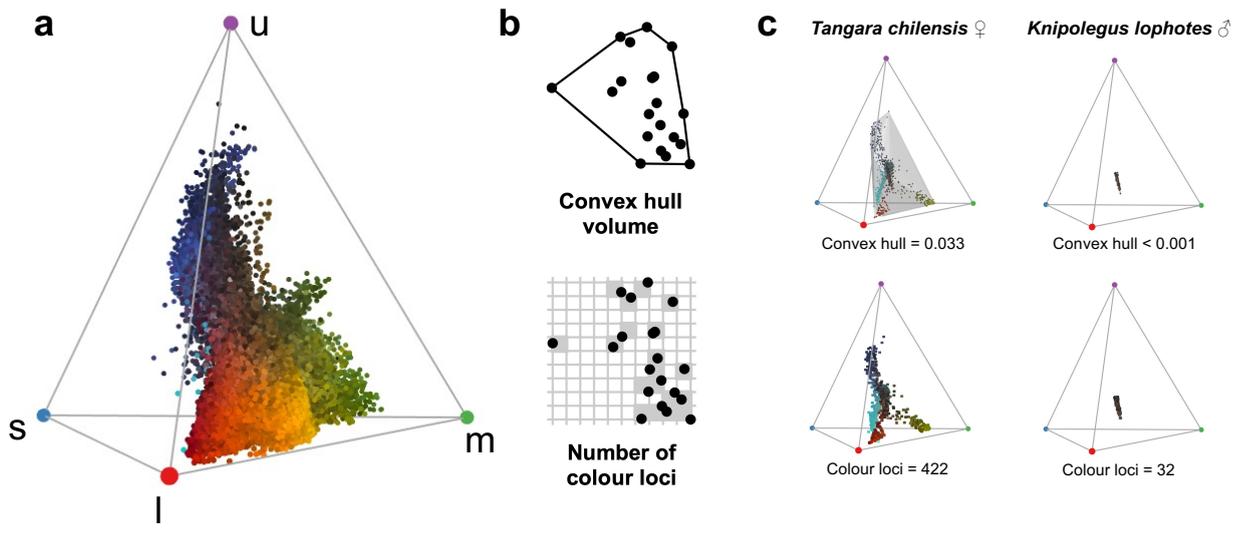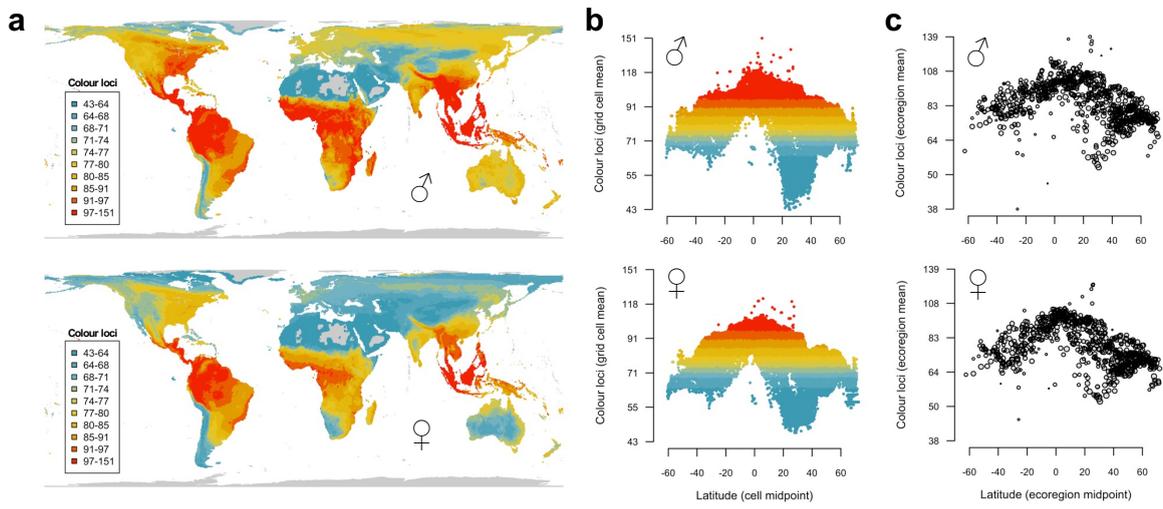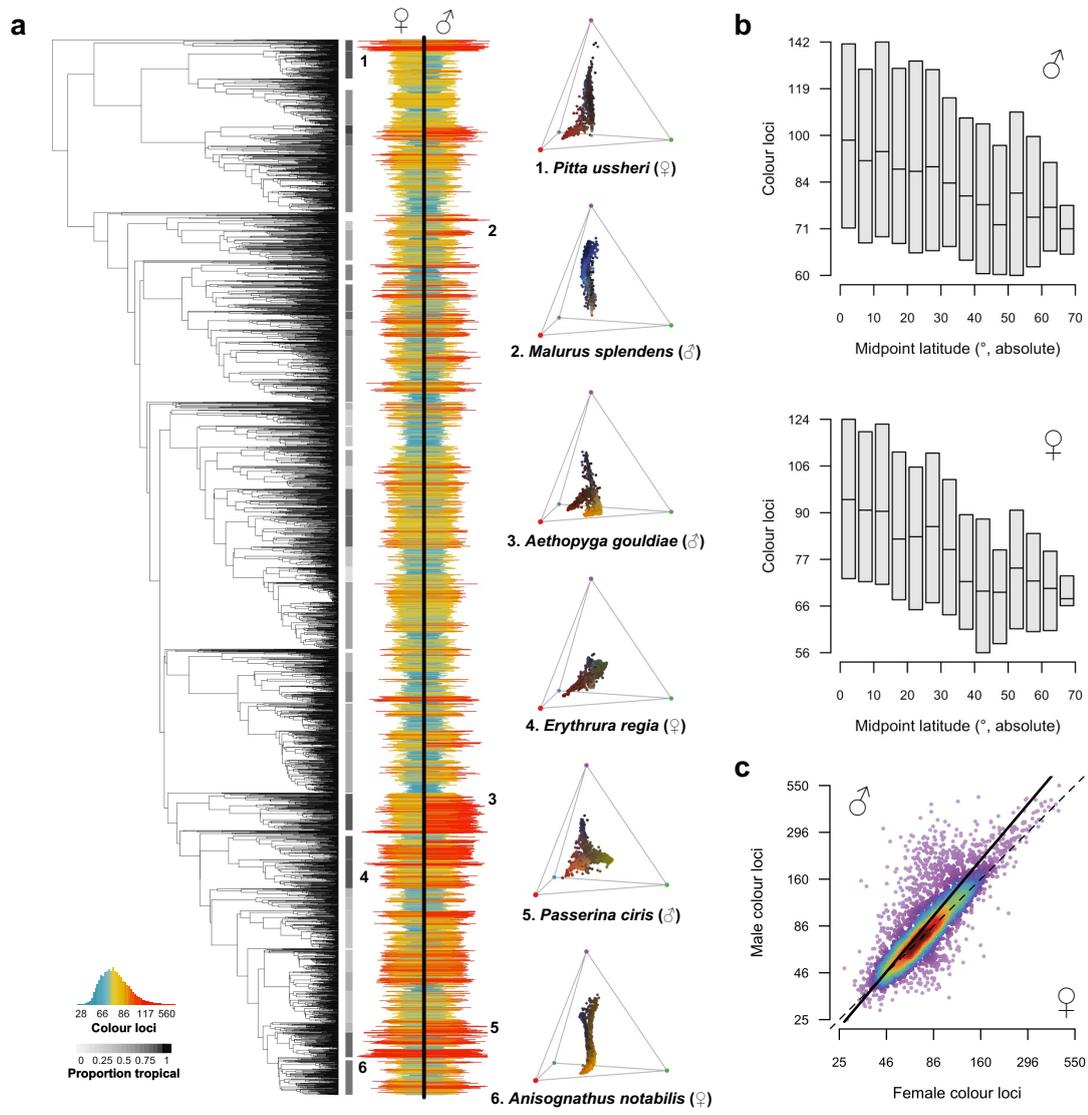759   (2014).

760

a

u

s

l

m

b

Convex hull
volume

Number of
colour loci

c

Tangara chilensis ♀

Knipolegus lophotes ♂

Convex hull = 0.033

Convex hull < 0.001

Colour loci = 422

Colour loci = 32

Figure 1.

Figure 2.

a

♀ ♂

1

2

3

4

5

6

28 66 86 117 560
Colour loci

0 0.25 0.5 0.75 1
Proportion tropical

1. *Pitta ussheri* (♀)

2. *Malurus splendens* (♂)

3. *Aethopyga gouldiae* (♂)

4. *Erythrura regia* (♀)

5. *Passerina ciris* (♂)

6. *Anisognathus notabilis* (♀)

b

♂

142
119
100
84
71
60

Colour loci

0 10 20 30 40 50 60 70
Midpoint latitude (°, absolute)

♀

124
106
90
77
66
56

Colour loci

0 10 20 30 40 50 60 70
Midpoint latitude (°, absolute)

c

♂

550
296
160
86
46
25

Male colour loci

25 46 86 160 296 550
Female colour loci

♀

Figure 3.

Figure 4.

a

b

Oscines

Suboscines

c

1. UV-Vis image acquisition

2. Image segmentation

3. Normalised pixel value extraction

4. Downsampling

5. Mapping to avian colour space

6. Final sample of 500 points

Proportion sampled

0   0.2   0.4   0.6   0.8   1

d

Colour volume (UVS)

42.63

12.26

3.52

1.01

0.29

0.08

Colour loci (UVS)

25   47   87   162   302   563

Extended Data Figure 1.

Extended Data Figure 2.

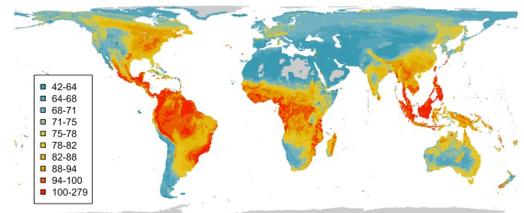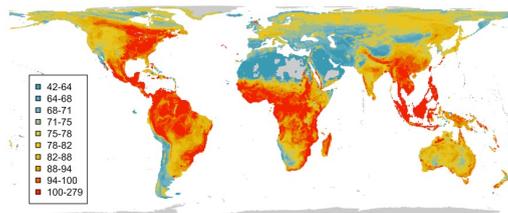**Males**   **Females**
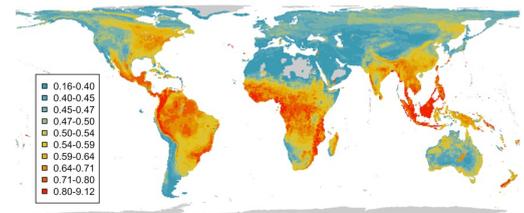
Colour volume
(VS)
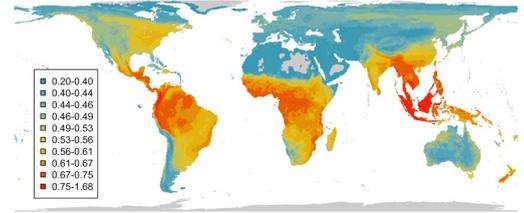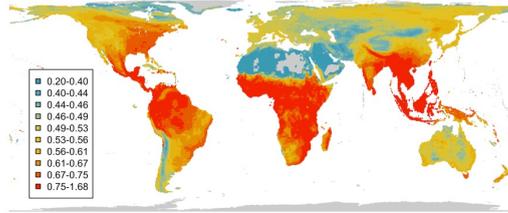
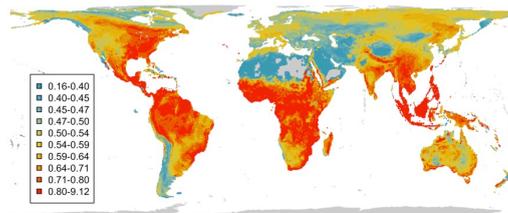
Colour loci
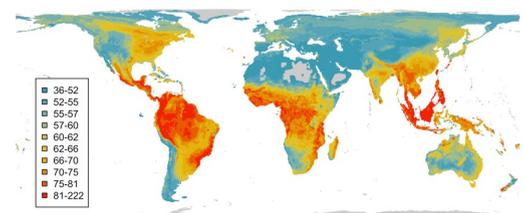(VS)
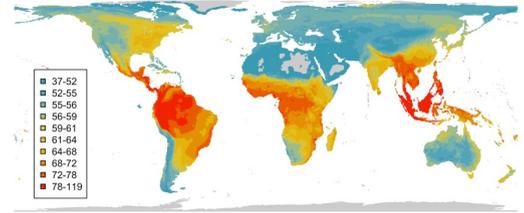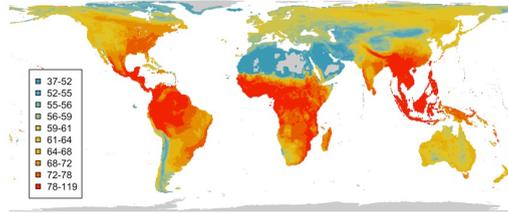
Colour volume
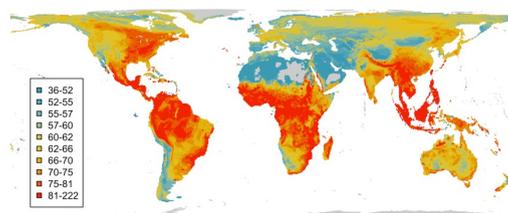(UVS, range weighted)
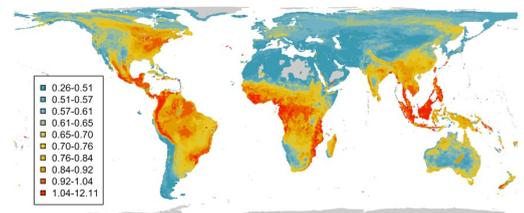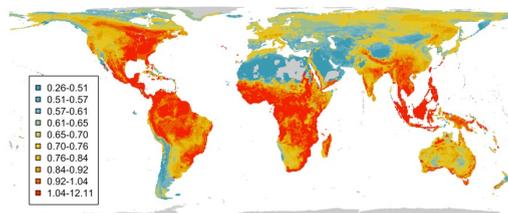
Colour loci
(UVS, range weighted)

Colour volume
(VS, range weighted)

Colour loci
(VS, range weighted)
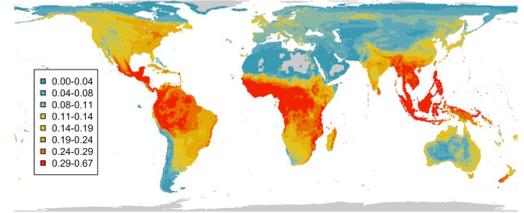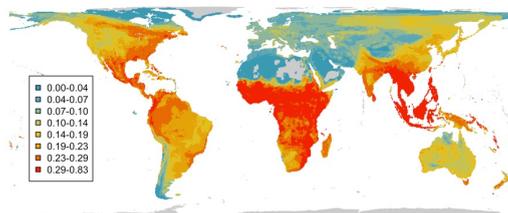

Extended Data Figure 3.

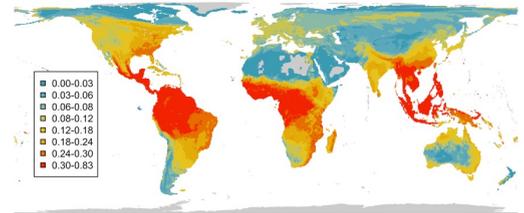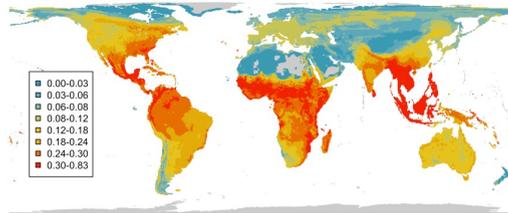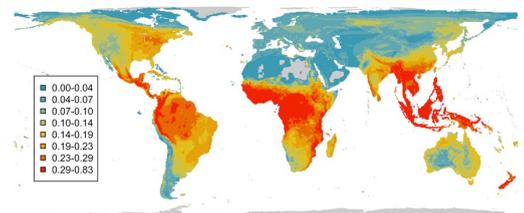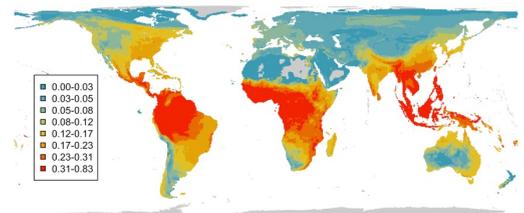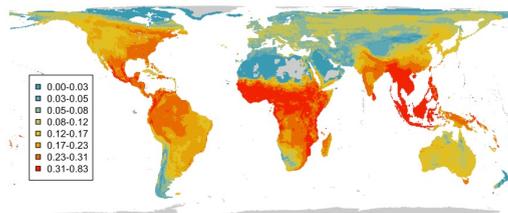**Extended Data Figure 4.**

Supplementary Information:

Latitudinal gradients in avian colourfulness

Authors: Christopher R. Cooney[1]*, Yichen He[1], Zoë K. Varley[1,6], Lara O. Nouri[1], Christopher J. A. Moody[1], Michael D. Jardine[1], András Liker[2,3], Tamás Székely[4,5], Gavin H. Thomas[1,6]

Affiliations:

[1] Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield; Alfred Denny Building, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

[2] MTA-PE Evolutionary Ecology Research Group, University of Pannonia, Veszprém H-8210, Hungary

[3] Behavioral Ecology Research Group, Center for Natural Sciences, University of Pannonia, Veszprém H-8210, Hungary

[4] Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom

[5] *Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen H-4032, Hungary*

[6] Bird Group, Department of Life Sciences, The Natural History Museum at Tring; Akeman Street, Tring, HP23 6AP, UK.

*Corresponding author. Email: c.cooney@sheffield.ac.uk

Study	Taxa	Geographic extent	Colour data	Conclusions	Notes
Adams et al. (2014) [6]	Butterflies (*n* = 247)	New World (Ecuador, Florida, Maine)	Digital photographs of museum specimens (VIS only)	<u>Gradient present</u> – Ecuadorian species more variable in colour intensity, saturation, and hue than species of other regions	Incomplete colour measurements (no UV), limited geographical extent.
Bailey (1978) [7]	Passerine birds (*n* = 784)	North and Central America (Alaska/Canada to Panama)	Human scores of field guide illustrations	<u>No gradient present</u> – Some significant differences between regions but overall weak support for enhanced tropical colorfulness	Qualitative, subjective scores of colourfulness, limited geographic extent
Dale *et al.* (2015) [11]	Passerine birds (*n* = 2,471)	Global	'Maleness' scores based on RGB data for front-facing body regions measured from handbook illustrations	<u>Gradient present</u> – Species with tropical life histories have more elaborate plumages (higher 'maleness' scores)	Incomplete colour measurements (no UV), colour elaboration rather than colourfulness *per se*, composite predictor variable (latitude + clutch size + environmental stability)
Dalrymple *et al.* (2015, 2018) [9, 5]	Birds (*n* = 570), butterflies (*n* = 424), flowers (*n* = 339)	Eastern Australia	Reflectance spectrometry (300-700 nm; birds, flowers) and UV/VIS digital photography (butterflies)	<u>No gradient present</u> – High rather than low latitude regions tend to contain the most colourful species	Limited geographical extent
Dunn et al. (2015) [12]	Birds (*n* = 977)	Global	Reflectance spectrometry (320-700 nm)	<u>Equivocal</u> – In monomorphic species (*n* = 489), subtropical taxa were brighter but tropical taxa were duller than non-tropical taxa	Colour quantified in terms of brightness and hue; colourfulness *per se* not measured
Friedman & Remeš (2017) [10]	Australian passerines (Meliphagidae, *n* = 97; Acanthizidae, *n* = 40)	Australia, New Guinea	Reflectance spectrometry (300-700 nm)	<u>No gradient present</u> – birds living close to the equator were not more colourful	Limited taxonomic and geographic extent
Wilson & Von Neaumann (1972) [8]	Birds (*n* = 1,678)	N and S America, Europe	Binary categorisation of species as 'colourful' or 'not so' based on pictures and written descriptions	<u>Gradient present</u> – Birds of the South American lowland tropics were more frequently colourful than those of South American extra-tropics, North America and Europe	Qualitative, subjective classification of colourfulness based on photos and/or written descriptions, somewhat geographically limited

Supplementary Table 1. Summaries of studies addressing latitudinal gradients in organismal colourfulness. Numbers in square brackets in the 'Study' column indicate the corresponding reference number in the main text.

		Mean colourfulness				SES colourfulness			
Variable	Sex	Slope	P	I	P	Slope	P	I	P
Volume (UVS)	M	-0.462	0	0.047	0.029	-0.231	3.18×10^{-14}	0.032	0.100
	F	-0.472	0	0.061	0.008	-0.226	6.51×10^{-14}	0.050	0.025
Loci (UVS)	M	-0.461	0	0.059	0.010	-0.220	7.51×10^{-14}	0.046	0.035
	F	-0.490	0	0.063	0.007	-0.211	4.02×10^{-14}	0.058	0.012
Volume (VS)	M	-0.438	0	0.043	0.041	-0.217	1.07×10^{-12}	0.030	0.119
	F	-0.517	0	0.054	0.016	-0.237	2.44×10^{-15}	0.048	0.031
Loci (VS)	M	-0.486	0	0.054	0.017	-0.233	3.77×10^{-15}	0.045	0.040
	F	-0.509	0	0.051	0.021	-0.211	5.11×10^{-14}	0.052	0.022
Volume (UVS, RW)	M	-0.383	2.73×10^{-12}	0.042	0.048	-0.260	1.99×10^{-07}	0.026	0.148
	F	-0.437	0	0.061	0.009	-0.319	9.56×10^{-12}	0.048	0.031
Loci (UVS, RW)	M	-0.353	1.52×10^{-11}	0.036	0.077	-0.228	9.82×10^{-07}	0.021	0.200
	F	-0.400	0	0.048	0.031	-0.247	1.70×10^{-09}	0.031	0.109
Volume (VS, RW)	M	-0.410	3.95×10^{-14}	0.041	0.051	-0.275	1.58×10^{-08}	0.026	0.147
	F	-0.464	0	0.056	0.015	-0.333	7.72×10^{-13}	0.047	0.034
Loci (VS, RW)	M	-0.380	2.16×10^{-13}	0.034	0.092	-0.244	1.42×10^{-07}	0.023	0.178
	F	-0.429	0	0.037	0.073	-0.258	2.42×10^{-10}	0.025	0.161
Volume (UVS, PTQ)	M	-0.551	0	0.054	0.017	-0.267	0	0.031	0.108
	F	-0.570	0	0.053	0.015	-0.266	0	0.041	0.054
Loci (UVS, PTQ)	M	-0.647	0	0.066	0.004	-0.275	0	0.036	0.081
	F	-0.662	0	0.055	0.014	-0.267	0	0.058	0.013
Volume (VS, PTQ)	M	-0.650	0	0.062	0.007	-0.314	0	0.030	0.117
	F	-0.582	0	0.068	0.003	-0.290	0	0.056	0.014
Loci (VS, PTQ)	M	-0.666	0	0.054	0.015	-0.292	0	0.033	0.094
	F	-0.711	0	0.061	0.008	-0.298	0	0.065	0.006

Supplementary Table 2. Spatial simultaneous autoregressive (SAR) models for the effect of absolute latitude on male and female colourfulness across terrestrial ecoregions (*n* = 800) using different datasets. Slope refers to the estimated slope of the relationship between colourfulness score (loci or volume) and absolute latitude in each model, with asterisks indicating significant effects (two-sided test, no adjustments for multiple tests). Moran's *I* refers to the global Moran's *I* estimate for each model assessing the presence of residual spatial autocorrelation in the model residuals, with asterisks indicating associated significance level. All variables were standardised (mean = 0, sd = 1) prior to model fitting. SES, standardised effect size; UVS, ultraviolet sensitive; VS, violet sensitive; RW, range weighted; PTQ, proportion of species in the top (25%) colour diversity quartile.

Variable	Sex	Estimate (95% CI)	P_{MCMC}
Volume (UVS)	M	-0.034 (-0.059, -0.008)	0.010
	F	-0.107 (-0.136, -0.078)	3.00×10^{-06}
Loci (UVS)	M	-0.043 (-0.068, -0.017)	9.15×10^{-04}
	F	-0.118 (-0.144, -0.090)	3.00×10^{-06}
Volume (VS)	M	-0.038 (-0.064, -0.012)	0.004
	F	-0.121 (-0.151, -0.092)	3.00×10^{-06}
Loci (VS)	M	-0.049 (-0.075, -0.024)	1.10×10^{-04}
	F	-0.140 (-0.167, -0.113)	3.00×10^{-06}

Supplementary Table 3. Bayesian phylogenetic mixed model results for the effect of absolute latitude on male and female colourfulness across passerine species (n = 4,527). All variables were standardised (mean = 0, sd = 1) prior to model fitting. Tests were two-sided and no adjustments for multiple tests were made. UVS, ultraviolet sensitive; VS, violet sensitive. All models were run over 100 posterior phylogenetic trees.

Variable	Term	Males		Females	
		Estimate (95% CI)	P_{MCMC}	Estimate (95% CI)	P_{MCMC}
Loci (UVS)	(Intercept)	0.140 (-0.691, 0.971)	0.739	0.228 (-0.643, 1.115)	0.609
	Temperature	0.019 (-0.024, 0.061)	0.379	0.046 (-0.001, 0.092)	0.055
	Precipitation	**0.040 (0.005, 0.074)**	**0.022**	**0.065 (0.027, 0.102)**	**0.001**
	Net primary productivity	**0.052 (0.019, 0.085)**	**0.002**	**0.086 (0.049, 0.123)**	**5.00 x 10^{-06}**
	Solar radiation	0.013 (-0.021, 0.046)	0.445	-0.021 (-0.059, 0.016)	0.257
	UV-B radiation	-0.024 (-0.059, 0.011)	0.175	-0.024 (-0.062, 0.015)	0.227
	Body mass	**-0.143 (-0.188, -0.098)**	**2.50 x 10^{-06}**	**-0.123 (-0.172, -0.073)**	**2.50 x 10^{-06}**
	Sexual dichromatism	**0.250 (0.221, 0.279)**	**2.50 x 10^{-06}**	0.005 (-0.027, 0.036)	0.753
	Forest dependency	**0.045 (0.021, 0.070)**	**3.25 x 10^{-04}**	**0.073 (0.046, 0.101)**	**2.50 x 10^{-06}**
	Frugivore-nectarivore	**0.036 (0.006, 0.068)**	**0.021**	**0.041 (0.006, 0.074)**	**0.019**
	Migratory	-0.015 (-0.041, 0.011)	0.272	**-0.040 (-0.069, -0.012)**	**0.006**
	Ground nesting	-0.007 (-0.033, 0.019)	0.592	-0.007 (-0.035, 0.021)	0.642
	Territoriality	0.002 (-0.035, 0.039)	0.932	-0.012 (-0.052, 0.028)	0.572
	Community diversity	**0.087 (0.055, 0.118)**	**2.50 x 10^{-06}**	**0.086 (0.051, 0.121)**	**5.00 x 10^{-06}**
Loci (VS)	(Intercept)	0.159 (-0.666, 0.982)	0.703	0.279 (-0.599, 1.150)	0.527
	Temperature	0.010 (-0.031, 0.053)	0.628	0.045 (-0.004, 0.091)	0.064
	Precipitation	**0.056 (0.021, 0.090)**	**0.001**	**0.089 (0.051, 0.127)**	**5.00 x 10^{-06}**
	Net primary productivity	**0.051 (0.018, 0.085)**	**0.002**	**0.084 (0.047, 0.122)**	**2.50 x 10^{-06}**
	Solar radiation	0.022 (-0.011, 0.056)	0.194	-0.019 (-0.056, 0.019)	0.330
	UV-B radiation	-0.019 (-0.054, 0.015)	0.285	-0.017 (-0.056, 0.022)	0.405
	Body mass	**-0.141 (-0.185, -0.096)**	**2.50 x 10^{-06}**	**-0.123 (-0.171, -0.074)**	**2.50 x 10^{-06}**
	Sexual dichromatism	**0.258 (0.229, 0.287)**	**2.50 x 10^{-06}**	-0.006 (-0.038, 0.026)	0.713
	Forest dependency	**0.040 (0.016, 0.065)**	**0.002**	**0.060 (0.032, 0.087)**	**5.00 x 10^{-06}**
	Frugivore-nectarivore	0.026 (-0.004, 0.057)	0.093	**0.037 (0.003, 0.072)**	**0.032**
	Migratory	-0.009 (-0.035, 0.017)	0.486	**-0.039 (-0.068, -0.010)**	**0.008**
	Ground nesting	-0.006 (-0.032, 0.020)	0.638	-0.004 (-0.033, 0.024)	0.788
	Territoriality	0.003 (-0.034, 0.039)	0.872	0.006 (-0.034, 0.046)	0.756
	Community diversity	**0.086 (0.055, 0.118)**	**2.50 x 10^{-06}**	**0.090 (0.054, 0.125)**	**2.50 x 10^{-06}**

Supplementary Table 4. Bayesian phylogenetic mixed model results for the effect of predictor variables on male and female colour loci scores across passerine species (*n* = 4,415). All variables were standardised (mean = 0, sd = 1) prior to model fitting. Tests were two-sided and no adjustments for multiple tests were made. UVS, ultraviolet sensitive; VS, violet sensitive. All models were run over 100 posterior phylogenetic trees.

Variable	Term	Males Estimate (95% CI)	P_{MCMC}	Females Estimate (95% CI)	P_{MCMC}
Volume (UVS)	(Intercept)	0.181 (-0.576, 0.931)	0.635	0.221 (-0.569, 1.012)	0.581
	Temperature	-0.001 (-0.045, 0.042)	0.951	-0.002 (-0.053, 0.049)	0.948
	Precipitation	**0.054 (0.019, 0.090)**	**0.003**	**0.086 (0.044, 0.127)**	**4.50 x 10^{-06}**
	Net primary productivity	**0.035 (0.000, 0.069)**	**0.048**	**0.068 (0.027, 0.108)**	**0.001**
	Solar radiation	**0.040 (0.005, 0.075)**	**0.023**	0.031 (-0.009, 0.071)	0.139
	UV-B radiation	-0.031 (-0.068, 0.005)	0.092	**-0.045 (-0.087, -0.004)**	**0.035**
	Body mass	**-0.171 (-0.215, -0.127)**	**2.50 x 10^{-06}**	**-0.163 (-0.212, -0.112)**	**2.50 x 10^{-06}**
	Sexual dichromatism	**0.235 (0.206, 0.264)**	**2.50 x 10^{-06}**	**-0.044 (-0.078, -0.011)**	**0.009**
	Forest dependency	**0.034 (0.008, 0.059)**	**0.010**	**0.079 (0.049, 0.108)**	**2.50 x 10^{-06}**
	Frugivore-nectarivore	**0.032 (0.000, 0.063)**	**0.048**	**0.037 (0.000, 0.073)**	**0.045**
	Migratory	-0.010 (-0.037, 0.017)	0.477	**-0.046 (-0.077, -0.014)**	**0.004**
	Ground nesting	-0.002 (-0.028, 0.025)	0.901	0.016 (-0.015, 0.046)	0.318
	Territoriality	0.000 (-0.036, 0.037)	0.985	0.015 (-0.025, 0.056)	0.459
	Community diversity	**0.089 (0.057, 0.122)**	**2.50 x 10^{-06}**	**0.106 (0.069, 0.144)**	**2.50 x 10^{-06}**
Volume (VS)	(Intercept)	0.236 (-0.514, 0.979)	0.531	0.316 (-0.434, 1.059)	0.406
	Temperature	-0.005 (-0.050, 0.039)	0.818	-0.011 (-0.063, 0.041)	0.684
	Precipitation	**0.062 (0.027, 0.099)**	**0.001**	**0.109 (0.067, 0.151)**	**2.50 x 10^{-06}**
	Net primary productivity	**0.035 (0.001, 0.071)**	**0.047**	**0.067 (0.026, 0.108)**	**0.001**
	Solar radiation	**0.042 (0.006, 0.077)**	**0.021**	0.035 (-0.005, 0.078)	0.097
	UV-B radiation	-0.026 (-0.063, 0.011)	0.167	-0.038 (-0.081, 0.005)	0.085
	Body mass	**-0.175 (-0.219, -0.130)**	**2.50 x 10^{-06}**	**-0.170 (-0.219, -0.120)**	**2.50 x 10^{-06}**
	Sexual dichromatism	**0.233 (0.203, 0.262)**	**2.50 x 10^{-06}**	**-0.050 (-0.084, -0.017)**	**0.003**
	Forest dependency	**0.030 (0.004, 0.056)**	**0.021**	**0.066 (0.035, 0.096)**	**1.50 x 10^{-06}**
	Frugivore-nectarivore	0.017 (-0.015, 0.049)	0.310	0.031 (-0.005, 0.069)	0.094
	Migratory	-0.003 (-0.030, 0.024)	0.826	**-0.043 (-0.075, -0.012)**	**0.008**
	Ground nesting	0.003 (-0.025, 0.029)	0.848	0.019 (-0.013, 0.050)	0.240
	Territoriality	-0.001 (-0.037, 0.035)	0.949	0.021 (-0.019, 0.062)	0.303
	Community diversity	**0.090 (0.057, 0.123)**	**2.50 x 10^{-06}**	**0.110 (0.072, 0.148)**	**2.50 x 10^{-06}**

Supplementary Table 5. Bayesian phylogenetic mixed model results for the effect of predictor variables on male and female colour volume scores across passerine species (*n* = 4,415). All variables were standardised (mean = 0, sd = 1) prior to model fitting. Tests were two-sided and no adjustments for multiple tests were made. UVS, ultraviolet sensitive; VS, violet sensitive. All models were run over 100 posterior phylogenetic trees.

Variable	Term[a]	Estimate (95% CI)	P_{MCMC}
Volume (UVS)	Absolute latitude	-0.059 (-0.082, -0.036)	3.00×10^{-06}
	Sex	-0.111 (-0.123, -0.100)	3.00×10^{-06}
	Absolute latitude x Sex	-0.003 (-0.015, 0.009)	0.606
Loci (UVS)	Absolute latitude	-0.066 (-0.090, -0.042)	3.00×10^{-06}
	Sex	-0.094 (-0.103, -0.084)	3.00×10^{-06}
	Absolute latitude x Sex	-0.018 (-0.027, -0.008)	3.25×10^{-04}
Volume (VS)	Absolute latitude	-0.069 (-0.092, -0.045)	3.00×10^{-06}
	Sex	-0.112 (-0.124, -0.099)	3.00×10^{-06}
	Absolute latitude x Sex	-0.004 (-0.017, 0.008)	0.488
Loci (VS)	Absolute latitude	-0.081 (-0.104, -0.058)	3.00×10^{-06}
	Sex	-0.099 (-0.110, -0.089)	3.00×10^{-06}
	Absolute latitude x Sex	-0.081 (-0.028, -0.008)	4.30×10^{-04}

Supplementary Table 6. Bayesian phylogenetic mixed model results for the effects of absolute latitude and sex on male and female colourfulness across passerine species (*n* = 4,527). All variables were standardised (mean = 0, sd = 1) prior to model fitting. Tests were two-sided and no adjustments for multiple tests were made. UVS, ultraviolet sensitive; VS, violet sensitive. All models were run over 100 posterior phylogenetic trees. [a], For Sex, 'Male' is the reference category.

Variable	Term	Males		Females	
		Estimate (95% CI)	P_{MCMC}	Estimate (95% CI)	P_{MCMC}
Loci (UVS)	(Intercept)	-0.119 (-0.765, 0.556)	0.715	-0.201 (-0.890, 0.488)	0.554
	Temperature	0.036 (-0.204, 0.279)	0.769	0.141 (-0.126, 0.407)	0.302
	Precipitation	-0.090 (-0.237, 0.056)	0.228	-0.024 (-0.186, 0.139)	0.770
	Net primary productivity	0.133 (-0.009, 0.275)	0.066	0.118 (-0.041, 0.277)	0.146
	Solar radiation	-0.003 (-0.194, 0.186)	0.971	-0.140 (-0.352, 0.069)	0.191
	UV-B radiation	0.088 (-0.145, 0.316)	0.455	0.055 (-0.203, 0.310)	0.671
	Body mass	**-0.226 (-0.329, -0.124)**	**1.00×10^{-05}**	**-0.203 (-0.314, -0.092)**	**4.65×10^{-04}**
	Sexual dichromatism	**0.327 (0.248, 0.405)**	**2.50×10^{-06}**	0.006 (-0.079, 0.091)	0.891
	Social mating system	-0.028 (-0.111, 0.055)	0.504	-0.022 (-0.112, 0.070)	0.640
	Forest dependency	**0.083 (0.012, 0.155)**	**0.023**	**0.121 (0.042, 0.200)**	**0.003**
	Frugivore-nectarivore	0.053 (-0.027, 0.132)	0.193	0.061 (-0.026, 0.148)	0.165
	Migratory	0.021 (-0.067, 0.110)	0.644	-0.055 (-0.153, 0.042)	0.268
	Ground nesting	-0.004 (-0.071, 0.065)	0.920	0.003 (-0.071, 0.078)	0.946
	Territoriality	**-0.096 (-0.177, -0.013)**	**0.022**	-0.036 (-0.125, 0.055)	0.437
	Community diversity	0.080 (-0.022, 0.185)	0.126	**0.116 (0.000, 0.230)**	**0.048**
Volume (UVS)	(Intercept)	-0.164 (-0.787, 0.473)	0.603	-0.303 (-0.951, 0.345)	0.347
	Temperature	0.082 (-0.152, 0.315)	0.492	0.141 (-0.129, 0.418)	0.312
	Precipitation	-0.092 (-0.232, 0.049)	0.201	-0.096 (-0.261, 0.071)	0.254
	Net primary productivity	**0.146 (0.010, 0.283)**	**0.035**	**0.171 (0.009, 0.332)**	**0.039**
	Solar radiation	0.059 (-0.125, 0.242)	0.529	-0.062 (-0.277, 0.155)	0.578
	UV-B radiation	-0.026 (-0.249, 0.196)	0.819	-0.035 (-0.302, 0.226)	0.796
	Body mass	**-0.247 (-0.345, -0.148)**	**2.50×10^{-06}**	-0.220 (-0.331, -0.110)	**1.45×10^{-04}**
	Sexual dichromatism	**0.288 (0.211, 0.363)**	**2.50×10^{-06}**	-0.057 (-0.144, 0.030)	0.194
	Social mating system	0.041 (-0.039, 0.120)	0.316	-0.022 (-0.113, 0.071)	0.644
	Forest dependency	0.053 (-0.017, 0.121)	0.134	**0.091 (0.009, 0.170)**	**0.027**
	Frugivore-nectarivore	0.059 (-0.018, 0.136)	0.132	0.082 (-0.007, 0.168)	0.068
	Migratory	0.004 (-0.081, 0.090)	0.933	-0.072 (-0.172, 0.028)	0.157
	Ground nesting	0.005 (-0.060, 0.071)	0.875	0.007 (-0.069, 0.084)	0.868
	Territoriality	**-0.116 (-0.195, -0.037)**	**0.004**	-0.038 (-0.130, 0.053)	0.415
	Community diversity	0.096 (-0.002, 0.196)	0.057	**0.145 (0.027, 0.262)**	**0.016**

Supplementary Table 7. Bayesian phylogenetic mixed model results for the effect of predictor variables on male and female colour loci scores across passerine species (*n* = 608), including the effect of social mating system. All variables were standardised (mean = 0, sd = 1) prior to model fitting. Tests were two-sided and no adjustments for multiple tests were made. UVS, ultraviolet sensitive; VS, violet sensitive. All models were run over 100 posterior phylogenetic trees.