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Latitudinal gradients in avian colourfulness

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

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

61 Part of the challenge in resolving this controversy revolves around the difficulty of
62 obtaining accurate, meaningful measurements of organismal colouration, and doing so
63 on a scale that permits a global-scale test of these ideas. Due to practical constraints,
64 previous studies have been limited to addressing this question using subjective and/or
65 incomplete measures of colourfulness (e.g. human scoring) or else by studying
66 radiations of species that span only a limited fraction of the Earth's latitudinal gradient⁵⁻
67 ¹² (see Supplementary Table 1). While some of these studies have found patterns
68 consistent with a latitudinal colourfulness gradient in birds and other taxa, other studies
69 have found no such effect, and an explicit, broad-scale test of the latitudinal
70 colourfulness hypothesis is currently lacking. Fortunately, recent advances in cost-
71 effective imaging technology, combined with the increasing availability of accurate
72 geographic information for many taxa, now make it possible to test for the existence of
73 latitudinal gradients in species' colourfulness on a truly global scale.

74 We tested whether a latitudinal gradient in species' colourfulness exists for the global
75 radiation of passerine birds (Order: Passeriformes)—the largest avian order comprising
76 ~60% of the ~10,000 bird species. Our approach is centred around a novel dataset of
77 plumage colouration based on >140,000 calibrated visible and ultraviolet light
78 photographs of male and female museum specimens for 4,527 species (~76% of
79 passerine diversity; Supplementary Fig. 1a,b). For each included specimen, we took
80 photographs from three different angles (dorsal, lateral, ventral), extracted calibrated
81 pixel values from each image using machine learning approaches, and mapped these
82 into avian tetrahedral colour space (see Methods). We then sampled 500 points from
83 each view to give a total of 1,500 measurements capturing whole-body plumage
84 reflectance for each specimen (Supplementary Fig. 1c). This process resulted in a
85 dataset consisting of >24,000 photographed specimens and >36 million unique
86 measurements of passerine plumage colouration (Fig. 1a), which together occupy a
87 colour space that is comparable to that estimated for all birds¹³.

88 Colourfulness can be considered in multiple ways. Here we follow the sensory ecology
89 literature by defining colourfulness in terms of within-individual colour diversity; that is,
90 the overall colour contrast of a multi-coloured pattern¹⁴. Defined in this way,
91 colourfulness arises when an organism displays a range of colours (potentially
92 produced by different colour producing mechanisms) that are perceptually different from
93 one another, and can be quantified using metrics that measure the spread of colour
94 traits in colour space¹⁴. Importantly, this characterisation of colourfulness is distinct from
95 other notions of colourfulness that include uniform plumage colouration of a particular
96 (often conspicuous) hue and also differs from approaches used by other broad-scale
97 bird colouration studies, which have variously quantified plumage colouration in terms of
98 brightness and hue¹² and degree of elaboration (e.g. the 'maleness' metric introduced
99 by Dale et al.)¹¹, rather than colourfulness (i.e. colour diversity) *per se*. Here we use two
100 established metrics of colourfulness: convex hull volume^{13,15} and the number of
101 occupied colour loci¹⁶. The former reliably captures the breadth of colours in a sample
102 but is heavily influenced by extreme values, whereas the latter reflects that species will
103 generally not occupy all areas of colour space within the extent of occurrence (Fig. 1b).
104 Values of the two metrics are strongly correlated across specimens in our dataset ($r =$
105 0.85 , $P < 0.001$, $n = 24,345$; Supplementary Figure 1d) but because the colour loci
106 metric is generally less sensitive to noise, outliers and large 'gaps' in colour space
107 occupation that can bias estimates of colourfulness^{14,16} (Fig. 1b), we focus in the main
108 text on results based on colour loci scores, with colour volume results provided as
109 Supplementary Information.

110 We separately mapped mean male and mean female colourfulness scores for grid cell
111 assemblages and find evidence for a strong latitudinal gradient in species' colourfulness
112 in passerine birds (Fig. 2). Analysis of per-cell mean species' colour loci values revealed
113 a pronounced tropical peak in species' colourfulness with respect to latitude that was
114 evident for both male and female birds (Fig. 2a,b). For example, mean male and mean

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

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

143 To corroborate our grid cell-based results, we also tested the relationship between
144 species' colourfulness and midpoint latitude using species-level phylogenetic
145 comparative analyses (see Methods). Consistent with our previous findings, equatorial-
146 zone species (midpoint latitude $<23.5^{\circ}$) are generally characterised by higher
147 colourfulness scores than extra-tropical species (Fig. 3a) and as expected, there is a
148 strong relationship between midpoint latitude and colourfulness across species for both
149 sexes (Fig. 3b,c). However, an important consideration is that both midpoint latitude and
150 the degree of male and female colourfulness exhibit considerable phylogenetic
151 conservatism, with mean phylogenetic heritability¹⁹ values of 0.83 [95% credible interval
152 (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)
153 for male and female colourfulness, respectively. It is therefore possible that the
154 latitudinal gradient in colourfulness we observe is the result of phylogenetic non-
155 independence between tropical residency and elevated colourfulness—for example, if

156 the ancestors of speciose tropically-restricted passerine clades happened to be
157 colourful, and both traits have simply been retained by descendent lineages over
158 evolutionary time². However, testing the relationship between colourfulness and
159 species' absolute latitudinal position while controlling for phylogenetic history, we find
160 significant negative correlations with latitude for both male [standardised slope
161 coefficient: -0.04 (95% CI: -0.07, -0.02)] and female colourfulness scores [-0.12 (95%
162 CI: -0.14, -0.09)] (Supplementary Table 3). This indicates that the observed gradient in
163 species' colourfulness cannot be explained solely by phylogenetic conservatism of both
164 latitudinal position and degree of colourfulness.

165 Our finding of a clear latitudinal increase in passerine bird colourfulness towards the
166 equator is in line with related findings of other broad scale studies of avian
167 colouration^{11,12} which together support the notion that tropical zone species tend to be
168 generally more colourful than those in the temperate zone¹⁻³. Although unambiguous
169 empirical support for this belief has so far remained elusive (see Supplementary Table
170 1), several explanations for tropical peaks in species' colourfulness have nonetheless
171 been proposed. These explanations broadly fall into hypotheses focused on latitudinal
172 variation in climatic conditions, (e.g. energy, temperature, precipitation, or productivity),
173 species' behavioural and/or ecological traits, or biotic interactions (particularly inter-
174 specific competition and signalling). For example, early explanations focused on 'the
175 direct action of heat and light from the sun'² in promoting tropical colourfulness, but the
176 importance of climatic factors such as temperature, precipitation and solar radiation
177 have been hotly debated^{2,3,5,20}. Another broad class of hypotheses emphasises the role
178 of species' ecological and behavioural traits in promoting colourfulness. This includes
179 dark, closed habitat types (e.g. forests) selecting for increased reflectivity^{21,22} and the
180 positive effects of particular foraging (e.g. frugivorous, nectarivorous) and life-history
181 strategies (e.g. sedentary, territorial breeding) that are common in the tropics and may
182 deterministically promote the evolution of colourful plumages^{2,11}. Furthermore, the
183 strength of biotic interactions has long been argued to increase towards the equator^{23,24},
184 due in part to greater numbers of co-existing species in tropical systems²⁵. In theory,
185 elevated levels of colourfulness in tropical taxa may also emerge as a response to
186 increased selection for more distinguishable visual signals for recognising conspecifics
187 in diverse tropical communities^{2,5,6}.

188 To explore the factors promoting passerine colourfulness and to illuminate potential
189 explanations for the latitudinal gradients in colourfulness we observe, we used multi-
190 predictor Bayesian phylogenetic mixed models²⁶ to assess the relative importance of
191 variables capturing relevant environmental and ecological axes of variation among
192 species ($n = 4,415$) (see Methods). Importantly, the majority of these predictor variables
193 (11 of 13) were significantly correlated with species' midpoint latitude ($P < 0.001$ in all
194 cases; for correlation coefficients see Fig. 4), indicating that they indeed represent
195 viable explanations for the observed latitudinal gradients. The only exceptions to this
196 were species' mean body mass ($P = 0.535$) and degree of sexual dichromatism ($P =$

197 0.802) – the latter representing a useful proxy for sexual selection acting on visual
198 signalling traits^{27,28}.

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

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

224 While these associations provide insight in the factors contributing to variation in
225 passerine colourfulness (i.e. Fig 3a), they are unable to account for a tropical
226 colourfulness peak as neither dichromatism nor body mass is correlated with latitude.
227 However, our analyses also identified significant effects of several latitude-related
228 climatic and ecological variables that evidently contribute to generating latitudinal
229 gradients in passerine colourfulness (Fig. 4 and Supplementary Tables 4 and 5). First, it
230 has long been suggested that more benign environmental conditions promote elevated
231 colourfulness in the tropics, due to lower evolutionary constraints on elaborate plumage
232 colouration imposed by the types of harsh environmental conditions often found towards
233 the poles and in deserts². In support of this, we find that male and female colourfulness
234 scores are consistently and positively associated with precipitation and net primary
235 productivity (NPP), such that species are on average more colourful in wetter, more
236 productive areas. Second, we also find that species' occupying closed (i.e. forested)

237 habitat types and foraging niches associated with a high degree of resource defence
238 and carotenoid intake (i.e. frugivores and nectarivores) generally have increased levels
239 of colourfulness, supporting hypotheses linking signalling conditions^{21,22,33} and dietary
240 factors^{2,34} to interspecific differences in colourfulness. Third, a strong and consistent
241 positive association between colourfulness and community diversity (i.e. the average
242 number of co-occurring passerine species) supports the suggestion that latitudinal
243 gradients in species' colourfulness emerge at least in part due to selection on both
244 sexes for accurate conspecific recognition in species-rich tropical communities^{2,5,6,9}.
245 Finally, for female birds we find a strong negative effect of migration on colourfulness
246 that is absent in males. An association between migration and reduced female
247 colourfulness across passerines generalises earlier findings³⁵ (though see ¹²) and
248 reinforces the idea that in migratory passerine taxa at least, changes in selection acting
249 on females may play an important role in generating sex-differences in colouration (cf.
250 above)^{2,34}. As many high-latitude breeding passerines are migratory, this female-
251 specific reduction in colourfulness in migratory taxa may also help to explain a general
252 pattern emerging from our analysis: that latitudinal gradients in colourfulness tend to be
253 more pronounced in females than in males (e.g. Fig. 3b; Supplementary Table 6).

254 Together, our results support the existence of a strong latitudinal gradient in species'
255 colourfulness for passerine birds. This gradient exists for both male and female
256 colouration and is consistent across major tropical realms. We demonstrate that this
257 pronounced tropical-zone peak in colourfulness can be explained, in part, by latitude-
258 associated gradients in climatic conditions and species' ecological traits that facilitate
259 the evolution of increased colour diversity of tropical passerine species. However, we
260 note that many potentially important factors remain to be investigated, including
261 latitudinal gradients in predation pressure²⁴ and the intensity of social selection³¹,
262 particularly acting on females. More broadly we note that conceptions of the latitudinal
263 colourfulness gradient are not limited to the plumages of birds, with early naturalists
264 such as Alexander von Humboldt remarking on the apparent colourfulness of many
265 tropical taxa, including plants, insects, fish and 'even crayfish'³⁶. Thus, while our results
266 provide clear support for broad-scale latitudinal gradients in colourfulness for passerine
267 birds, the extent to which other global radiations follow the 'rule' that life in the tropics is
268 generally more colourful than in the temperate zones remains to be seen.

269 **Methods**

270 **Specimen selection.** We based our data collection on the taxonomic framework of Jetz
271 *et al.*³⁷, which currently represents the only integrated species-level taxonomic and
272 phylogenetic dataset for all (passerine) birds. We collected data on plumage colouration
273 using study skins housed at the Natural History Museum, Tring, UK. We focused on
274 species with representatives of both sexes and for which geographic range data were
275 available (see below). Where possible, we sampled specimens of three males and three
276 females, taking care to select only mature individuals in breeding plumage with no

277 obvious signs of moult. Based on these criteria, we were able to sample specimens of
278 both sexes for 4,527 (76%) of the 5,966 taxa represented in the Jetz *et al.* taxonomy,
279 with a mean sampling of 2.77 male and 2.61 female specimens per species and 24,345
280 specimens in total.

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

296 **Image segmentation using deep learning.** To facilitate the extraction of pixel
297 information from our photography dataset, we applied an automated image
298 segmentation protocol based on convolutional neural networks. Full details of this
299 approach and a comprehensive analysis of its performance, particularly in relation to
300 other methods, can be found in He *et al.*³⁸. A brief account is also provided below.

301 We used DeepLabv3+, which is a deep convolutional neural network architecture based
302 on fully convolutional networks³⁹, to build a pixel-wise semantic segmentation network
303 capable of accurately identifying specimen pixels in each of our images. DeepLabv3+
304 has been shown to outperform both classical computer vision techniques (e.g.
305 thresholding) and other neural network architectures for semantic segmentation on
306 benchmark tasks³⁹. It has also previously been shown to perform well when applied to a
307 similar task as ours, involving the segmentation of biological specimens from
308 photographic images of herbarium specimens⁴⁰.

309 To generate a dataset of expert labelled images for use in network training and
310 evaluation, we placed polygons on a diverse sample of bird specimen images using
311 Project Plumage (www.projectplumage.org), an online citizen science project with
312 bespoke image labelling protocols. These polygons were used to manually identify
313 plumage areas and to exclude non-plumage areas obscuring the specimen, such as
314 eye holes, feet, specimen labels and string. The images labelled as part of developing
315 this protocol form part of a broader effort to measure avian colouration. As such, across
316 the three views (dorsal, lateral ventral) a total of 5,094 images were labelled for 1,698

317 species distributed across the entire avian radiation (i.e. passerines and non-
318 passerines), encompassing representatives of more than 81% of all bird genera and 27
319 bird orders.

320 We used this 5,094-image dataset to train and validate the network and then to
321 generate specimen segmentation predictions for each of the >140,000 images in our
322 dataset³⁸, which took ~72 hours to complete on a desktop computer. Finally, each of the
323 resulting image masks was individually checked by eye and manually refined where
324 necessary using bespoke software (<https://github.com/EchanHe/PhenoLearn>).

325 **Image processing.** All raw (.NEF) images of specimens were linearised and exported
326 as linear TIFF files using DCRAW⁴¹. Pixel values were then normalised using mean
327 pixel intensity values from the five grey standards included in each image in order to
328 control for variation in lighting conditions, following established approaches^{27,42}. Finally,
329 the image was segmented using the image masks described above to leave only pixel
330 values corresponding to the specimen in each image. As individual pixel measurements
331 can be noisy—and because different specimens were represented by different numbers
332 of pixels in our raw dataset—we downsampled each specimen image to a comparable
333 resolution (see Supplementary Fig. 1c), prior to calculating cone catch values and
334 colourfulness metrics (see below). To do this, we treated each specimen image as a
335 raster and, using the aggregate() function in the R package ‘raster’ (version 3.4-5)⁴³, we
336 found the smallest aggregation factor in the range 100 to 1 that resulted in at least 500
337 aggregated cells (pixels) being returned, with aggregated cell values calculated as the
338 mean of relevant neighbouring values. We then randomly sampled 500 measurements
339 from this aggregated dataset to represent the plumage colouration of that specimen
340 view in all further analyses. Samples from the each of the three specimen views (dorsal,
341 lateral, ventral) were pooled to give a final set of 1,500 whole-body plumage colour
342 measurements per specimen.

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

354 **Visual modelling.** We used established methods⁴² to generate mapping functions to
355 convert sampled specimen RGB pixel values into avian cone-catch values. This
356 approach works by first estimating camera responses and visual system cone-catch

357 values to a library of natural spectra under a specific illuminate, and then uses multiple
358 regression to create mapping functions for each receptor channel from the camera's
359 responses. Using tools available in the IMAGEJ Multispectral Image Calibration and
360 Analysis Toolbox (version 2.2)⁴², we generated mapping functions for each
361 photoreceptor using equations containing second-order polynomial terms and three-way
362 interactions between channels. Note that this approach does not incorporate information
363 on camera responses in the UV G channel due to typically low sensitivities of the G
364 channel in the UV range⁴². We fit these equations to our data incorporating information
365 on the estimated spectral sensitivities of our camera set up and the irradiance spectrum
366 of our illuminant (i.e. flash units), both of which had estimated previously²⁷. For
367 modelling receptor responses, we assumed idealised illumination conditions^{13,15} and
368 receptor sensitivities corresponding either to an 'average' violet-sensitive (VS) or
369 'average' ultraviolet-sensitive (UVS) avian visual system, both extracted from the R
370 package pavo (version 2.6.1)⁴⁴. We used this information to generate mapping functions
371 for each cone class, and the resulting models were all characterised by a high degree of
372 mapping accuracy (R^2 values > 0.99). These mapping functions were then used to
373 convert linearised and normalised image RGB values into cone catch values (u/v , s , m ,
374 l) for use in downstream analyses. We have previously shown that cone catch values
375 generated by this photography-based approach are highly correlated ($r > 0.92$) with
376 corresponding values calculated from spectrophotometric measurements²⁷.

377 Following previous studies, we represented chromatic (i.e. colour) variation among
378 measurements using a standard avian colour space model in which raw cone catch
379 values are converted to relative cone catch values and projected in a tetrahedron^{13,15}.
380 This tetrahedron—in which the luminance (i.e. achromatic) dimension is removed and
381 each vertex represents one of the four cones characterising avian colour vision (i.e. u/v ,
382 s , m , l)—is the sensory equivalent of a morphospace, where similar colours fall in close
383 proximity in the colour space and disparate colours are far apart^{13,15,45}. As quantifying
384 the colour of patches with very low overall reflectance can be problematic⁴⁶, pixels
385 exhibiting a mean normalised reflectance value of <1% across all channels (uR , uB , vR ,
386 vG , vB) were re-cited to the achromatic centre.

387 **Colourfulness metrics.** We quantified colourfulness using two simple and intuitive
388 metrics for quantifying variation in organismal colourfulness¹⁴ (Fig. 1b). First, we
389 calculated the volume of the minimum convex polygon containing all colour
390 measurements for a given specimen, which represents the standard and most widely-
391 used metric of (avian) colourfulness employed in the literature^{13,15}. However, convex
392 hull polygon volume can strongly depend on extreme values¹⁴ and can generate
393 overinflated volume estimates when highly disparate colours are separated by large
394 areas of unoccupied colour space⁴⁷. Therefore we also employed a second metric of
395 colour space occupation that is less sensitive to these issues. This approach¹⁶ is based
396 on sub-dividing (rasterising) tetrahedral colour space into a series of equally-sized 3D
397 cells termed 'colour loci'. This is done by defining two 2D grid systems in the XY and YZ

398 axes of colour space that, when intersected, define a 3D grid system covering the
399 entirety of colour space. Each 3D cell (dimensions: 0.022 × 0.022 × 0.022) therefore
400 represents a ‘chromatic locus’ and provides a way of partitioning the continuous
401 variation in colour space into discrete units. The strength of this approach is that the
402 colour diversity (i.e. colourfulness) of a particular set of measurements can then be
403 assessed by simply counting the number of colour loci occupied ¹⁶, with these estimates
404 being less impacted by outlier values and intermediate areas of unoccupied colour
405 space.

406 We calculated estimates of convex hull volume and number of colour loci occupied for
407 each specimen separately, and then calculated species-level values for each sex as the
408 mean of log₁₀-transformed specimen-level values.

409 **Phylogenetic framework.** To provide a phylogenetic framework for the species
410 included in our analysis ($n = 4,527$), we downloaded 100 trees from the posterior
411 distribution of complete trees produced by Jetz *et al.* ³⁷ from <http://www.birdtree.org>,
412 which were then pruned to generate a distribution of trees containing only the focal
413 species set. All of our analyses incorporating phylogenetic information were run over
414 this distribution of 100 trees to incorporate phylogenetic uncertainty into our parameter
415 estimates. For plotting purposes, we identified a maximum clade credibility (MCC) tree
416 from this posterior distribution of trees using the `maxCladeCred()` function in the R
417 package ‘phangorn’ (version 2.5.5)⁴⁸.

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

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

433 Global spatial information on temperature, precipitation, solar radiation, ultraviolet-B
434 (UV-B) radiation and net primary productivity (NPP) were extracted from various
435 sources and then reprojected and resampled to match the resolution of our range
436 dataset. Annual mean temperature (bio1) and annual precipitation (bio12) data were

437 downloaded from the WorldClim (version 2.1) database⁴⁹ at 2.5 arc-minute resolution.
438 Monthly information on solar radiation was downloaded at 30 arc-second resolution and
439 monthly totals were summed to give a measure of total annual solar radiation.
440 Information on annual mean UV-B radiation was extracted from Beckmann *et al.*⁵⁰ at 15
441 arc-minute resolution. Information on NPP at 1 km was extracted from datasets
442 produced by Running *et al.*⁵¹. In all cases, species' values represent averages across
443 their geographic range.

444 Information on species-level ecological and behavioural traits were extracted from
445 several sources, specifically BirdLife International's Data Zone
446 (<http://www.datazone.birdlife.org>) (forest dependency) and Tobias and Pigot⁵² (foraging
447 niche, migration, nest placement, territoriality, body mass). To reduce the complexity of
448 the categorical variables included in these datasets, and to facilitate effect size
449 comparison in our multipredictor models, we re-coded variation in forest dependency,
450 foraging niche, migration, nest placement, and territoriality as binary variables that
451 aligned with our hypotheses (see main text). Specifically, species were coded as forest
452 dependent ('low', 'medium' or 'high' dependency) or not ('does not usually occur in
453 forest'), frugivorous/nectarivorous or not (all other dietary niches), migratory ('migratory'
454 or 'partially migratory') or not ('sedentary'), ground nesting ('exposed ground') or not
455 ('cavity' or 'exposed elevated'), and territorial ('strong' or 'weak') or not ('none'). Sexual
456 dichromatism was scored from handbook plates as the mean value of plumage
457 dimorphism estimated from five body regions (head, back, belly, wings and tail) using
458 the following scheme: -2, the female was substantially brighter and/or more patterned
459 than the male; -1, the female was brighter and/or more patterned than the male; 0, there
460 was no sex difference in the body region or there was a difference but neither could be
461 considered brighter than the other; 1, the male was brighter and/or more patterned than
462 the female; 2, the male was substantially brighter and/or more patterned than the
463 female. Thus these scores are independent of the data used in this study to quantify
464 colourfulness and positive values represent male-biased ornamentation, zero represent
465 unbiased ornamentation, and negative values represent female-biased ornamentation.
466 To assess the effect of variation in community diversity on species' colourfulness, we
467 generated a variable capturing the average richness of passerine species co-occurring
468 with each species in our dataset. To do this we used range data for all passerine
469 species (i.e. not just those sampled in our dataset) to calculate for each grid cell the
470 number of co-occurring passerine species. We then calculated the mean value of this
471 variable across species' geographic ranges to provide a measure of average community
472 diversity for each species, analogous to the community diversity metric generated by
473 Dalrymple *et al.*⁵. Overall, we were able to collect complete data on these variables for
474 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^{11,12,53}. 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
488 above (and on UVS colour scores) are presented. The lack of a clear effect of social
489 mating system on colourfulness using this dataset suggests that mating system
490 variation across species cannot account for any of the patterns we report in our main
491 analysis, particularly the effect of dichromatism, which remained significant even in this
492 reduced dataset (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
496 mean 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^{18,37} 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)^{18,37}.

504 To formally assess the relationship between latitude and assemblage-level
505 colourfulness, we followed the approach of Rabosky *et al.*¹⁸ by testing this relationship
506 at the scale of ecoregions rather than individual grid cells. We chose to do this to reduce
507 the computation burden of analysing the full 59,102 grid cell dataset and, more
508 importantly, to minimise levels of autocorrelation between assemblages, which is far
509 higher between adjacent grid cells than between adjacent ecoregions¹⁸. We therefore
510 calculated mean colourfulness scores for all cells within terrestrial ecoregions of the
511 world¹⁷ containing passerine species in our dataset ($n = 800$) and related this to the
512 absolute latitude of ecoregions' centroid position. To account for spatial autocorrelation
513 between ecoregions, we used simultaneous autoregressive error (SAR) models
514 implemented using the function `spautolm()` in the R package 'spdep' (version 1.1-5)⁵⁴.
515 For these models, neighbours were defined as those ecoregions with contiguous
516 boundaries and we then selected the appropriate weighting style using Akaike
517 information criterion (AIC) model selection based on code provided by Rabosky *et al.*¹⁸.
518 We used Moran's I to test for spatial autocorrelation in the residuals of SAR regressions

519 to determine the extent to which SAR models successfully accounted for spatial non-
520 independence in the data. These results showed that all models retained some
521 evidence of residual spatial autocorrelation, but to lesser degree in models based on
522 richness-corrected ecoregion colourfulness scores (see below) than raw ecoregion
523 scores (Supplementary Table 1).

524 An important consideration when analysing aggregated species-level variables in a
525 spatial context is that underlying species richness gradients can generate strong spatial
526 patterns in aggregated data⁵⁵. To address the extent to which the latitudinal
527 colourfulness gradients we observe in our spatial analyses are independent of
528 underlying species richness differences, we used a randomisation approach to calculate
529 colourfulness standardised effect size (SES) values for each ecoregion, which corrects
530 for the effect of species richness differences on aggregated trait scores⁵⁵. To do this we
531 generated 200 null communities for each ecoregion by randomising species'
532 colourfulness scores with respect to species' identity across our dataset. These null
533 communities were then used to generate a null distribution of mean colourfulness
534 scores for each ecoregion, against which observed colourfulness scores were
535 compared. The resulting SES scores, in which the effects of species richness on mean
536 colourfulness values have been factored out, were then analysed using the same SAR
537 modelling approach described above.

538 *Species-level analyses.* To test the relationship between species' absolute midpoint
539 latitude and colourfulness, and between species' colourfulness scores and variation in
540 the 13 predictor variables described above, we used multi-predictor Bayesian
541 phylogenetic mixed models implemented in the R package 'MCMCglmm'^{26,56}. All models
542 included a phylogenetic random effects term and were run over a posterior distribution
543 of 100 trees to incorporate phylogenetic uncertainty and posterior distributions of
544 parameter estimates associated with different trees were pooled to give model
545 estimates that incorporate phylogenetic error⁵⁷. In all cases, models were run for 55,000
546 iterations (sampled every 25th iteration) with a 5,000 iteration burn-in, and we used
547 standard non-informative priors [i.e. list(R=list(V=1, nu=0.002), G=list(G1=list(V=1,
548 nu=0.002)))]. All variables were standardised (mean = 0, standard deviation = 1) prior to
549 model fitting to facilitate effect size comparison. Before running models we also checked
550 for evidence of multi-collinearity among predictors in our multi-predictor models using
551 variance inflation factors (VIFs) and found no evidence of severe (VIF > 10) or even
552 moderate (VIF > 4) multi-collinearity in our models (median VIF = 1.60; range = 1.05 –
553 3.89).

554 Finally, phylogenetic heritability (H^2) values¹⁹ were estimated by fitting intercept-only
555 models for each variable of interest and then calculating the proportion of the total
556 variance explained by phylogenetic effects across the posterior distribution of parameter
557 estimates.

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706 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
707 analyses. C.R.C. wrote the manuscript, with input from all authors.

708

709 **Competing interests:** All authors have no competing interests.

710

711 **Materials and correspondence:** Correspondence and material requests should be
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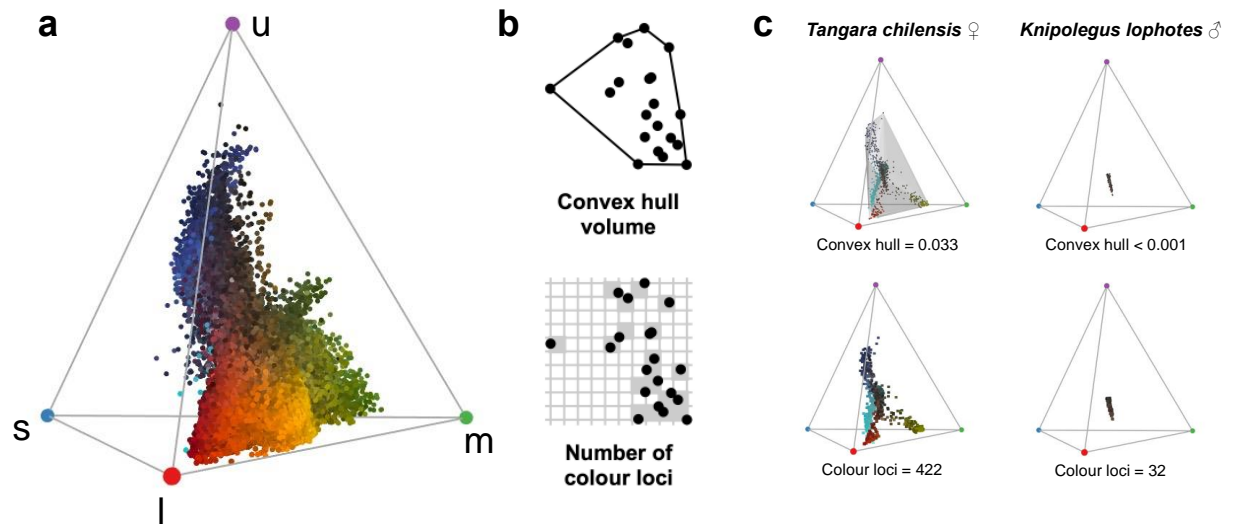
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714 **Data and materials availability:** All analysis data is available in the supplementary
715 materials. Analysis code is available from the corresponding author upon request.

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717 **Supplementary information:** An Excel file (Cooney_etal_data_S1.xlsx) containing the
718 dataset analysed in this study.

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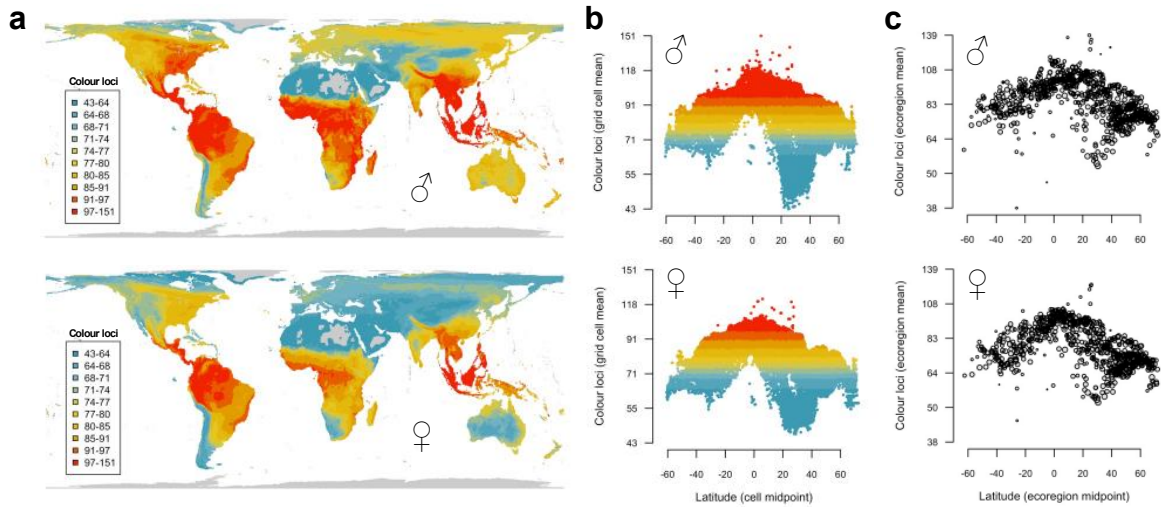
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Figure 1. The diversity of passerine plumage colours in avian tetrahedral colour space. **a**, A sample of one million passerine plumage colours analysed in this study, visualised in avian ultraviolet-sensitive (UVS) tetrahedral colour space where 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 colour space **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.



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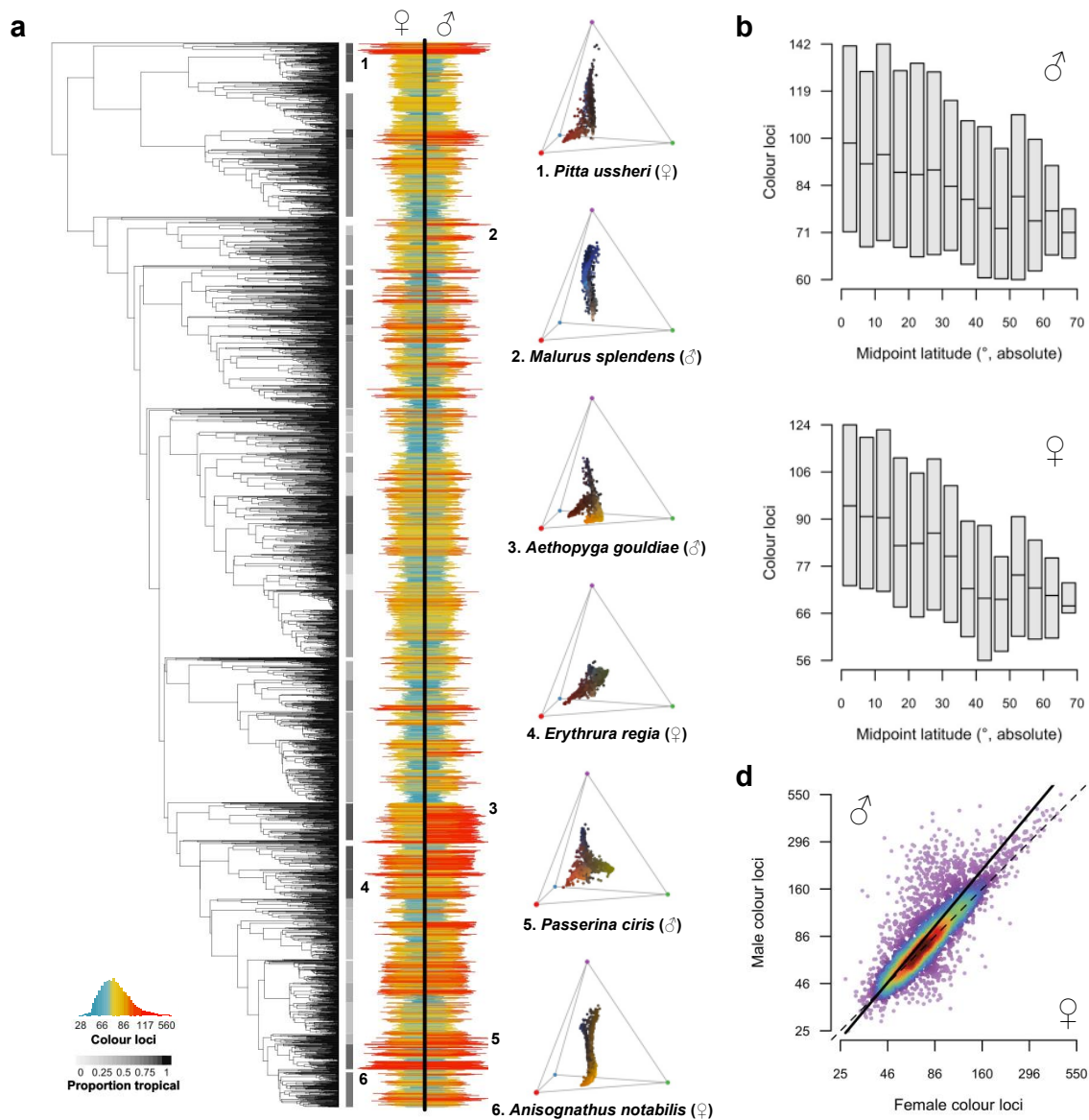
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Figure 2. Latitudinal gradients in male and female colourfulness in passerine birds. **a**, Mean colour loci scores for grid cell assemblages, separately for males (top) and females (bottom). **b**, **c**, Distributions of mean species' colour loci 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.



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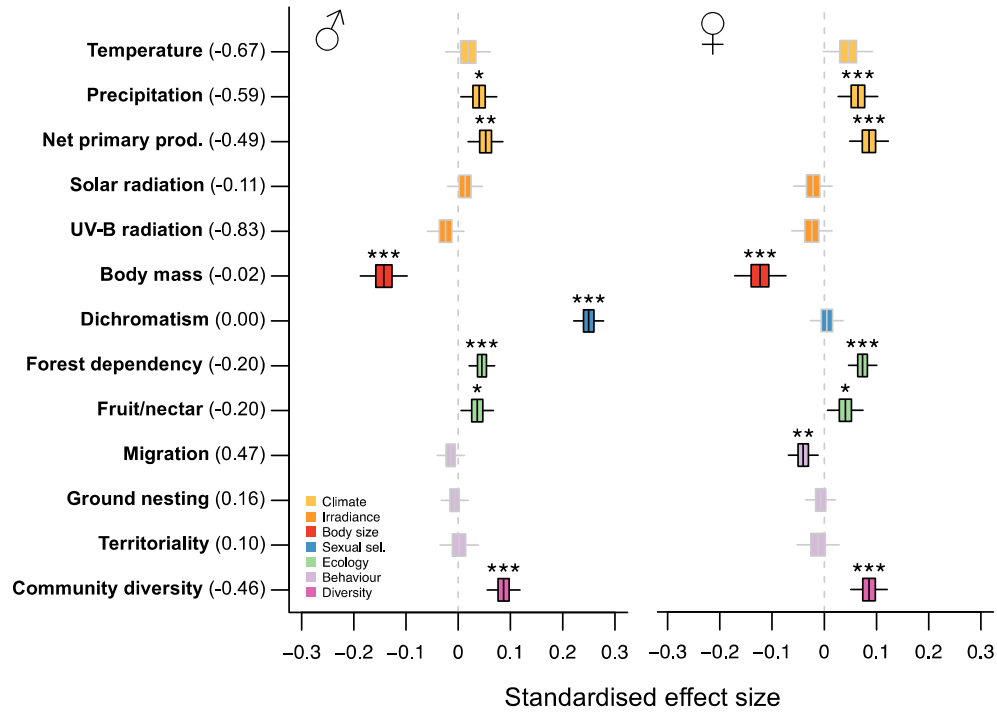
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Figure 3. The phylogenetic distribution of male and female colourfulness and its relation to species' midpoint latitude in passerine birds. a, Coloured bars indicate male and female colour loci scores for 4,527 passerine species. Grey segments indicate the proportion of tropical species (i.e. $|\text{midpoint latitude}| < 23.5^\circ$) 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.



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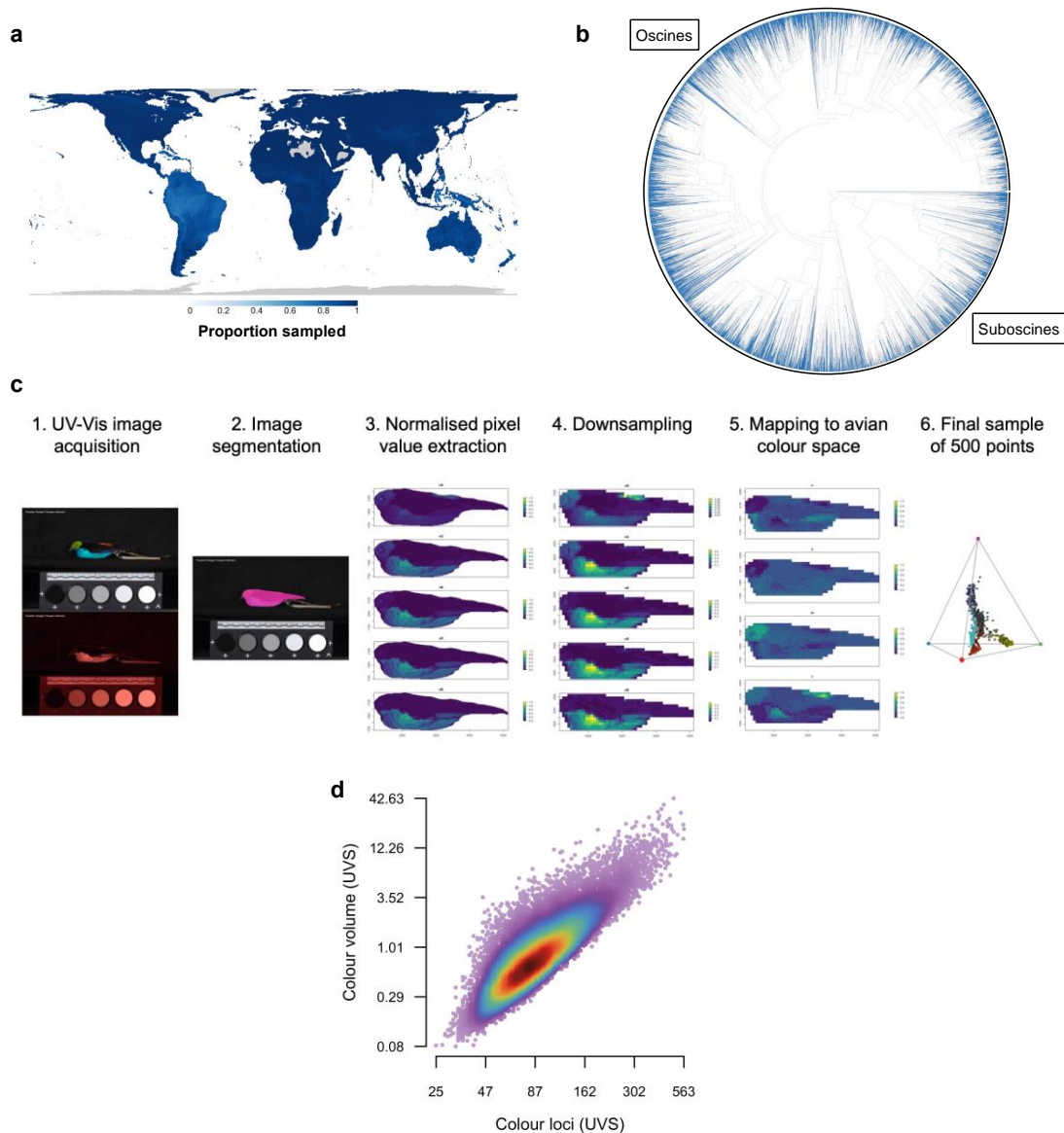
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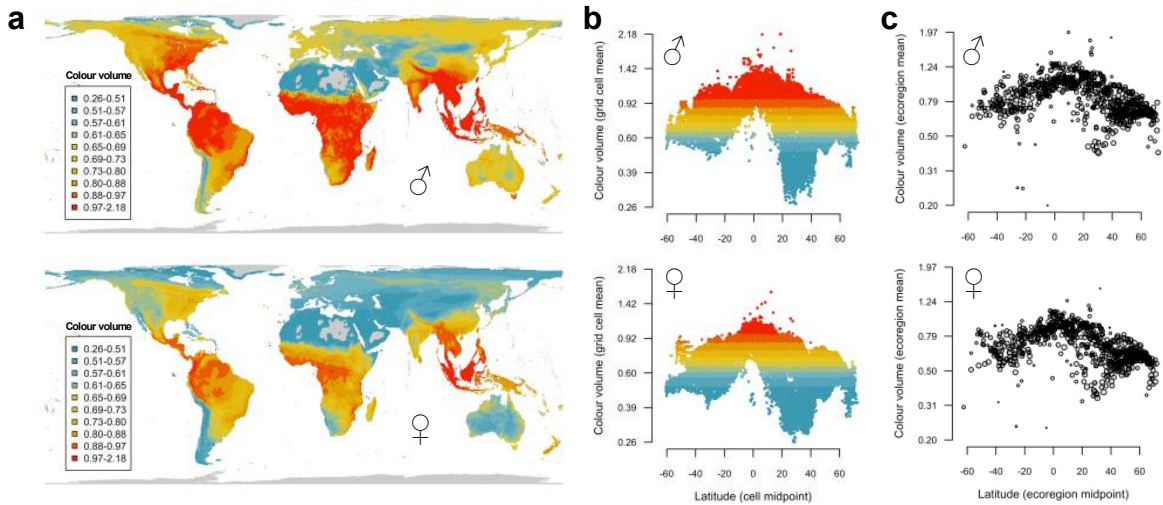
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Figure 4. Predictors of male and female colourfulness in passerine birds. Box plots summarise the posterior marginal distributions for all fixed-effects from Bayesian phylogenetic mixed models applied over a sample of 100 phylogenetic trees predicting male (left) and female (right) colour loci scores across 4,415 species. 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 ρ) 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.



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



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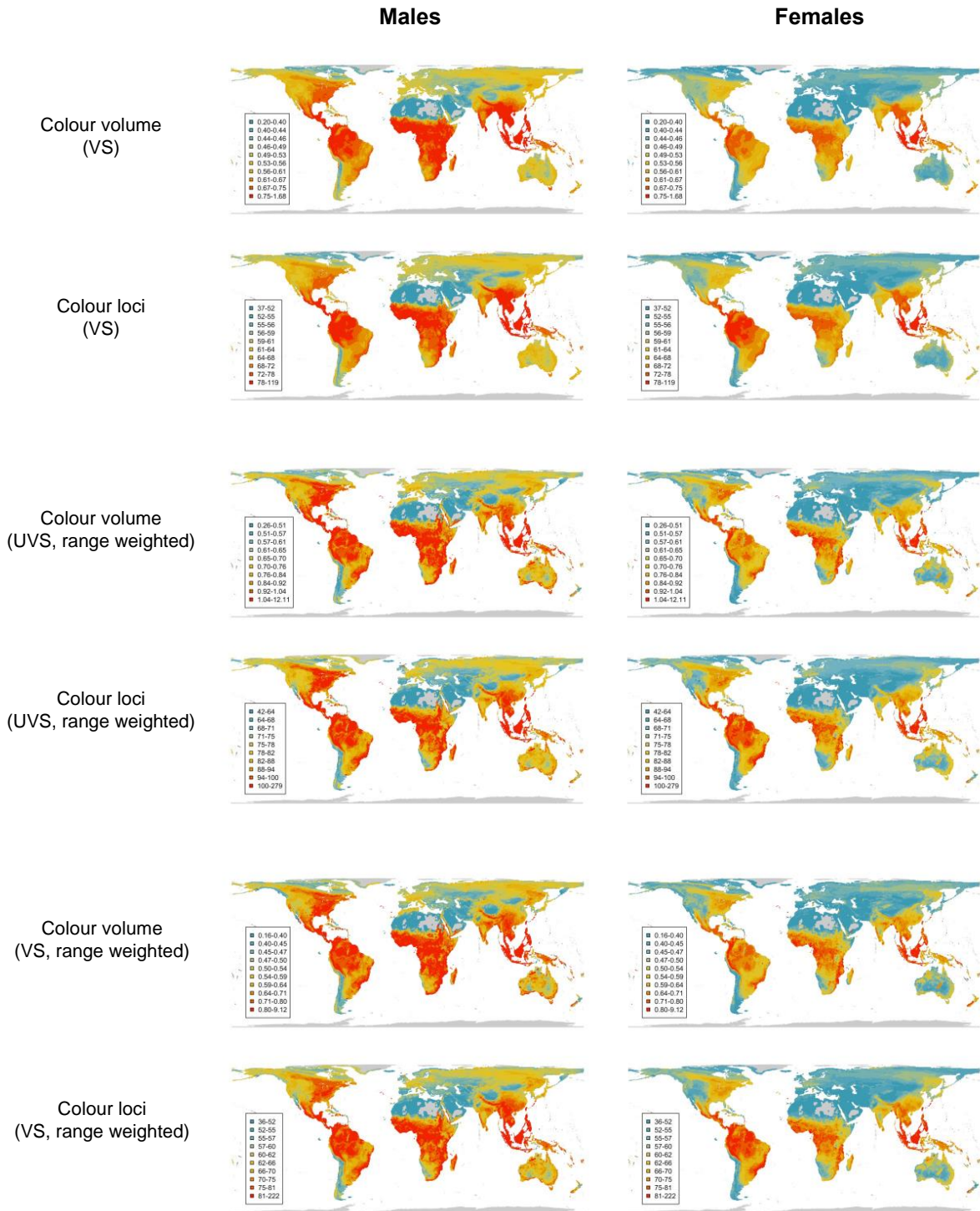
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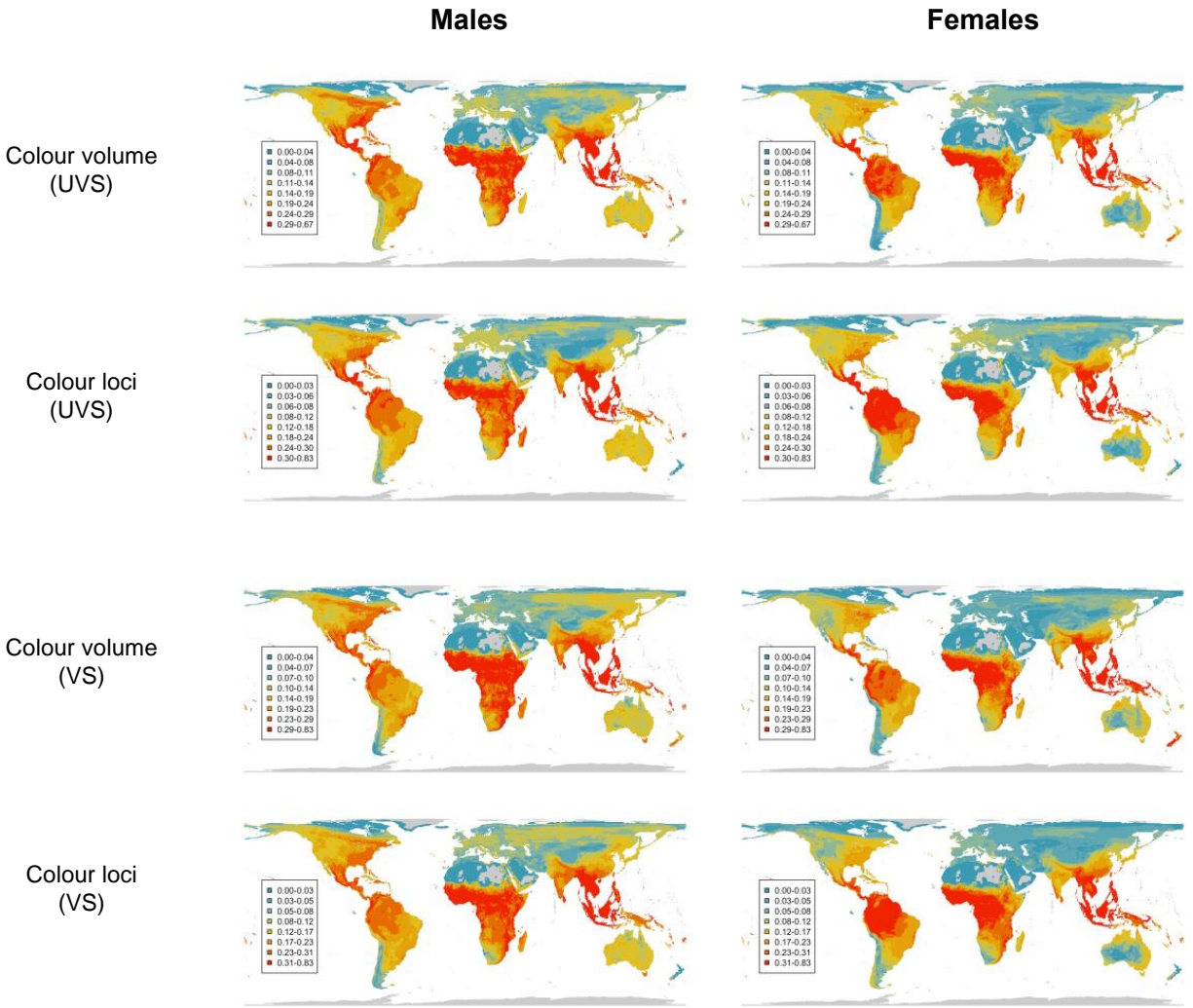
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Supplementary Figure 2. Latitudinal gradients in male and female colourfulness in passerine birds using colour volume. **a**, Mean colour volume scores for grid cell assemblages, separately for males (top) and females (bottom). **b**, **c**, Distributions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



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792 **Supplementary Figure 3. Geographic distributions of male and female**
 793 **colourfulness in passerine birds using different datasets.** Grid cell size is 50 x 50
 794 km for all panels (Behrman projection) and only cells containing at least 5 sampled
 795 species are plotted. UVS, ultraviolet sensitive; VS, violet sensitive. Note: colour volume
 796 values are multiplied by 1000.



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

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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 (US only)	Gradient present – Ecuadorian species more variable in colour intensity, saturation, and hue than species of other regions	Incomplete colour measurements (no UV), limited geographical extent.
Bailey (1976) [7]	Passerine birds (n = 784)	North and Central America (Alaska, Canada to Panama)	Human scores of field guide illustrations	No gradient present – Some significant differences between regions but overall weak support for enhanced tropical colourfulness	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	Gradient present – 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)
Daymple et al. (2015, 2018) [9, 5]	Birds (n = 570), butterflies (n = 424), flowers (n = 338)	Eastern Australia	Reflectance spectrometry (300-700 nm), birds, flowers, and UV/VS digital photography (butterflies)	No gradient present – 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 (300-700 nm)	Eurotropical – In monotropical species (n = 489), subtropical taxa were higher but tropical taxa were taller than non-tropical taxa	Colour quantified in terms of brightness and hue; colourfulness per se not measured
Friedman & Reines (2017) [10]	Australian passerines (Meliphagidae, n = 97; Acamitizidae, n = 40)	Australia, New Guinea	Reflectance spectrometry (300-700 nm)	No gradient present – birds living close to the equator were not more colourful	Limited taxonomic and geographic extent
Wilson & von Neumann (1972) [8]	Birds (n = 1,578)	N and S America, Europe	Binary categorisation of species as 'colourful' or 'not so' based on pictures and written descriptions	Gradient present – 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

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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	Moran's <i>I</i>	Slope	Moran's <i>I</i>
Volume (UVS)	M	-0.462***	0.047*	-0.231***	0.032
	F	-0.472***	0.061**	-0.226***	0.050*
Loci (UVS)	M	-0.461***	0.059**	-0.220***	0.046*
	F	-0.490***	0.063**	-0.211***	0.058*
Volume (VS)	M	-0.438***	0.043*	-0.217***	0.030
	F	-0.517***	0.054*	-0.237***	0.048*
Loci (VS)	M	-0.486***	0.054*	-0.233***	0.045*
	F	-0.509***	0.051*	-0.211***	0.052*
Volume (UVS, RW)	M	-0.383***	0.042*	-0.260***	0.026
	F	-0.437***	0.061**	-0.319***	0.048*
Loci (UVS, RW)	M	-0.353***	0.036	-0.228***	0.021
	F	-0.400***	0.048*	-0.247***	0.031
Volume (VS, RW)	M	-0.410***	0.041	-0.275***	0.026
	F	-0.464***	0.056*	-0.333***	0.047*
Loci (VS, RW)	M	-0.380***	0.034	-0.244***	0.023
	F	-0.429***	0.037	-0.258***	0.025
Volume (UVS, PTQ)	M	-0.551***	0.054*	-0.267***	0.031
	F	-0.570***	0.053*	-0.266***	0.041
Loci (UVS, PTQ)	M	-0.647***	0.066**	-0.275***	0.036
	F	-0.662***	0.055*	-0.267***	0.058*
Volume (VS, PTQ)	M	-0.650***	0.062**	-0.314***	0.030
	F	-0.582***	0.068**	-0.290***	0.056*
Loci (VS, PTQ)	M	-0.666***	0.054*	-0.292***	0.033
	F	-0.711***	0.061**	-0.298***	0.065*

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Supplementary Table 2. Models for the effect of absolute latitude on male and female colourfulness across 800 terrestrial ecoregions using different datasets.

Shown are results from spatial simultaneous autoregressive (SAR) models. 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. 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. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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)	<0.001***
Loci (UVS)	M	-0.043 (-0.068, -0.017)	0.001***
	F	-0.118 (-0.144, -0.090)	<0.001***
Volume (VS)	M	-0.038 (-0.064, -0.012)	0.004**
	F	-0.121 (-0.151, -0.092)	<0.001***
Loci (VS)	M	-0.049 (-0.075, -0.024)	<0.001***
	F	-0.140 (-0.167, -0.113)	<0.001***

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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. UVS, ultraviolet sensitive; VS, violet sensitive. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. 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)	<0.001***
	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)	<0.001***	-0.123 (-0.172, -0.073)	<0.001***
	Sexual dichromatism	0.250 (0.221, 0.279)	<0.001***	0.005 (-0.027, 0.036)	0.753
	Forest dependency	0.045 (0.021, 0.070)	<0.001***	0.073 (0.046, 0.101)	<0.001***
	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)	<0.001***	0.086 (0.051, 0.121)	<0.001***
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)	<0.001***
	Net primary productivity	0.051 (0.018, 0.085)	0.002**	0.084 (0.047, 0.122)	<0.001***
	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)	<0.001***	-0.123 (-0.171, -0.074)	<0.001***
	Sexual dichromatism	0.258 (0.229, 0.287)	<0.001***	-0.006 (-0.038, 0.026)	0.713
	Forest dependency	0.040 (0.016, 0.065)	0.002**	0.060 (0.032, 0.087)	<0.001***
	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)	<0.001***	0.090 (0.054, 0.125)	<0.001***

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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. UVS, ultraviolet sensitive; VS, violet sensitive. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. 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)	<0.001***
	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)	<0.001***	-0.163 (-0.212, -0.112)	<0.001***
	Sexual dichromatism	0.235 (0.206, 0.264)	<0.001***	-0.044 (-0.078, -0.011)	0.009**
	Forest dependency	0.034 (0.008, 0.059)	0.010*	0.079 (0.049, 0.108)	<0.001***
	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)	<0.001***	0.106 (0.069, 0.144)	<0.001***
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)	<0.001***
	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)	<0.001***	-0.170 (-0.219, -0.120)	<0.001***
	Sexual dichromatism	0.233 (0.203, 0.262)	<0.001***	-0.050 (-0.084, -0.017)	0.003**
	Forest dependency	0.030 (0.004, 0.056)	0.021*	0.066 (0.035, 0.096)	<0.001***
	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)	<0.001***	0.110 (0.072, 0.148)	<0.001***

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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. UVS, ultraviolet sensitive; VS, violet sensitive. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. 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)	<0.001***
	Sex	-0.111 (-0.123, -0.100)	<0.001***
	Absolute latitude x Sex	-0.003 (-0.015, 0.009)	0.601
Loci (UVS)	Absolute latitude	-0.066 (-0.090, -0.042)	<0.001***
	Sex	-0.094 (-0.103, -0.084)	<0.001***
	Absolute latitude x Sex	-0.018 (-0.027, -0.008)	<0.001***
Volume (VS)	Absolute latitude	-0.069 (-0.092, -0.045)	<0.001***
	Sex	-0.112 (-0.124, -0.099)	<0.001***
	Absolute latitude x Sex	-0.004 (-0.017, 0.008)	0.488
Loci (VS)	Absolute latitude	-0.081 (-0.104, -0.058)	<0.001***
	Sex	-0.099 (-0.110, -0.089)	<0.001***
	Absolute latitude x Sex	-0.081 (-0.028, -0.008)	<0.001***

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Supplementary Table 6. Bayesian phylogenetic mixed model results for the effects of absolute latitude and sex on male and female colourfulness across passerine species ($n = 4,527$ species). All variables were standardised (mean = 0, sd = 1) prior to model fitting. UVS, ultraviolet sensitive; VS, violet sensitive. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. 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)	<0.001***	-0.203 (-0.314, -0.092)	<0.001***
	Sexual dichromatism	0.327 (0.248, 0.405)	<0.001***	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	-0.247 (-0.874, 0.376)	0.424
	Temperature	0.082 (-0.152, 0.315)	0.492	0.022 (-0.249, 0.297)	0.873
	Precipitation	-0.092 (-0.232, 0.049)	0.201	-0.083 (-0.247, 0.083)	0.323
	Net primary productivity	0.146 (0.010, 0.283)	0.035*	0.223 (0.064, 0.387)	0.006***
	Solar radiation	0.059 (-0.125, 0.242)	0.529	-0.008 (-0.223, 0.209)	0.944
	UV-B radiation	-0.026 (-0.249, 0.196)	0.819	0.024 (-0.240, 0.286)	0.855
	Body mass	-0.247 (-0.345, -0.148)	<0.001***	-0.237 (-0.345, -0.127)	<0.001***
	Sexual dichromatism	0.288 (0.211, 0.363)	<0.001***	-0.059 (-0.146, 0.026)	0.179
	Social mating system	0.041 (-0.039, 0.120)	0.316	0.003 (-0.088, 0.094)	0.955
	Forest dependency	0.053 (-0.017, 0.121)	0.134	0.056 (-0.025, 0.137)	0.175
	Frugivore-nectarivore	0.059 (-0.018, 0.136)	0.132	0.074 (-0.012, 0.163)	0.094
	Migratory	0.004 (-0.081, 0.090)	0.933	-0.080 (-0.181, 0.020)	0.117
	Ground nesting	0.005 (-0.060, 0.071)	0.875	0.018 (-0.058, 0.094)	0.650
	Territoriality	-0.116 (-0.195, -0.037)	0.004**	-0.040 (-0.130, 0.050)	0.382
	Community diversity	0.096 (-0.002, 0.196)	0.057	0.133 (0.016, 0.250)	0.026*

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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. UVS, ultraviolet sensitive; VS, violet sensitive. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. All models were run over 100 posterior phylogenetic trees.