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35 **Abstract**

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

49 **Main text**

50 **Introduction**

51 Is life generally more colourful in the tropics? The possible existence of global-scale
52 trends in organismal colourfulness was suggested by 19th century European naturalists
53 such as von Humboldt, Darwin and Wallace, who upon being afforded the opportunity to
54 travel extensively in the tropics, remarked on the 'rich variety' and 'mixtures of colors' they
55 encountered during their travels¹⁻³. Since then, a variety of explanations focused on
56 latitude-associated gradients in biotic and abiotic factors have been proposed to account
57 for the assumed increases in tropical species' colourfulness, including positive effects of
58 more benign climatic conditions and particular ecological strategies that are more
59 prevalent at low latitudes^{2,4-8}. However, in the centuries following these early anecdotal
60 observations, biologists have struggled to conclusively test for the existence of global-
61 scale latitudinal gradients in species colourfulness, calling into question whether this long-
62 assumed biogeographic 'rule' really exists at all^{5,7,9,10}.

63 Part of the challenge in resolving this controversy revolves around the difficulty of
64 obtaining accurate, meaningful measurements of organismal colouration, and doing so
65 on a scale that permits a global-scale test of these ideas. Due to practical constraints,
66 previous studies have often addressed this question using subjective and/or incomplete
67 measures of colourfulness (e.g. human scoring) or by studying radiations of species that
68 span only a limited fraction of the Earth's latitudinal gradient⁵⁻¹² (see Supplementary Table
69 1). While some of these studies have found patterns consistent with a latitudinal
70 colourfulness gradient in birds and other taxa, other studies have found no such effect,
71 and controversy over the existence of this gradient remains. Fortunately, recent advances
72 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.

75 **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 birds¹³.

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 pattern¹⁴. 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 space¹⁴. 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 hue¹² 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 loci¹⁶. 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

113 **Testing for latitudinal colourfulness gradients.** We separately mapped mean male
114 and mean female colourfulness scores for grid cell assemblages and find evidence for a
115 strong latitudinal gradient in species' colourfulness in passerine birds (Fig. 2). Analysis of
116 per-cell mean species' colour loci values revealed a pronounced tropical peak in species'
117 colourfulness with respect to latitude that was evident for both male and female birds (Fig.
118 2a,b). For example, mean male and mean female colour loci scores for species in tropical
119 cell assemblages are 92 and 86, respectively (<23.5°; n = 16,997 cells), compared to
120 corresponding values of 76 and 70 for high-latitude assemblages (>45°; n = 22,412 cells).
121 Similar patterns were evident when using colour volume scores (Extended Data Fig. 2)
122 and when cell averages are calculated by downweighting the influence of geographically
123 widespread species (Extended Data Fig. 3; for methods see 'Statistical analyses'). To
124 formally test the relationship between latitudinal position and species' colourfulness while
125 minimising the impact of spatial autocorrelation, we calculated mean colourfulness scores
126 across species present in unique terrestrial ecoregions¹⁷ rather than individual grid cells
127 (Fig. 2c) and used spatial simultaneous autoregressive (SAR) models with absolute
128 ecoregion latitude as a predictor¹⁸. Regardless of how ecoregion colourfulness averages
129 are calculated (see Methods), all models had a highly significant effect of latitude on both
130 male and female colourfulness ($P < 0.001$ in all cases; Supplementary Table 2)
131 corresponding to steep declines in the average colourfulness of species within ecoregions
132 moving from the equator towards the poles (Fig. 2c and Extended Data Fig. 2c).

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

145 To corroborate our grid cell-based results, we also tested the relationship between
146 species' colourfulness and midpoint latitude using species-level phylogenetic
147 comparative analyses (see Methods). Consistent with our previous findings, equatorial-
148 zone species (midpoint latitude <23.5°) are generally characterised by higher
149 colourfulness scores than extra-tropical species (Fig. 3a) and as expected, there is a
150 strong relationship between midpoint latitude and colourfulness across species for both
151 sexes (Fig. 3b,c). However, an important consideration is that both midpoint latitude and
152 the degree of male and female colourfulness exhibit considerable phylogenetic
153 conservatism, with mean phylogenetic heritability¹⁹ 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 time². 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 zone¹⁻³. 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 systems²⁵. 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 models²⁶ 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

195 cases; for correlation coefficients see Fig. 4), indicating that they indeed represent viable
196 explanations for the observed latitudinal gradients. The only exceptions to this were
197 species' mean body mass ($P = 0.535$) and degree of sexual dichromatism ($P = 0.802$) –
198 the latter representing a useful proxy for sexual selection acting on visual signalling
199 traits^{27,28}.

200 We find that species' colourfulness is significantly predicted by several factors (Fig. 4 and
201 Supplementary Tables 4 and 5). Across all analyses, the strongest correlate of
202 colourfulness we identified is sexual dichromatism: males of highly dichromatic species
203 are far more colourful on average than males of less dichromatic species. This supports
204 the view that bright male colouration often evolves in response to increases in sexual
205 selection intensity^{12,29}. The lack of a similar, or negative, effect in females also implies
206 that dichromatism primarily indexes the intensity of sexual selection acting on males³⁰
207 and that variation in female colourfulness across species cannot be explained simply as
208 a correlated response of selection acting on males^{12,31}.

209 In addition to dichromatism, we also find a strong negative effect of body mass on
210 colourfulness in both sexes, with larger birds being less colourful than smaller birds. Body
211 size has been proposed as an important constraint for the evolution of colourful plumage,
212 due to physiological limits on both the relative number of body feathers and circulating
213 carotenoid levels in larger birds³². This hypothesis has received little prior support,
214 particularly considering that other broad-scale bird studies have found positive rather than
215 negative effects of body size on axes of plumage colour elaboration^{11,12}. However, these
216 results are difficult to compare due to differences in the taxonomic scope and metrics of
217 colouration used among studies (see Supplementary Table 1). Here, focusing only on
218 passerines and using colourfulness metrics that are closely aligned with the concept of
219 'plumage colour heterogeneity' forming the basis of the original hypothesis³², we find a
220 strong inverse relationship between body size and colourfulness across species. This
221 relationship is therefore consistent with large birds experiencing greater physiological
222 constraints on colourfulness than smaller birds³², but could also be explained by size-
223 related differences in visual communication requirements, if individuals of smaller species
224 tend to interact at closer viewing distances and in denser habitats than larger species³³.
225 Nonetheless, our results argue against the idea that increased predation risks associated
226 with being small strongly constrain the evolution of plumage colourfulness¹¹.

227 While these associations provide insight in the factors contributing to variation in
228 passerine colourfulness (i.e. Fig 3a), they are unable to account for a tropical
229 colourfulness peak as neither dichromatism nor body mass is correlated with latitude.
230 However, our analyses also identified significant effects of several latitude-related climatic
231 and ecological variables that evidently contribute to generating latitudinal gradients in
232 passerine colourfulness (Fig. 4 and Supplementary Tables 4 and 5). First, it has long
233 been suggested that more benign environmental conditions promote elevated
234 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 deserts². 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 findings³⁶ (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 pressure²⁴ and the intensity of social selection³¹, 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**

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

285 **Digital photography.** Whole-specimen plumage colouration was measured using
286 calibrated ultraviolet (UV) and visible (Vis) light photography²⁷. To do this we used a
287 modified Nikon D7000 digital single-lens reflex camera with a Nikon 105mm f/4.5 UV
288 Nikkor lens combined with two Baader photographic lens filters: one permitting human
289 visible wavelengths (400–680 nm; Baader UV/IR Cut filter / L filter) and another permitting
290 UV wavelengths (320–380 nm; Baader U-Venus-Filter). Specimens were illuminated
291 using two Broncolor Pulso G 1600 J lamps (with UV filters removed) connected to a
292 single Broncolor Scoro 1600 S Power Pack. The same camera settings were used for all
293 photographs (1/250 sec, f/16.0, ISO 100, ‘Daylight’ white balance, RAW photo format),
294 with the exception that a higher ISO sensitivity (2000) was used for UV images to achieve
295 correct exposure. Each image also contained five Labsphere Spectralon Diffuse
296 Reflectance standards of known relative reflectance (2%, 40%, 60%, 80% and 99%). All
297 specimens were photographed through each filter (UV, Vis) from three different angles
298 (dorsal, lateral, ventral), resulting in six images per specimen. Therefore our digital
299 photography dataset consisted of 6 x 24,345 = 146,070 images.

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

305 We used DeepLabv3+, which is a deep convolutional neural network architecture based
306 on fully convolutional networks⁴⁰, to build a pixel-wise semantic segmentation network
307 capable of accurately identifying specimen pixels in each of our images. DeepLabv3+ has
308 been shown to outperform both classical computer vision techniques (e.g. thresholding)
309 and other neural network architectures for semantic segmentation on benchmark tasks⁴⁰.
310 It has also previously been shown to perform well when applied to a similar task as ours,
311 involving the segmentation of biological specimens from photographic images of
312 herbarium specimens⁴¹.

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

323 We used this 5,094-image dataset to train and validate the network and then to generate
324 specimen segmentation predictions for each of the >140,000 images in our dataset³⁹,
325 which took ~72 hours to complete on a desktop computer. Finally, each of the resulting
326 image masks was individually checked by eye and manually refined where necessary
327 using bespoke software (<https://github.com/EchanHe/PhenoLearn>).

328 **Image processing.** All raw (.NEF) images of specimens were linearised and exported as
329 linear TIFF files using DCRAW (<https://www.dechifro.org/dcrawl/>). Pixel values were then
330 normalised using mean pixel intensity values from the five grey standards included in
331 each image in order to control for variation in lighting conditions, following established
332 approaches^{27,42}. Finally, the image was segmented using the image masks described
333 above to leave only pixel values corresponding to the specimen in each image. As
334 individual pixel measurements can be noisy—and because different specimens were
335 represented by different numbers of pixels in our raw dataset—we downsampled each
336 specimen image to a comparable resolution (see Extended Data Fig. 1c), prior to
337 calculating cone catch values and colourfulness metrics (see below). To do this, we
338 treated each specimen image as a raster and, using the aggregate() function in the R
339 package raster (version 3.4-5), we found the smallest aggregation factor in the range 100
340 to 1 that resulted in at least 500 aggregated cells (pixels) being returned, with aggregated
341 cell values calculated as the mean of relevant neighbouring values. We then randomly
342 sampled 500 measurements from this aggregated dataset to represent the plumage
343 colouration of that specimen view in all further analyses. Samples from the each of the
344 three specimen views (dorsal, lateral, ventral) were pooled to give a final set of 1,500
345 whole-body plumage colour measurements per specimen.

346 As well as helping to reduce the impact of measurement noise on our colour
347 measurements, another benefit of this procedure of downsampling each image to a
348 comparable resolution is that it ensures that a comparable proportion of the surface of
349 each specimen view is sampled when taking a sample of a set number of measurements.
350 For example, taking a random sample of 500 pixels from raw specimen datasets
351 represented by 1,000 and 5,000 pixel values, respectively, would result in 50% coverage
352 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 methods⁴² 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 range⁴². 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 previously²⁷. 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 measurements²⁷.

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 problematic⁴⁵, 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 colourfulness¹⁴ (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 values¹⁴ and can generate overinflated
396 volume estimates when highly disparate colours are separated by large areas of
397 unoccupied colour space⁴⁶. Therefore we also employed a second metric of colour space
398 occupation that is less sensitive to these issues. This approach¹⁶ 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 occupied¹⁶, 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 log₁₀-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).

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

435 Global spatial information on temperature, precipitation, solar radiation, ultraviolet-B (UV-
436 B) radiation and net primary productivity (NPP) were extracted from various sources and
437 then reprojected and resampled to match the resolution of our range dataset. Annual
438 mean temperature (bio1) and annual precipitation (bio12) data were downloaded from the
439 WorldClim (version 2.1) database⁴⁸ (<https://worldclim.org/>) at 2.5 arc-minute resolution.
440 Monthly information on solar radiation was downloaded at 30 arc-second resolution and
441 monthly totals were summed to give a measure of total annual solar radiation. Information
442 on annual mean UV-B radiation was extracted from Beckmann *et al.*⁴⁹ at 15 arc-minute
443 resolution. Information on NPP at 1 km was extracted from datasets produced by Running
444 *et al.*⁵⁰. In all cases, species' values represent averages across their geographic range.

445 Information on species-level ecological and behavioural traits were extracted from several
446 sources, specifically BirdLife International's Data Zone (<http://www.datazone.birdlife.org>)
447 (forest dependency) and Tobias and Pigot⁵¹ (foraging niche, migration, nest placement,
448 territoriality, body mass). To reduce the complexity of the categorical variables included
449 in these datasets, and to facilitate effect size comparison in our multipredictor models, we
450 re-coded variation in forest dependency, foraging niche, migration, nest placement, and
451 territoriality as binary variables that aligned with our hypotheses (see main text).
452 Specifically, species were coded as forest dependent ('low', 'medium' or 'high'
453 dependency) or not ('does not usually occur in forest'), frugivorous/nectarivorous or not
454 (all other dietary niches), migratory ('migratory' or 'partially migratory') or not ('sedentary'),
455 ground nesting ('exposed ground') or not ('cavity' or 'exposed elevated'), and territorial
456 ('strong' or 'weak') or not ('none'). Sexual dichromatism was scored from handbook plates
457 as the mean value of plumage dimorphism estimated from five body regions (head, back,
458 belly, wings and tail) using the following scheme: -2, the female was substantially brighter
459 and/or more patterned than the male; -1, the female was brighter and/or more patterned
460 than the male; 0, there was no sex difference in the body region or there was a difference
461 but neither could be considered brighter than the other; 1, the male was brighter and/or
462 more patterned than the female; 2, the male was substantially brighter and/or more
463 patterned than the female. Thus these scores are independent of the data used in this
464 study to quantify colourfulness and positive values represent male-biased ornamentation,
465 zero represent unbiased ornamentation, and negative values represent female-biased
466 ornamentation. To assess the effect of variation in community diversity on species'
467 colourfulness, we generated a variable capturing the average richness of passerine
468 species co-occurring with each species in our dataset. To do this we used range data for
469 all passerine species (i.e. not just those sampled in our dataset) to calculate for each grid
470 cell the number of co-occurring passerine species. We then calculated the mean value of
471 this variable across species' geographic ranges to provide a measure of average
472 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 ecoregions¹⁸. We therefore calculated mean colourfulness
510 scores for all cells within terrestrial ecoregions of the world¹⁷ 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

513 simultaneous autoregressive error (SAR) models implemented using the function
514 `spautolm()` in the R package `spdep` (version 1.1-5). For these models, neighbours were
515 defined as those ecoregions with contiguous boundaries and we then selected the
516 appropriate weighting style using Akaike information criterion (AIC) model selection
517 based on code provided by Rabosky *et al.*¹⁸. We used Moran's *I* to test for spatial
518 autocorrelation in the residuals of SAR regressions to determine the extent to which SAR
519 models successfully accounted for spatial non-independence in the data. These results
520 showed that all models retained some evidence of residual spatial autocorrelation, but to
521 lesser degree in models based on richness-corrected ecoregion colourfulness scores
522 (see below) than raw ecoregion scores (Supplementary Table 1).

523 An important consideration when analysing aggregated species-level variables in a
524 spatial context is that underlying species richness gradients can generate strong spatial
525 patterns in aggregated data⁵³. To address the extent to which the latitudinal colourfulness
526 gradients we observe in our spatial analyses are independent of underlying species
527 richness differences, we used a randomisation approach to calculate colourfulness
528 standardised effect size (SES) values for each ecoregion, which corrects for the effect of
529 species richness differences on aggregated trait scores⁵³. To do this we generated 200
530 null communities for each ecoregion by randomising species' colourfulness scores with
531 respect to species' identity across our dataset. These null communities were then used
532 to generate a null distribution of mean colourfulness scores for each ecoregion, against
533 which observed colourfulness scores were compared. The resulting SES scores, in which
534 the effects of species richness on mean colourfulness values have been factored out,
535 were then analysed using the same SAR modelling approach described above.

536 *Species-level analyses.* To test the relationship between species' absolute midpoint
537 latitude and colourfulness, and between species' colourfulness scores and variation in
538 the 13 predictor variables described above, we used multi-predictor Bayesian
539 phylogenetic mixed models implemented in the R package `MCMCglmm` (version
540 2.32)^{26,54}. All models included a phylogenetic random effects term and were run over a
541 posterior distribution of 100 trees to incorporate phylogenetic uncertainty and posterior
542 distributions of parameter estimates associated with different trees were pooled to give
543 model estimates that incorporate phylogenetic error⁵⁵. In all cases, models were run for
544 55,000 iterations (sampled every 25th iteration) with a 5,000 iteration burn-in, and we used
545 standard non-informative priors [i.e. `list(R=list(V=1, nu=0.002), G=list(G1=list(V=1,
546 nu=0.002)))`]. All variables were standardised (mean = 0, standard deviation = 1) prior to
547 model fitting to facilitate effect size comparison. Before running models we also checked
548 for evidence of multi-collinearity among predictors in our multi-predictor models using
549 variance inflation factors (VIFs) and found no evidence of severe (VIF > 10) or even
550 moderate (VIF > 4) multi-collinearity in our models (median VIF = 1.60; range = 1.05 –
551 3.89).

552 Finally, phylogenetic heritability (H^2) values¹⁹ 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).

557 **Data availability:** All analysis data is available in Supplementary Data 1.xlsx. In addition,
558 phylogenetic trees were downloaded from <http://www.birdtree.org>, geographic and
559 ecological data were accessed via BirdLife International's Data Zone
560 (<http://www.datazone.birdlife.org>), and global climate data were downloaded from
561 WorldClim (<https://worldclim.org/>).

562

563 **Code availability:** R code is available at [https://github.com/christophercooney/Avian-](https://github.com/christophercooney/Avian-colourfulness)
564 [colourfulness](https://github.com/christophercooney/Avian-colourfulness).

565

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581 the analyses. C.R.C. wrote the manuscript, with input from all authors.

582

583 **Competing interests statement:** The authors have no competing interests.

584

Figure Legends

585

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.

599

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.

606

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.

618

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

623

624 black outlines and asterisks indicating evidence for a non-zero effect of the relevant
625 variable. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values in parentheses next to each
626 predictor give the correlation coefficient (Spearman's ρ) for the relationship between
627 each predictor and species' absolute midpoint latitude. Results shown are for colour loci
628 scores calculated assuming an ultraviolet-sensitive (UVS) visual system. In all cases, $n =$
629 4,415 species. Full statistical results can be found in Supplementary Table 4.

630

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632

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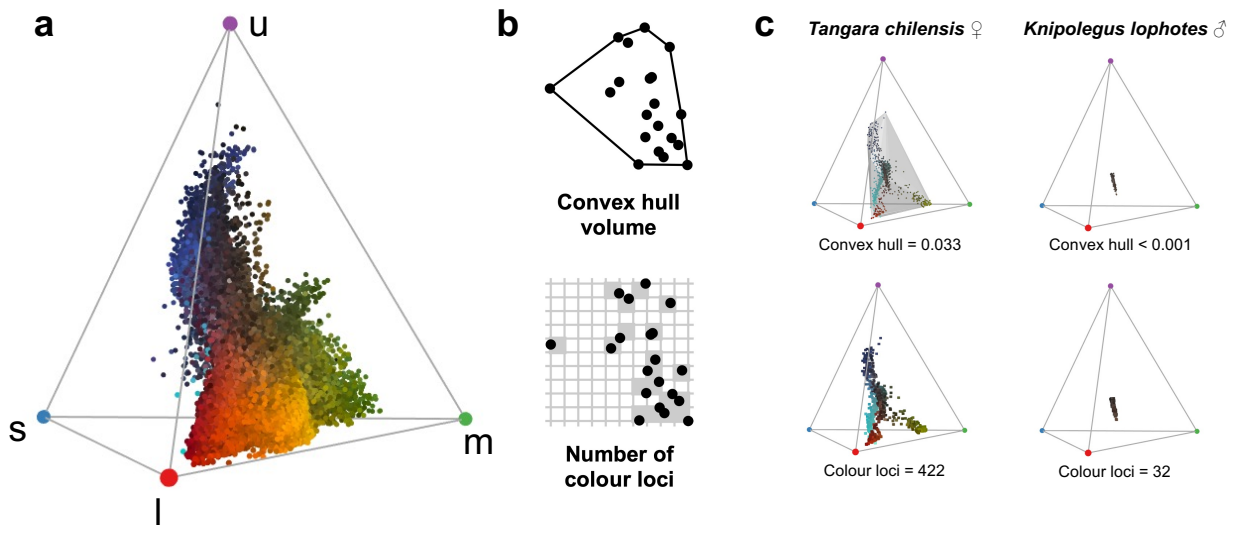


Figure 1.

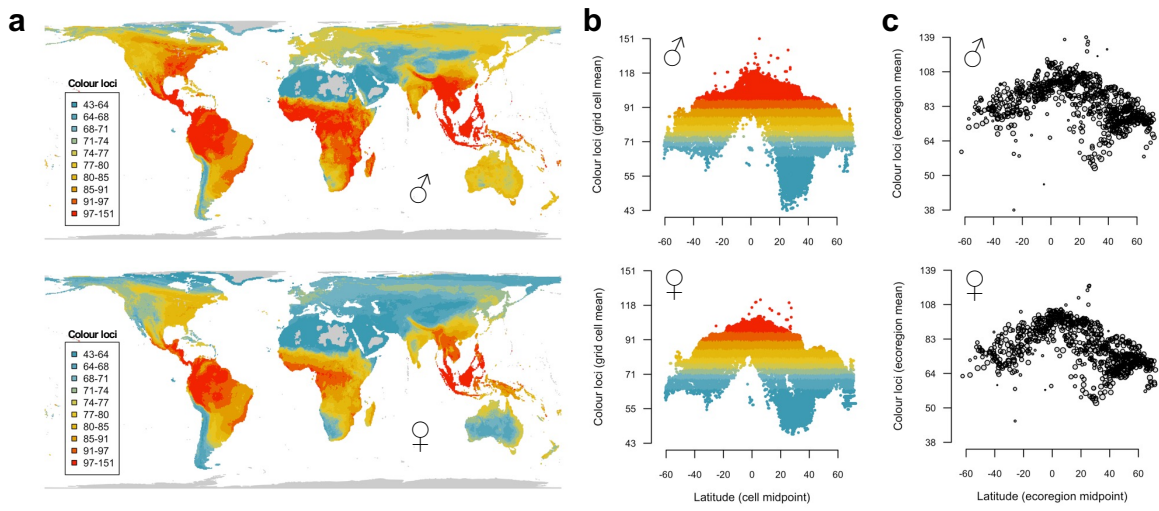


Figure 2.

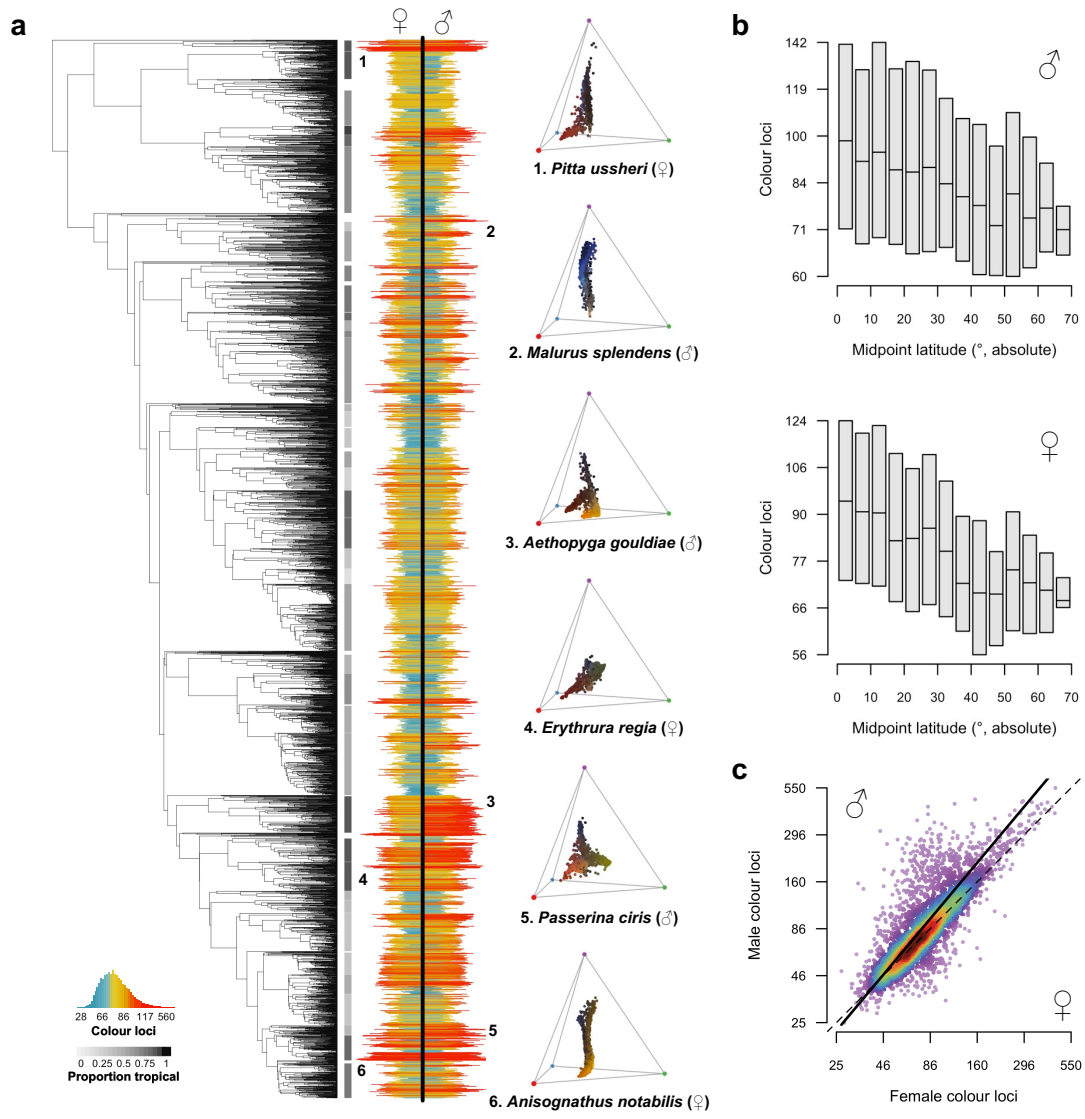


Figure 3.

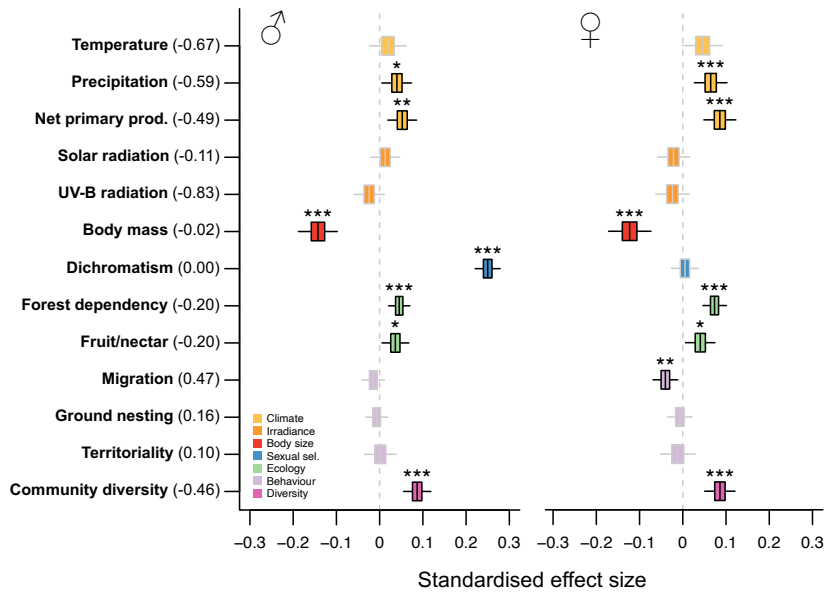
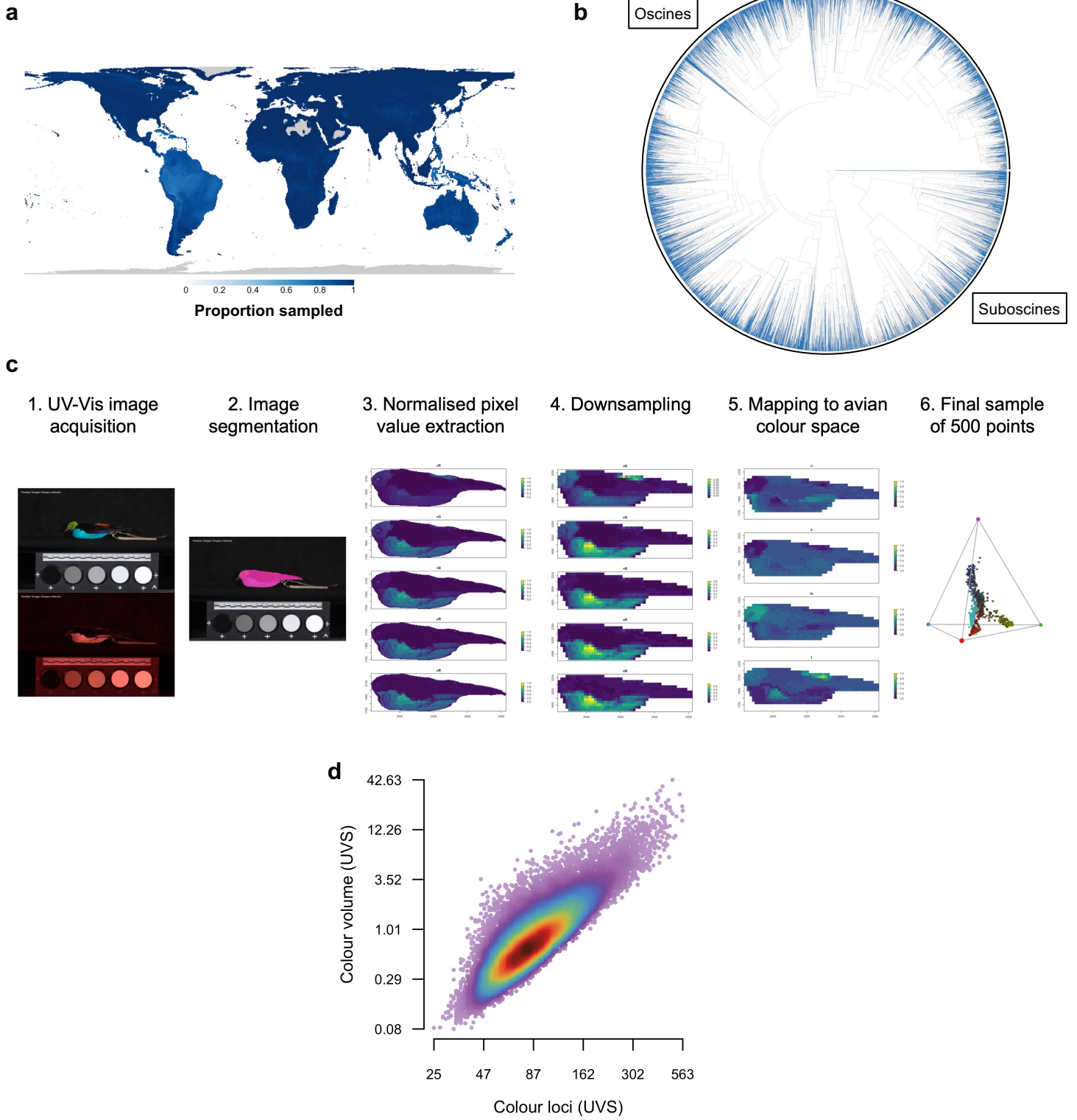
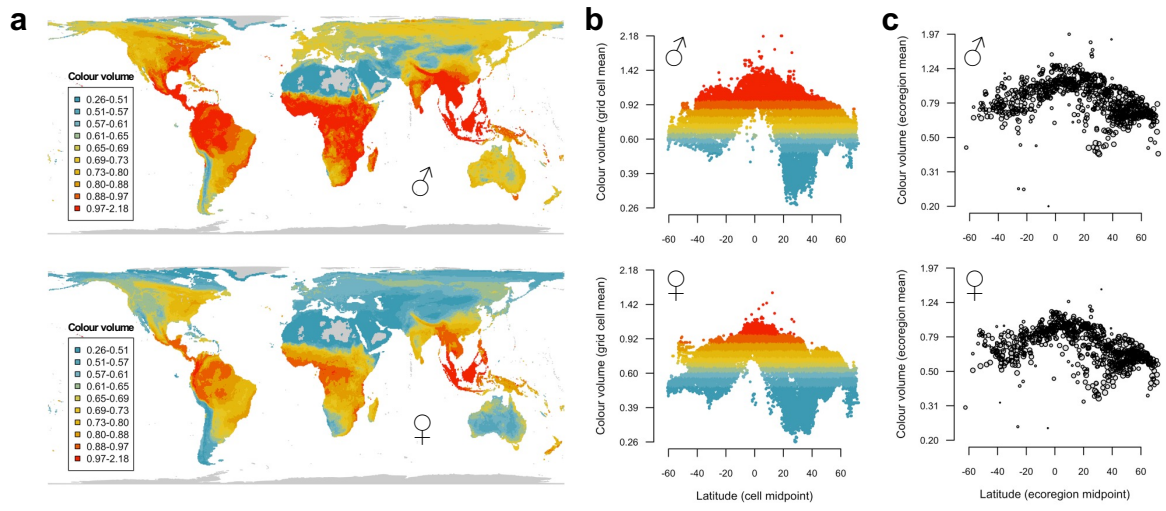


Figure 4.



Extended Data Figure 1.

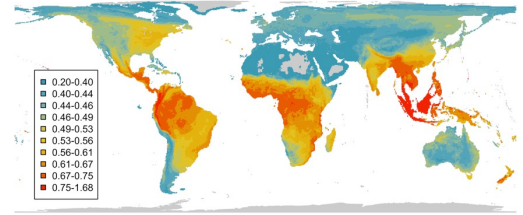
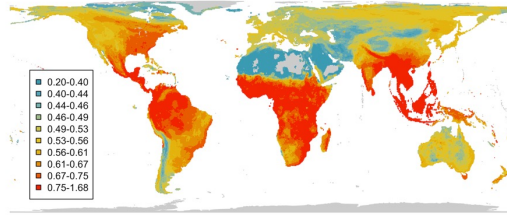


Extended Data Figure 2.

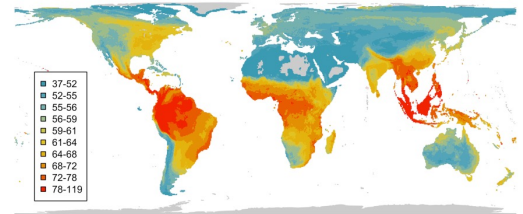
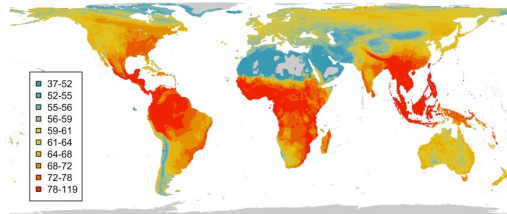
Males

Females

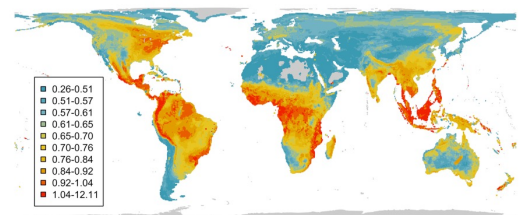
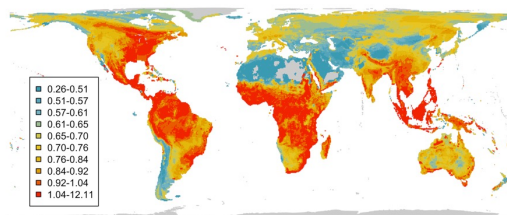
Colour volume
(VS)



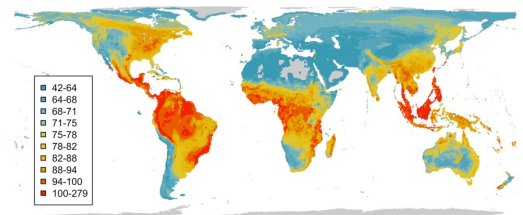
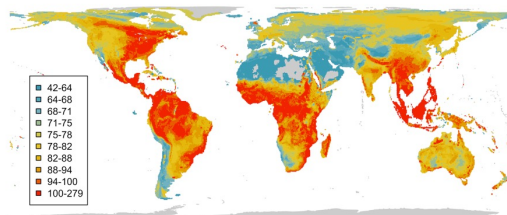
Colour loci
(VS)



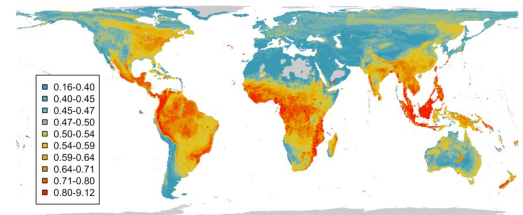
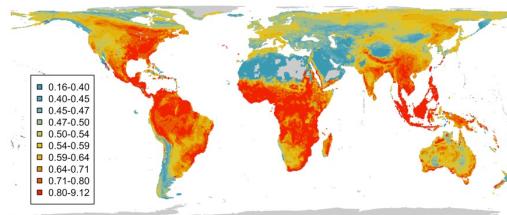
Colour volume
(UVS, range weighted)



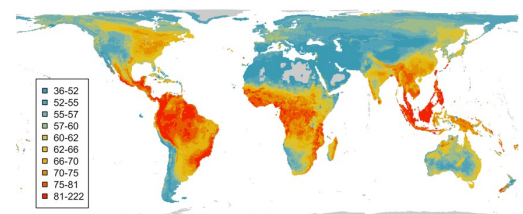
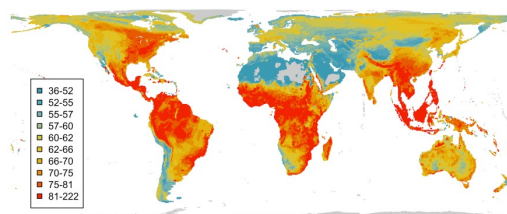
Colour loci
(UVS, range weighted)



Colour volume
(VS, range weighted)



Colour loci
(VS, range weighted)

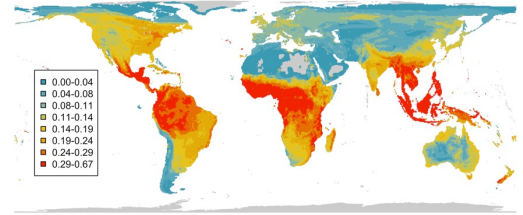
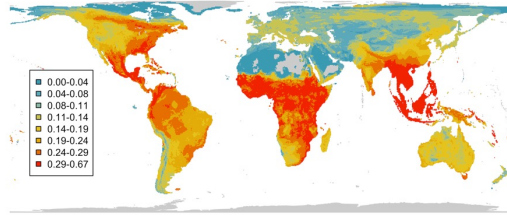


Extended Data Figure 3.

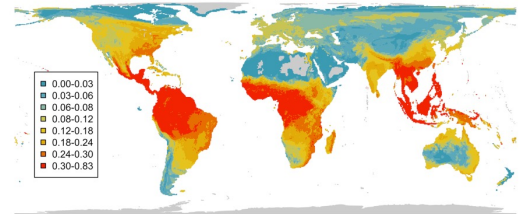
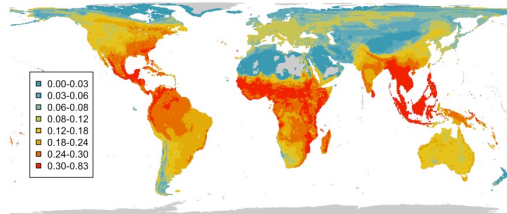
Males

Females

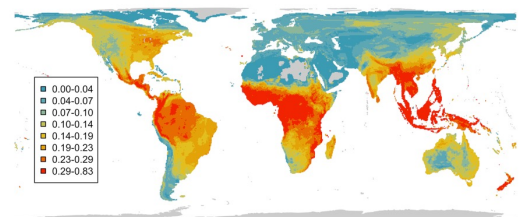
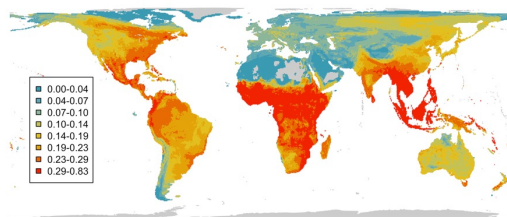
Colour volume
(UVS)



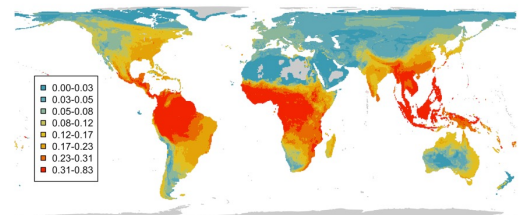
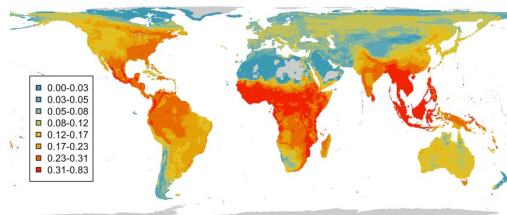
Colour loci
(UVS)



Colour volume
(VS)



Colour loci
(VS)



Extended Data Figure 4.

Supplementary Information:

Latitudinal gradients in avian colourfulness

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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 <i>per se</i> , 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 <i>per se</i> 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 Neumann (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.

Variable	Sex	Mean colourfulness				SES colourfulness			
		Slope	<i>P</i>	<i>I</i>	<i>P</i>	Slope	<i>P</i>	<i>I</i>	<i>P</i>
Volume (UVS)	M	-0.462	0	0.047	0.029	-0.231	3.18 x 10 ⁻¹⁴	0.032	0.100
	F	-0.472	0	0.061	0.008	-0.226	6.51 x 10 ⁻¹⁴	0.050	0.025
Loci (UVS)	M	-0.461	0	0.059	0.010	-0.220	7.51 x 10 ⁻¹⁴	0.046	0.035
	F	-0.490	0	0.063	0.007	-0.211	4.02 x 10 ⁻¹⁴	0.058	0.012
Volume (VS)	M	-0.438	0	0.043	0.041	-0.217	1.07 x 10 ⁻¹²	0.030	0.119
	F	-0.517	0	0.054	0.016	-0.237	2.44 x 10 ⁻¹⁵	0.048	0.031
Loci (VS)	M	-0.486	0	0.054	0.017	-0.233	3.77 x 10 ⁻¹⁵	0.045	0.040
	F	-0.509	0	0.051	0.021	-0.211	5.11 x 10 ⁻¹⁴	0.052	0.022
Volume (UVS, RW)	M	-0.383	2.73 x 10 ⁻¹²	0.042	0.048	-0.260	1.99 x 10 ⁻⁰⁷	0.026	0.148
	F	-0.437	0	0.061	0.009	-0.319	9.56 x 10 ⁻¹²	0.048	0.031
Loci (UVS, RW)	M	-0.353	1.52 x 10 ⁻¹¹	0.036	0.077	-0.228	9.82 x 10 ⁻⁰⁷	0.021	0.200
	F	-0.400	0	0.048	0.031	-0.247	1.70 x 10 ⁻⁰⁹	0.031	0.109
Volume (VS, RW)	M	-0.410	3.95 x 10 ⁻¹⁴	0.041	0.051	-0.275	1.58 x 10 ⁻⁰⁸	0.026	0.147
	F	-0.464	0	0.056	0.015	-0.333	7.72 x 10 ⁻¹³	0.047	0.034
Loci (VS, RW)	M	-0.380	2.16 x 10 ⁻¹³	0.034	0.092	-0.244	1.42 x 10 ⁻⁰⁷	0.023	0.178
	F	-0.429	0	0.037	0.073	-0.258	2.42 x 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^{-6}
Loci (UVS)	M	-0.043 (-0.068, -0.017)	9.15×10^{-4}
	F	-0.118 (-0.144, -0.090)	3.00×10^{-6}
Volume (VS)	M	-0.038 (-0.064, -0.012)	0.004
	F	-0.121 (-0.151, -0.092)	3.00×10^{-6}
Loci (VS)	M	-0.049 (-0.075, -0.024)	1.10×10^{-4}
	F	-0.140 (-0.167, -0.113)	3.00×10^{-6}

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		Females	
		Estimate (95% CI)	P_{MCMC}	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 x 10⁻⁰⁵	-0.203 (-0.314, -0.092)	4.65 x 10⁻⁰⁴
	Sexual dichromatism	0.327 (0.248, 0.405)	2.50 x 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 x 10⁻⁰⁶	-0.220 (-0.331, -0.110)	1.45 x 10⁻⁰⁴
	Sexual dichromatism	0.288 (0.211, 0.363)	2.50 x 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.