Climate, habitat, and geographic range overlap drive plumage evolution

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Organismal appearances are shaped by selection from both abiotic and biotic drivers¹⁻⁵. For example, Gloger's rule describes the pervasive pattern that more pigmented populations are found in more humid areas^{1,6,7}, and substrate matching as a form of camouflage to reduce predation is widespread across the tree of life⁸⁻¹⁰. Sexual selection is a potent driver of plumage elaboration^{5,11}, and species may also converge on nearly identical colours and patterns in sympatry, often to avoid predation by mimicking noxious species^{3,4}. To date, no study has taken an integrative approach to understand how these factors determine the evolution of colour and pattern across a large clade of organisms. Here we show that both habitat and climate profoundly shape avian plumage. However, we also find a strong signal that many species exhibit remarkable convergence not explained by these factors nor by shared ancestry. Instead, this convergence is associated with geographic overlap between species, suggesting strong, albeit occasional, selection for interspecific mimicry. Consequently, both abiotic and biotic factors, including interspecific interactions, are potent drivers of phenotypic evolution.

Birds are frequently studied for the insights they can offer to our understanding of phenotypic evolution^{11,12}. Yet, we still do not understand how factors such as climate, substrate matching, and sexual selection interact to influence phenotypic evolution across a large clade of birds (or any other large organismal radiation, for that matter). Here, we employ a novel phylogenetic comparative framework, coupled with remote-sensing data and a large citizen science dataset, to examine the combined effects of climate, habitat, evolutionary history, and social selection for mimicry on plumage pattern and colour evolution in woodpeckers. This diverse avian clade of 230 species is an excellent group to examine how external phenotypes evolve because they occupy a broad range of climates across many habitats globally, and display

patterns of rapid divergence in appearance, as well as striking convergences. A complete, time-calibrated phylogeny, which we incorporated into our analyses here, recently highlighted the magnitude of some of these convergences¹³. Woodpeckers have evolved a wide range of plumages; from species with boldly marked black and white patterns and others with large bright red patches, to other species that are entirely dull olive (Fig. 1). This variation provides the raw material with which to disentangle the contribution of the various abiotic and biotic factors that may drive plumage evolution. Moreover, there are several cases of ostensible plumage mimicry within woodpeckers^{14,15}; whether such cases represent biotic or socially driven convergence, or whether they can be explained by shared ancestry, climate, or habitat space remains untested.

We used multidimensional-colour and pattern-quantification tools to measure species' colouration and patterns, quantifying species' plumages from a standardized source (Figs. 2-3)^{11,16,17}. Evidence suggests that pattern and colour are likely processed separately in vertebrate brains, with achromatic (i.e., luminance) channels being used to process pattern information¹⁸ and differential stimulation of cones encoding chromatic information¹⁹. While both plumage colour and pattern are inherently multivariate, we reduced this complexity into a composite matrix of pairwise species differences. We could then address whether purported convergences were a mere by-product of shared evolutionary history or, if not, which of the aforementioned factors were responsible. We incorporated the potential for interactions between pairs of species into the analysis by quantifying pairwise geographic range overlap using globally crowd-sourced citizen science data from eBird²⁰; species in complete allopatry have no chance of interacting, while increasing degrees of sympatry should correlate with the probability of evolutionarily meaningful interactions.

Comparing species-level pairwise distance matrices revealed that variation in climate ($r = 0.055$, $p = 0.006$), habitat ($r = 0.106$, $p = 0.007$) and, to a lesser degree, phylogenetic relationships ($r = 0.001$, $p = 0.015$) are all correlated with woodpecker plumage similarity scores. Overall, woodpecker species in similar climates and habitats tend to look alike, even after accounting for shared ancestry. However, we also found that close sympatry was a strong predictor of plumage similarity for the most similar-looking species pairs (Extended Data Fig. 1). We interpret this result as evidence for widespread plumage mimicry *per se*, separate from any broader patterns of environmentally-driven plumage convergence. Following this result, we developed a novel method to identify the species pairs that powered this striking result. Many previously suggested mimicry complexes were, in fact, responsible, including the Downy-Hairy Woodpecker system (Fig. 1)²¹, repeated convergences between members of *Veniliornis* and *Piculus*²², *Dinopium* and *Chrysocolaptes*, *Dryocopus* and *Campephilus*²³, and the remarkable convergence of *Celeus galeatus* on the latter two genera¹⁵. Collectively, this combination of distance matrix-based analyses provides powerful understanding of the importance of various factors in driving evolutionary patterns of mimicry and divergence. To gain further insight into the evolutionary drivers of particular colours and patterns, we delved deeper with species-level phylogenetic comparative approaches.

We found that precipitation consistently drives global patterns of plumage pigmentation and patterning in woodpeckers. We show that darker species tend to inhabit areas of higher precipitation (phylogenetic generalized least squares [PGLS], $r^2 = 0.08$, $p < 0.001$), supporting Gloger's rule¹. While not unexpected, this is the first time that Gloger's rule has been quantitatively assessed for a large, globally distributed clade. The mechanism underlying Gloger's rule remains debated, but may include a response to increased predation pressure in the

tropics²⁴ via background matching²⁵, or defence against feather-degrading parasites²⁶. In addition to providing support for Gloger's rule, wherein precipitation is correlated with dark plumage, we show that precipitation is also associated with reduced patterning (PGLS $r^2 = 0.15$, $p < 0.001$). These results could be interpreted as support for either or both proposed mechanisms. For example, there are some boldly marked woodpecker species in humid areas, but they invariably achieve these conspicuous phenotypes with minimal use of white plumage, suggesting an evolutionary trade-off wherein Gloger's rule is due, at least in part, to the ability of melanin to forestall feather wear²⁶. Alternatively, unconcealed large, white plumage patches might simply subject humid forest-dwelling birds to evolutionarily unacceptable levels of predation. While additional research is necessary to pin down the mechanism(s) responsible, our results expand the generality of Gloger's rule and show that it may be involved in phenotypic convergence among disparate lineages inhabiting similar forests. For example, *Micropternus brachyurus* is not closely related to the members of *Celeus*, as was long thought, and instead simply occupies Asian forests of similar physiognomy to those inhabited by some Neotropical *Celeus*.

Seasonality, in addition to total precipitation, also exerts significant influence on woodpecker plumage. The gradient from dark- to light-plumaged woodpeckers (colorPC1) was best explained by a model that included body mass, latitude, and seasonality in precipitation. Darker birds are larger, are found at lower latitudes, and in climates that receive much precipitation throughout the year (PGLS $r^2 = 0.08$, $p < 0.001$, Fig. 4a). The gradient from red to green plumaged woodpeckers (colorPC2) was best explained by a model that included variation in temperature seasonality, and included the dichotomy between open habitats and closed forests. Specifically, green birds tend to be found in climates that experience seasonal temperature fluctuations, and in open habitats (PGLS $r^2 = 0.07$, $p < 0.001$, Fig. 4b). Moreover, boldly marked

birds tend to be found in seasonal climates, open habitats, and temperate forests, and the gradient from boldly to subtly marked birds was best explained by a model that included variation in temperature seasonality, and the dichotomies between open habitats and closed forests, and between dense tropical forests and temperate forests (PGLS $r^2 = 0.15$, $p < 0.001$, Fig. 4c). We had suspected that variation along the gradient from species with large plumage elements to those with barring and spotting (pattern PC2) might be associated with sexual selection, but after accounting for body mass, pattern PC2 was not associated with sexual size dimorphism; instead, smaller birds simply tended to be more finely marked (PGLS $r^2 = 0.04$, $p = 0.01$, Fig. 4d). This plumage pattern gradient was not closely associated with any climate or habitat gradient, and we could find no evidence that sexual selection shapes woodpecker plumage in any consistent way across taxa.

Although climate and habitat appear responsible for some of the convergence in external appearance in woodpeckers, our analyses confirmed the decades-old suggestions²⁷ that some species have converged above and beyond what would be expected based only on selection pressures from the environments they inhabit. Sympatry, a proxy for the likelihood of evolutionarily meaningful interspecific interactions, was a strong predictor of plumage similarity for species exhibiting large geographic range overlaps (Extended Data Fig. 1). Given that sympatry itself is implicated in plumage convergence, the evidence indicates that such convergence is true mimicry, i.e., phenotypic evolution by one or both parties in response to a shared signal receiver^{3,4}. Indeed, our study almost certainly underestimates the degree to which close sympatry leads to mimicry in woodpeckers: some mimetic dyads are well known to track one another at the subspecific level. Recent taxonomic revision of *Chrysocolaptes*²⁸ that is not yet matched by equivalent efforts in *Dinopium* means that additional parallel mimicry in this

complex was not entirely accounted for in our study (e.g., the extraordinary convergence between the Sri Lankan endemics *C. stricklandii* and *D. benghalense psarodes*). There are two contested questions regarding plumage mimicry: whether it truly occurs^{23,27,29} and, if it does, what process(es) drive the pattern^{30–33}. Here we have shown that plumage mimicry does indeed occur and is pervasive across the woodpecker evolutionary tree, indicating that the processes deserve further study.

Few studies^{21,34} have empirically demonstrated that convergence on the scale which we document among woodpeckers is not exclusively a product of shared evolutionary history. Nevertheless, several mechanisms have been proposed to explain convergent evolutionary trajectories of external appearance^{27,31,32,35,36}. Recently, it has been shown³³ that the smaller species in plumage mimicry complexes may derive a benefit by fooling third parties into believing they are the socially dominant model species, and currently this remains the only empirically supported hypothesis. An open question is how distantly related lineages genomically achieve plumage convergence. It is unclear whether multiple mutations are required, each of which increases the degree of plumage convergence, or if selection acts on genetic modules controlled by fewer loci that shape overall plumage and are shared across all woodpeckers, or if possibly rare hybridization events between sympatric species have resulted in adaptive introgression of relevant plumage control loci^{22,37}.

In summary, we provide the first demonstration of selection promoting the evolution of mimicry at a broad phylogenetic scale. Additionally, we provide novel, comprehensive tests of longstanding hypotheses about the relative importance of abiotic and biotic factors to the evolution of organisms' external appearances. Because we incorporated enormous variation in plumage, climate, habitat, and geographic range overlap into our phylogenetic comparative

framework, our explanatory power was limited. Nevertheless, our simplified univariate PGLS approach corroborated the finding that climate and habitat can drive phenotypic evolution in predictable ways across a globally distributed clade of birds. Moreover, we showed that the convergence predicted by shared climate, habitat, and evolutionary history is insufficient to explain the prominent, geographically-widespread convergent events that we detected between closely sympatric, but distantly related woodpecker species. The modern union of comprehensive, time-calibrated molecular phylogenies, massive distributional databases like eBird, and powerful computing techniques like pattern analysis enables rigorous testing of hypotheses first put forth centuries ago. Within this framework, our results provide quantitative details of the abiotic and biotic factors, including interspecific signalling, that act as potent drivers of phenotypic evolution.

METHODS

Taxonomic reconciliation and creation of a complete woodpecker phylogeny A time-dated phylogeny containing nearly all known woodpecker species was recently published by Shakya and colleagues ¹³. As described below, we used illustrations from the Handbook of the Birds of the World Alive ¹⁶ to quantify woodpecker plumage, and we used eBird ²⁰, a massively crowd-sourced database, to define spatial, climate, and habitat overlap between species. Each of these references uses a slightly different taxonomy. Our goal was to use the species-level concepts from the most recent eBird/Clements taxonomy ³⁸ as our final classification system.

To reconcile these three taxonomies (HBW, Shakya et al., and eBird/Clements), we first identified any taxon that was represented by multiple tips in the Shakya et al. (2017) tree. All of the species represented by multiple tips were monophyletic except one: *D. moluccensis*. However, eBird only recognizes a single taxon of this species. Thus, we simply dropped all but one instance of all species represented by multiple tips in the Shakya tree. In the process, we noted that *Dendrocopos medius* is represented by multiple tips in the Shakya tree, but the second instance is listed under *Leiopicus medius*. The two sequenced specimens are monophyletic, so we dropped the latter. We then identified all named woodpecker taxa in eBird. We allocated these to their respective terminals in the Shakya tree manually, to ensure accurate matches. For example, *Picus miniaceus* eBird records were allocated to *Chrysophlegma miniaceum* from the Shakya tree, and the tip renamed accordingly. This process made it clear which species, as recognized by eBird, were missing from the Shakya tree.

Twenty-one such missing taxa were identified: *Picumnus fuscus*, *P. limae*, *P. fulvescens*, *P. granadensis*, *P. cinnamomeus*, *Dinopium everetti*, *Gecinulus viridis*, *Mulleripicus fulvus*,

Piculus simplex, *Dryocopus hodgei*, *Melanerpes pulcher*, *Xiphidiopicus percussus*, *Veniliornis maculifrons*, *Dendrocopos analis*, *Dendrocopos ramsayi*, *Colaptes fernandinae*, *Chrysocolaptes festivus*, *C. xanthocephalus*, *C. strictus*, *C. guttacristatus*, and *C. stricklandi*. We added these using the R package *addTaxa*³⁹, and taxonomic hypotheses outlined in previous work (reviewed in¹³). Eighteen of these taxa have fairly precise hypothesized taxonomic positions which we were able to leverage to carefully circumscribe where they were bound into the tree. As an example, *Dinopium everetti* was recently split from *D. javanense*, so it was simply added as sister to the latter species in the final tree. The precise phylogenetic positions of the remaining three taxa are less well known. For these, we first added *C. fernandinae* as sister to *Colaptes sensu stricto* (as previously found⁴⁰), then added *Piculus simplex* into the clade *Piculus* + *Colaptes*, as previous work showed some members of the former genus to actually belong to the latter⁴⁰. We added *X. percussus* as sister to *Melanerpes striatus* (reasons summarized in Shakya et al. (2017); and we added *P. cinnamomeus* into *Picumnus* while ensuring that the Old World *P. innominatus* remained sister to the rest of the genus (it is very likely the New World *Picumnus* form a clade). Finally, we dropped a few tips from the phylogeny that represent splits not currently recognized by eBird: *Celeus ochraceus*, *Melanerpes santacruzi*, and *Picus sharpei*. The resulting tree contained 230 species. For each of these taxa, we identified the illustration that best represented it in the Handbook of the Birds of the World Alive. When the latter recognized multiple subspecies for a given taxon from the final tree, we used the nominate subspecies as our unit of analysis for colour and pattern (see below).

Quantifying plumage colour and pattern from illustrations We calculated plumage colour and pattern scores for males of 230 species of woodpeckers using digital images of colour plates

obtained from *The Handbook of the Birds of the World Alive* ¹⁶. Each image was imported to Adobe Photoshop (Adobe Inc. San Jose, CA) at 300 dots per inch, scaled to a uniform size, and saved as a Tagged Image File (.TIF). Following creation of .TIF files, we ran a custom macro in ImageJ ⁴¹ to sample the red (R), green (G), and blue (B) pixel values for each of 1,000 random, 9-pixel-diameter circles from each woodpecker image (macro code will be made available with data upon acceptance). RGB values were transformed to CIELAB coordinates, which is an approximately perceptually-uniform colour space (distance between points is perceptually equivalent in all directions) ^{42,43}. To calculate pairwise colour dissimilarity scores, we plotted the 1,000 colour measurements from the first species (e.g., species A) in 3-dimensional CIELAB space, as well as the 1,000 measurements for the second species (e.g., species B) in the dyadic comparison. We then calculated the average Mahalanobis distance ⁴⁴ between the colours representing species A and the colours representing species B. We repeated this process for every possible combination (26,335 unique dyadic combinations) to generate an overall colour dissimilarity matrix. Additionally, to facilitate a more in-depth investigation of the underlying variation in colour among species, as well as how such variation is related to environmental, genetic, and geographic influences we conducted principal components analysis (PCA) on all 230,000 colour measurements. Following PCA, we averaged principal component (PC) scores for each species to create mean PC scores describing the average colour values for each species (Fig. 2). PC1 describes a dark-to-bright continuum, as well as a blue-to-yellow continuum (high loadings for L* and b*; Extended Data Table 1; Fig. 2), while PC2 primarily describes a red-to-green continuum (high loadings for a*; Extended Data Table 1; Fig. 2).

We conducted pattern analyses on the same, scaled .TIF files for each species in ImageJ ⁴¹. First, we split each image into R, G, B slices and then used the G layer for pattern analysis

because this channel corresponds most closely to known avian luminance channels^{45,46}, which is thought to be primarily responsible for processing of pattern information^{18,19}. We then used the Image Calibration and Analysis Toolbox⁴⁷ in ImageJ to conduct granularity-based pattern analysis. In this process, widely used to study animal patterning^{48–51}, images are Fast Fourier band pass filtered into a number of granularity bands that correspond to different spatial frequencies. For each filtered image, the “energy” at that scale is quantified as the standard deviation of filtered pixel values and corresponds to the contribution to overall appearance from pattern elements of that size. Pattern energy spectra were calculated for each species in a comparison across 17 bandwidths (from 2 pixels to 512 pixels, by multiples of $\sqrt{2}$), which we used for both pairwise pattern comparisons (pattern maps can be created to visualize differences; Fig. 3a), and to categorize overall plumage pattern with PCA (Fig. 3c,d). Pattern difference values were calculated by summing absolute differences between energy spectra at each bandwidth⁴⁷, and principal components analyses revealed that the first three PCs explained ~93% of the variance in overall pattern energy (Fig. 3c; Extended Data Table 2) across species (Fig. 3d). Pattern PC1 has large positive loadings for most element sizes/granularities, indicating that species with high PC1 scores have numerous pattern elements of different sizes (whereas species with low PC1 are relatively homogenous and with little overall patterning; Fig. 3d). Pattern PC2 has large positive loadings for small pattern elements, and negative loadings for intermediate and large pattern sizes such that species with high PC2 scores have lots of small pattern components, and species with low PC2 scores have more intermediate and large pattern size contributions (Fig. 3d).

Photographic quantification of woodpecker plumage colour and pattern To validate the use of colour plates for quantifying meaningful interspecific variation in plumage colour and pattern among woodpeckers, we employed digital photographic and visual ecology methods to quantify the appearance of museum specimens and compared these results to those obtained using the colour plates. Specifically, we used ultraviolet and visible spectrum images to create standardized multispectral image stacks and then converted these multispectral image stacks into woodpecker visual space. Photos were taken with a Canon 7D camera with full-spectrum quartz conversion fitted with a Novoflex Noflexar 35 mm lens, and two Baader (Mammendorf, Germany) lens filters (one transmitting only UV light, one transmitting only visible light). We took profile-view photograph pairs (one visible, one UV) under full-spectrum light (eyeColor arc lamps, Iwasaki: Tokyo, Japan, with UV-coating removed), then converted these image stacks into woodpecker visual space using data from *Dendrocopos major*⁵² and average visual sensitivities for other violet-sensitive bird species⁵³. The inferred peak-sensitivity (λ_{max}) for the short-wavelength sensitive 1 (SWS1) cone of Great Spotted Woodpeckers, based on opsin sequence, is 405 nm⁵². After generating images corresponding to the quantum catch values (i.e., stimulation of the different photoreceptor types), we performed granularity-based pattern analyses with the Image Calibration and Analysis Toolbox⁴⁷ in ImageJ⁴¹ using the image corresponding to the stimulation of the avian double-cone, responsible for luminance detection^{45,46}, because this photoreceptor type is assumed to be involved in processing pattern information from visual scenes^{18,19}. Additionally, because relative stimulation values do not generate perceptually-uniform colour spaces^{54,55}, we implemented visual models⁵⁶ to generate Cartesian coordinates for the colour values from each of 1,000 randomly selected, 9-pixel diameter circles for each specimen and viewpoint (as we did with colour plates). Cartesian coordinates in this

perceptually-uniform woodpecker colour space were then used to calculate pair-wise Mahalanobis distances⁴⁴ for each dyadic combination of measured specimens.

As with our colour plate-based analysis, we Z-score transformed colour and pattern distances (mean = 0, $SD = 1$), then combined these distances to create a composite plumage dissimilarity matrix incorporating overall plumage colour and pattern. Based on specimens available at the Cornell University Museum of Vertebrates, we endeavoured to measure up to three male specimens from at least one species of every woodpecker genus. We were able to measure 56 individuals from 23 woodpecker species (Extended Data Table 3). To compare the museum-based results to those from the colour plates, we derived species-level pairwise distances. We did so by finding the mean plumage distance between all specimens of one species and all of those of another, and repeating for all possible species pair comparisons. We repeated this process for both the colour only dissimilarity matrix, and the combined colour and pattern matrix. We subset the larger, plate-based colour-only and colour-plus-pattern matrices to the corresponding species, and compared the relevant matrices with Mantel tests. Our results from the museum specimens substantiated those from the illustrations—we found tight correlations between colour dissimilarity (measured from specimens vs. measured from illustrations; $r = 0.74, p < 0.001$) and overall plumage dissimilarity (measured from specimens vs. measured from illustrations $r = 0.72, p < 0.001$).

eBird data management, curation, and analysis On 24 November, 2017 we queried the eBird database for all records of each of the 230 species in our final woodpecker phylogeny. We excluded records for which we had low confidence in the associated locality information. Specifically, we excluded: 1) historical records, which are prone to imprecise locality

information and are not associated with effort information, 2) records from (0°, 0°), 3) records that were considered invalid after review by a human (thus, flagged but unreviewed records were included), and 4) records that came from transects of longer than 5 km in length. Because eBird has grown exponentially in recent years, we connected directly to the database to ensure maximal data coverage for infrequently reported species. We made this analytical decision because the automatic filters that flag unusual observations can be imprecise in regions of the globe infrequently visited by eBirders; flagged observations remain unconfirmed (and not included in products such as the eBird basic dataset) until they are reviewed, and backlogs of unreviewed observations exist in some infrequently birded regions. This approach allowed us to increase our sample size for infrequently observed species. In contrast, other species are very well represented in the database. To reduce downstream computational loads, we used the R package *ebirdr* (<https://github.com/eliotmiller/ebirdr>) to downsample overrepresented species in a spatially stratified manner. Specifically, for each of the 230 species, we laid a grid of 100 x 100 cells over the species' extent, and randomly sampled and retained 60 points per cell. For most species, this had little to no effect, and fewer than 10% of points were thinned and removed from analysis; for a small number of well-sampled North American species, this excluded over 90% of points from analysis (Extended Data Table 4). In sum, this process reduced the original dataset from 13,513,441 to 1,037,628 records.

We used the R package *hypervolume*⁵⁷ to create pseudo-range maps around each species' point locations. Hypervolumes account for the density in the underlying points and can have holes in them, and are therefore much better suited to describing species' ranges than are, e.g., minimum convex polygons⁵⁷. For every dyadic comparison (i.e., for every species pair comparison), we used *hypervolume* to calculate the Sørensen similarity index between the

species' inferred geographic ranges. We summarized these similarities in a pairwise matrix, which we subsequently converted to a dissimilarity matrix such that a value of 1 represented complete allopatry (no overlap in geographic distributions), and a value of 0 represented perfect sympatry (complete overlap in geographic distributions).

We used the *raster* package to match each species' point locations to climatic data at each point using WorldClim bioclimatic data⁵⁸. These data describe the annual and seasonal climatic conditions around the globe. After querying species' climatic data, we bound the resulting files together and ran a single large correlation matrix PCA across all climate variables except bio7, which is simply the difference between bio5 and bio6. We retained species' scores along the different PC axes, and used scores along the first two PC axes to calculate species-level hypervolumes in climate space. These first two axes explained 85% of the variance in the climates occupied by woodpeckers. The first axis described a gradient from places that are warm in general, and that are not cold in winter, to areas that show seasonal variation in temperature and large diurnal shifts in temperature. The second axis described a gradient from areas that receive precipitation in seasonal pulses, have some hot months and have large swings in temperature over the course of a day, to areas that always receive lots of rain. Again, for each dyadic comparison, we calculated a Sørensen similarity index, and then converted the resulting values to a dissimilarity matrix.

Querying habitat data We used *ebirdr*, which harnesses GDAL (<http://www.gdal.org/>), to bind species' point locations into ~50 MB-sized tables, then converted the resulting tables into KML (Keyhole Markup Language) files, which we uploaded and converted into Google Fusion Tables (<https://fusiontables.google.com>). This particular file size was chosen after we employed a trial-

and-error process to determine the most efficient query size for Google Earth Engine (see below). Once accessible as a Fusion Table, we fed the tables into custom Google Earth Engine scripts. For every eBird observation, these scripts identified the MODIS satellite reflectance values⁵⁹ from the observation location within a 16-day window of the observation. We queried data specifically from the MODIS MCD43A4 Version 6 Nadir Bidirectional reflectance distribution function Adjusted Reflectance (NBAR) data set, a daily 16-day product which “provides the 500 meter reflectance data of the MODIS ‘land’ bands 1-7 adjusted using the bidirectional reflectance distribution function to model the values as if they were collected from a nadir view” (<https://lpdaac.usgs.gov/node/891>). At the time of query, this dataset was available for the time period 18 February 2000 to 14 March 2017, which corresponded to the time period in which most of our eBird records were recorded. The year of all other records was adjusted up or down to fall within the available satellite data, e.g., observations from 10 November 2017 became 10 November 2016. This method is appealing in that it incorporates species’ spatiotemporal variation in habitat availability and use, although for most woodpecker species such variation is minimal.

After querying species’ habitat data, we downloaded and combined the resulting files from Google Earth Engine, dropping any records that were matched to incomplete MODIS data. *ebirdr* contains functions to automatically combine and process these files from Google Earth Engine. We then ran a single large correlation matrix PCA across all 7 MODIS bands. Before doing so, we natural log-transformed bands 1, 3, and 4, as a few extreme values along these bands hampered our initial efforts to ordinate this dataset. We retained the first two PC axes, which explained 81% of the variance in the habitats occupied by woodpeckers. The first described a gradient from closed forests to open, reflective habitats. The second described a

gradient from regions with high visible and low infrared reflectance to those with low visible and high infrared reflectance. This dichotomy is used to identify snow in MODIS snow products (https://modis.gsfc.nasa.gov/data/atbd/atbd_mod10.pdf). Thus, at the species-average level, the second habitat PC axis functionally described a gradient between seasonally snow-covered (temperate) forests and tropical woodland. Again, for each dyadic comparison, we calculated a Sørensen similarity index, and then converted the resulting matrix to a dissimilarity matrix.

Multiple distance matrix regression After the steps described above, we had data of four variables hypothesized to explain plumage variation across woodpeckers in the form of four pairwise distance matrices: genetic distances, climate dissimilarity, habitat dissimilarity, and geographic range dissimilarity. We combined the plumage colour and the plumage pattern dissimilarity matrices into a single matrix by independently standardizing each using z-scores, then calculating the element-wise sum of each dyadic comparison. We then related the four explanatory matrices to the single dependent plumage dissimilarity matrix using multiple distance matrix regression, with 999 permutations⁶⁰. The resulting model was highly significant ($p = 0.001$), but fairly low in explanatory power ($r^2 = 0.03$), reflecting the massive variation incorporated into these five 230 x 230 matrices. Three of the four dissimilarity matrices were significantly and positively associated with plumage dissimilarity: increasing genetic distance ($p = 0.02$), climate dissimilarity ($p = 0.007$), and habitat dissimilarity ($p = 0.006$) all lead to increasing plumage dissimilarity. At this scale, geographic range dissimilarity was not significantly associated with plumage dissimilarity.

Modified Mantel correlogram The likelihood that sympatric species evolve plumage mimicry is not thought to be monotonically related to range overlap. Instead, hypotheses to explain plumage mimicry propose that only certain species pairs that are both closely sympatric and ecologically similar will converge dramatically in appearance¹⁴. Thus, we did not expect a continuous relationship between geographic range dissimilarity and plumage dissimilarity; rather, we expect plumage convergence in only dyads with high geographic overlap (greater than some threshold). We therefore implemented a modified Mantel correlogram approach to test whether such a threshold existed⁶¹. For this, we manually created a series of matrices where we converted all elements in the plumage dissimilarity matrix to values of 1, except for dyads with plumage dissimilarity scores in a certain range. Specifically, the dissimilarity scores within a given range for a given analysis (ranges tested: 0-0.1, 0.1-0.2, 0.2-0.25, 0.25-0.3, 0.3-0.35, 0.35-0.4, 0.4-0.5, 0.5-0.6, 0.6-0.7, 0.7-0.8, 0.8-0.9, and 0.9-1) were set to a value of 0, and all other dissimilarity scores remained unmanipulated. We then sequentially input these matrices as the dependent variable into the same multiple distance matrix regression described above, repeatedly calculating the significance and partial correlation coefficient of the geographic range dissimilarity matrix with that of plumage dissimilarity. This approach allowed us to examine how the correlation between plumage and range dissimilarities varied across a range of plumage dissimilarities, while simultaneously incorporating the influences of evolutionary relationships, and climate and habitat dissimilarities.

We found that geographic range dissimilarity was significantly associated with plumage dissimilarity for the most similar looking species pairs (Extended Data Fig. 1). Dyadic comparisons with plumage dissimilarities of 0-0.2 include such pairs as *Picoides pubescens* and *Picoides villosus* (purported plumage mimics), *Gecinulus grantia* and *Blythipicus pyrrhotis*

(which are quite similar looking), and *Picus awokera* and *Melanerpes striatus* (not closely similar, but do share colour and pattern elements). Notably, the relationship was reversed at intermediate levels of plumage dissimilarity; species pairs that phenotypically differed by 25-35% were associated with partial but incomplete range overlap. Dyadic comparisons with dissimilarities in this range include *Campethera abingoni* and *C. maculosa* and *Veniliornis spilogaster* and *Celeus obrieni*. This pattern mirrors recent results showing the greatest degree of plumage differentiation between pairs of birds at intermediate levels of sympatry⁶². The fact that some degree of sympatry is associated with rapid plumage divergence is expected by theory⁶³, and is likely due to strong selection to avoid unsuccessful hybridization (i.e., reinforcement), or to avoid accidentally targeting heterospecifics for aggression⁶⁴. Whether the relaxation of plumage divergence in closer sympatry could be attributed to shared habitats or climates, or to some other selective pressure, was heretofore unknown⁶². We show that, remarkably, in woodpeckers, after accounting for other likely selective forces, either one or both of the species in pairs that have attained close sympatry may evolve towards the phenotype of the species with which they co-occur.

Identification of putative plumage mimics We developed a novel and powerful method to identify high-leverage dyadic comparisons in Mantel tests and multiple distance matrix regressions. We used this to identify species pairs that have converged above and beyond that expected by shared climates and habitats. The process works as follows. In the first step, the observed correlation statistic is calculated. In our case, that was the correlation coefficient of a thresholded plumage dissimilarity matrix (values from 0-0.2 set to 0, all others set to 1) with the geographic range dissimilarity matrix. The statistic can also be the correlation coefficient from a

regular or partial Mantel test; we confirmed that the method yielded similar results when we employed it with a partial Mantel test between the continuous plumage dissimilarity matrix, geographic range dissimilarity, and genetic distance. In the second step, each element (dyad) in the relevant matrix is modified in turn, and the relevant correlation statistic calculated and retained after each modification. We tested three methods of modifying dyads, i.e., three different approaches to this second step. All yielded similar results. (A) The value can be randomly sampled from the off-diagonal elements in the matrix. (B) The value can be set to NA and the correlation statistic calculated using all complete observations. (C) For the thresholded matrix, the test element can be swapped for the other value; zeros become ones, and ones become zeros. In the third step, only necessary for approach A, the process is iterated multiple times, and the modified correlation coefficient for every element, at each iteration, is stored as a list of matrices. In the fourth step, again only necessary for approach A, these matrices are summarized by taking the element-wise average. In the fifth step, the leverage of each dyad is calculated by subtracting the observed correlation statistic from each element in the averaged matrix. Finally, the matrix can be decomposed into a pairwise table and sorted by the leverage of each dyad. In our case, dyads that have high leverage, and are large contributors to the positive correlation between close plumage similarity and geographic range overlap, have the largest negative values (i.e., modifying their observed plumage dissimilarity score most diminished the observed positive correlation between range and plumage).

We used this method to identify the most notable plumage mimics across woodpeckers, after accounting for shared evolutionary history, climate, and habitat use. Many purported mimicry complexes were responsible, including the Downy-Hairy system²¹, and repeated convergences between members of *Veniliornis* and *Piculus*²², *Dinopium* and *Chrysocolaptes*,

and *Dryocopus* and *Campephilus*²³. Convergence between the Helmeted Woodpecker (*Dryocopus*=*Celeus galeatus*) and *Campephilus robustus* was also detected¹⁵, as was convergence between members of *Thripias* and *Campethera*, *Meiglyptes* and *Blythipicus*, and *Hemicircus* and *Meiglyptes*.

Phylogenetic least squares regression We derived species' average scores along the first two axes of a plumage colour principal components analysis (PCA, Fig. 2), a plumage pattern PCA (Fig. 3), the climate PCA described above, the habitat PCA described above, and species' average latitude (absolute value) and longitude of distribution. Additionally, we mined body mass data from Dunning (2007). For those species for which mass was listed separately for males and females, we calculated sexual size dimorphism *sensu* Miles et al. (2018). These authors additionally reported dimorphism measures from a number of species not available in Dunning (2007). We then combined these datasets, resulting in sexual size dimorphism measures for 94 of 230 species. During this process, we noticed that one of the most well-known of sexually size-dimorphic species, *Melanerpes striatus*, was characterized in both databases as having larger females than males. This is incorrect—males are much larger than females—and we replaced the values with the midpoint of ranges given in del Hoyo et al. (2017). We used *Rphylopars*⁶⁷ to impute missing body mass and size dimorphism data, which we did using a Brownian motion model and the observed variance-covariance matrix between all traits except for plumage colour and pattern.

Treating climate, habitat, latitude, longitude, natural log body mass, and sexual size dimorphism as explanatory variables, we used multi-model inference to identify phylogenetic generalized least squares (PGLS) regression models that explained each of the four PCA

plumage axes of interest. We also visualized pairwise correlations and distributions of these traits using *corrplotter*⁶⁸ (Extended Data Fig. 2). We used a model averaging approach to determine which explanatory variables strongly influenced plumage (Fig. 4).

Code availability All computer code necessary to run these analyses is available in the purpose-built R package *ebirdr*, available at <https://github.com/eliotmiller/ebirdr>.

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Acknowledgements We thank T. Auer, D. Caetano, D. Fink, R. Grant, L. Harmon, W. Hochachka, K. Horton, S. Kelling, R. Maia, A. Patton, M. Pennell, M. Strimas-Mackey, D. Toews, J. Uyeda, C. Wood, and R. Zenil-Ferguson for statistical, graphical, and intellectual input. ETM, GML, and RAL were supported by NSF grants 1402506, 1523748, and 1523895,

respectively. ETM, GML, RAL, and ACL were supported by the Cornell Lab of Ornithology.
BGF was supported by Banting Canada (379958) and the Biodiversity Research Centre at the
University of British Columbia.

Author contributions ETM, GML, BGF, ACL, and RAL were responsible for
conceptualization and writing of the manuscript. ETM and RAL were responsible for analysis
and visualization.

Data deposition statement All data is available in the manuscript or the supplementary
materials.

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Competing interests The authors declare no competing interests.

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Fig. 1 | Evolutionary relationships and plumage similarity among exemplar species that shared a common ancestor ~6.5 mya. Climate partially determines variation in woodpecker plumage. Lines lead from tips of phylogeny (left) to centroid of each species' geographic distribution, and are coloured according to mean climate regime of each species. The colour scale depicts a gradient from warm (yellow) to seasonally cold regions (blue). eBird records for these species are plotted in the same colours as large points on the map. All other eBird woodpecker records are overlaid as smaller points and coloured similarly. Plumage dendrogram (right) shows the plumage dissimilarity relationships among the same set of species. *Veniliornis mixtus*, long classified as a member of *Picoides*, is inferred to have invaded seasonal climates in

667 the southern hemisphere, and accordingly evolved bold black and white plumage. *Picoides*
668 *fumigatus*, long classified as a member of *Veniliornis*, is inferred to have invaded warm climates
669 near the equator, and accordingly evolved dark, subtly marked plumage. *Picoides pubescens* and
670 *P. villosus* are rather distantly related but largely sympatric; they are inferred to have converged
671 on one another in plumage above and beyond what would be expected based on shared climate,
672 habitat, and evolutionary history. Illustrations © HBW Alive/Lynx Edicions.

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Fig. 2 | Principal components analysis (PCA) of species-averaged woodpecker colour values, used for species-level analyses (e.g., Fig. 4.). Principal component one (colourPC1) explains 45% of the variation in measured colour scores. Higher PC1 scores correspond to greater luminance values, and more yellow and less blue. Principal component two (colourPC2) explains an additional 36% of variation in overall colour scores. Higher PC2 scores correspond to more green and less red colouration. Coloured circles behind each woodpecker species

correspond to the average CIE L*a*b scores for the 1,000 randomly drawn colour samples from that species. Illustrations © HBW Alive/Lynx Edicions.

Fig. 3 | Major axes of plumage pattern variation quantified using granularity analysis, then summarized with a principal components analysis (PCA) for species-level approaches. (a) Pattern energy spectra for exemplar species characterized by maximally divergent PC scores (i = *Picoides villosus*, ii = *Mulleripicus funebris*, iii = *Colaptes fernandinae*, iv = *Melanerpes erythrocephalus*). These show information on relative contributions of different granularities to overall appearance. (b) Pattern maps of exemplar species enable visualization of energy at subsets of isotropic band-pass filter sizes (2, 32, 64, 128, 256, and 512 pixels). (c) Principal component loadings of pattern energy spectra across filter size for all species reveals how pattern

693 elements of different sizes influence PC scores. (d) Pattern PC1 and PC2, collectively, account
 694 for 82.1% of variation across woodpeckers. Exemplar species (i-iv) illustrate extreme variation
 695 in PC1: (i) exhibits high energy scores across most pattern element sizes, with small, medium,
 696 and large pattern elements; (ii) has low energy scores across the spectrum, with few pattern
 697 elements of any size. And, extreme variation in PC2: (iii) has many small pattern elements and
 698 few of any other sizes; (iv) has only medium and large size pattern elements. Illustrations ©
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Fig. 4 | Variable importance scores and model-averaged parameter estimates from

phylogenetic generalized least squares regressions. These quantify how colour and pattern

vary as a function of climate, habitat, body mass, sexual size dimorphism, latitude and longitude,

with summaries of the climate and habitat principal component analyses (PCA). Model-averaged

p-values of explanatory factors are colour-coded from yellow to blue; only factors with *p*-values

< 0.05 are coloured yellow and discussed here. (a) Dark birds are heavier and occur in wetter

709 climates. (b) Greenish (as opposed to reddish) birds are found in more open habitats. (c) Less-
 710 patterned birds are found in aseasonal climates, open habitats, and temperate forests. (d) Birds
 711 patterned in large plumage elements, such as large colour patches, tend to be larger in body size.
 712 (e) Climate PCA results, illustrating the distribution of woodpeckers in climate space, with
 713 qualitative descriptions of the first two PC axes. (f) Habitat PCA results, showing the distribution
 714 of woodpeckers across global habitats, with qualitative descriptions of the first two PC axes.
 715 Illustrations © HBW Alive/Lynx Edicions.

Extended Data Table 1 | Principal components analysis of 230,000 CIELAB color values (1,000 samples from each of 230 woodpecker species). The first two PCs explain ~82% of the variance in color. PC1 has high loading values for luminance (L*) and yellowness (positive values of b*), and PC2 has high loading values for greenness (negative values of a*).

	PC1	PC2	PC3
<i>Eigenvalues</i>	1.17	1.04	0.74
<i>Proportion of Variance</i>	0.46	0.36	0.18
<i>Cumulative Proportion of Variance</i>	0.46	0.82	1
Color variable	<i>PC loadings</i>		
L*	0.70	0.29	-0.65
a*	0.01	-0.92	-0.39
b*	0.71	-0.27	0.65

Extended Data Table 2 | Principal components analysis of pattern energy spectra across 230 species of woodpeckers. The three PC axes explain ~93% of the variance in pattern across all species.

	PC1	PC2	PC3
Standard deviation	3.08	2.12	1.34
Proportion of Variance	0.56	0.26	0.11
Cumulative Proportion	0.56	0.82	0.93

Extended Data Table 3 | Synopsis of specimens from the Cornell University Museum of Vertebrates (CUMV) used for color and pattern analyses.

Species (our taxonomy)	Species (on CUMV tag)	CUMV tag subspecies	CUMV collection number	Location
<i>Xiphidiopicus percussus</i>	<i>Xiphidiopicus percussus</i>	<i>percussus</i>	22746	Cuba
<i>Xiphidiopicus percussus</i>	<i>Xiphidiopicus percussus</i>	<i>percussus</i>	6498	Cuba
<i>Xiphidiopicus percussus</i>	<i>Xiphidiopicus percussus</i>	<i>percussus</i>	6497	Cuba
<i>Sphyrapicus varius</i>	<i>Sphyrapicus varius</i>	NA	55875	NY
<i>Sphyrapicus varius</i>	<i>Sphyrapicus varius</i>	NA	53166	NY
<i>Sphyrapicus varius</i>	<i>Sphyrapicus varius</i>	NA	30185	NY
<i>Melanerpes carolinus</i>	<i>Melanerpes carolinus</i>	NA	51400	NY
<i>Melanerpes carolinus</i>	<i>Melanerpes carolinus</i>	NA	55391	NY
<i>Melanerpes carolinus</i>	<i>Melanerpes carolinus</i>	NA	6198	TN
<i>Dendrocopos major</i>	<i>Dendrocopos major</i>	NA	6542	France
<i>Dendrocopos major</i>	<i>Dendrocopos major</i>	NA	6540	Germany
<i>Dendrocopos major</i>	<i>Dendrocopos major</i>	NA	6541	Italy
<i>Colaptes rubiginosus</i>	<i>Colaptes rubiginosus</i>	NA	34519	Chiapas
<i>Colaptes rubiginosus</i>	<i>Colaptes rubiginosus</i>	NA	6335	Motzorongo, Veracruz
<i>Mesopicos goertae</i>	<i>Mesopicos goertae</i>	NA	33636	Uganda
<i>Mesopicos goertae</i>	<i>Dendropicos spodocephalus</i>	NA	33640	Kenya
<i>Mesopicos goertae</i>	<i>Dendropicos spodocephalus</i>	<i>rhodeogaster</i>	6524	illegible
<i>Picoides villosus</i>	<i>Picoides villosus</i>	<i>villosus</i>	6406	NY
<i>Picoides villosus</i>	<i>Picoides villosus</i>	<i>villosus</i>	6407	NY
<i>Picoides villosus</i>	<i>Picoides villosus</i>	<i>villosus</i>	6415	NY
<i>Picoides albolarvatus</i>	<i>Picoides albolarvatus</i>	<i>albolarvatus</i>	6736	CA
<i>Picoides albolarvatus</i>	<i>Picoides albolarvatus</i>	<i>albolarvatus</i>	6733	CA
<i>Picoides albolarvatus</i>	<i>Picoides albolarvatus</i>	NA	22183	WA
<i>Picus viridis</i>	<i>Picus viridis</i>	<i>virescens</i>	7762	England
<i>Picus viridis</i>	<i>Picus viridis</i>	<i>virescens</i>	7763	England
<i>Dendropicos fuscescens</i>	<i>Dendropicos fuscescens</i>	<i>fuscescens</i>	6530	Angola
<i>Dendropicos fuscescens</i>	<i>Dendropicos fuscescens</i>	<i>fuscescens</i>	6529	Angola
<i>Dendropicos fuscescens</i>	<i>Dendropicos fuscescens</i>	NA	32433	Southwest Africa
<i>Picoides pubescens</i>	<i>Picoides pubescens</i>	<i>medianus</i>	6569	NY
<i>Picoides pubescens</i>	<i>Picoides pubescens</i>	<i>medianus</i>	6593	NY
<i>Picoides pubescens</i>	<i>Picoides pubescens</i>	<i>medianus</i>	6571	NY

<i>Veniliornis kirkii</i>	<i>Veniliornis kirkii</i>	NA	26606	Colombia
<i>Veniliornis kirkii</i>	<i>Veniliornis kirkii</i>	<i>neglectus</i>	6518	Costa Rica
<i>Dryocopus pileatus</i>	<i>Dryocopus pileatus</i>	NA	52879	NY
<i>Dryocopus pileatus</i>	<i>Dryocopus pileatus</i>	NA	54931	NY
<i>Dryocopus pileatus</i>	<i>Dryocopus pileatus</i>	NA	53082	NY
<i>Dinopium benghalense</i>	<i>Dinopium benghalense</i>	<i>benghalense</i>	23454	India
<i>Campephilus guatemalensis</i>	<i>Campephilus guatemalensis</i>	NA	29193	Honduras
<i>Campephilus guatemalensis</i>	<i>Campephilus guatemalensis</i>	<i>guatemalensis</i>	6397	Costa Rica
<i>Campephilus guatemalensis</i>	<i>Campephilus guatemalensis</i>	<i>regius</i>	6402	Mexico
<i>Campethera nivos</i>	<i>Campethera nivos</i>	<i>efulenensis</i>	6519	Cameroon
<i>Campethera nivos</i>	<i>Campethera nivos</i>	NA	29775	Nigeria
<i>Campethera nivos</i>	<i>Campethera nivos</i>	NA	33632	Uganda
<i>Gecinulus grantia</i>	<i>Gecinulus grantia</i>	NA	6464	India
<i>Blythipicus pyrrhotis</i>	<i>Blythipicus pyrrhotis</i>	NA	6479	India
<i>Hemicircus canente</i>	<i>Hemicircus canente</i>	<i>canente</i>	6501	India
<i>Chrysocolaptes guttacristatus</i>	<i>Chrysocolaptes guttacristatus</i>	NA	6486	illegible
<i>Chrysocolaptes guttacristatus</i>	<i>Chrysocolaptes guttacristatus</i>	NA	23486	Burma
<i>Colaptes auratus</i>	<i>Colaptes auratus</i>	NA	48699	NY
<i>Colaptes auratus</i>	<i>Colaptes auratus</i>	NA	28168	NY
<i>Colaptes auratus</i>	<i>Colaptes auratus</i>	NA	14975	NY
<i>Colaptes auratus</i>	<i>Colaptes auratus</i>	NA	48717	NY
<i>Meiglyptes tristis</i>	<i>Meiglyptes tristis</i>	<i>grammithorax</i>	6466	India
<i>Celeus castaneus</i>	<i>Celeus castaneus</i>	NA	6471	Mexico
<i>Celeus castaneus</i>	<i>Celeus castaneus</i>	NA	6473	Costa Rica
<i>Celeus castaneus</i>	<i>Celeus castaneus</i>	NA	6472	Costa Rica

Extended Data Table 4 | Species-level sample sizes of eBird point locations before and after spatial downsampling.

Species	Before thinning	After thinning	Proportion thinned
<i>Blythipicus pyrrhotis</i>	660	660	0.00
<i>Blythipicus rubiginosus</i>	457	432	0.05
<i>Campephilus gayaquilensis</i>	1034	643	0.38
<i>Campephilus guatemalensis</i>	11400	6291	0.45
<i>Campephilus haematogaster</i>	268	267	0.00
<i>Campephilus imperialis</i>	5	5	0.00
<i>Campephilus leucopogon</i>	582	581	0.00
<i>Campephilus magellanicus</i>	559	559	0.00
<i>Campephilus melanoleucos</i>	5625	3842	0.32
<i>Campephilus pollens</i>	1014	576	0.43
<i>Campephilus principalis</i>	11	11	0.00
<i>Campephilus robustus</i>	577	575	0.00
<i>Campephilus rubricollis</i>	1650	1508	0.09
<i>Campethera abingoni</i>	902	902	0.00
<i>Campethera bennettii</i>	101	100	0.01
<i>Campethera cailliautii</i>	93	92	0.01
<i>Campethera caroli</i>	97	97	0.00
<i>Campethera maculosa</i>	50	50	0.00
<i>Campethera mombassica</i>	27	27	0.00
<i>Campethera nivosa</i>	182	181	0.01
<i>Campethera notata</i>	73	73	0.00
<i>Campethera nubica</i>	823	668	0.19
<i>Campethera punctuligera</i>	112	112	0.00
<i>Campethera scriptoricauda</i>	44	43	0.02
<i>Campethera tullbergi</i>	74	74	0.00
<i>Celeus brachyurus</i>	3687	2743	0.26
<i>Celeus castaneus</i>	3043	1783	0.41
<i>Celeus elegans</i>	926	865	0.07
<i>Celeus flavescens</i>	2576	2009	0.22
<i>Celeus flavus</i>	1140	1116	0.02
<i>Celeus grammicus</i>	793	764	0.04
<i>Celeus loricatus</i>	3454	1559	0.55
<i>Celeus lugubris</i>	345	344	0.00
<i>Celeus obrieni</i>	63	63	0.00
<i>Celeus spectabilis</i>	132	132	0.00
<i>Celeus torquatus</i>	627	541	0.14

<i>Celeus undatus</i>	306	305	0.00
<i>Chrysocolaptes erythrocephalus</i>	65	65	0.00
<i>Chrysocolaptes festivus</i>	693	693	0.00
<i>Chrysocolaptes guttacristatus</i>	4893	3267	0.33
<i>Chrysocolaptes haematribon</i>	197	194	0.02
<i>Chrysocolaptes lucidus</i>	141	141	0.00
<i>Chrysocolaptes stricklandi</i>	172	172	0.00
<i>Chrysocolaptes strictus</i>	13	13	0.00
<i>Chrysocolaptes xanthocephalus</i>	10	10	0.00
<i>Colaptes atricollis</i>	428	409	0.04
<i>Colaptes auratus</i>	2627294	85664	0.97
<i>Colaptes auricularis</i>	526	371	0.29
<i>Colaptes campestris</i>	8531	7166	0.16
<i>Colaptes chrysoides</i>	14305	7320	0.49
<i>Colaptes fernandinae</i>	375	366	0.02
<i>Colaptes melanochloros</i>	9414	6731	0.29
<i>Colaptes pitius</i>	2967	2747	0.07
<i>Colaptes punctigula</i>	3357	3023	0.10
<i>Colaptes rivolii</i>	2655	1721	0.35
<i>Colaptes rubiginosus</i>	20306	7879	0.61
<i>Colaptes rupicola</i>	2132	1887	0.11
<i>Dendrocopos analis</i>	824	762	0.08
<i>Dendrocopos assimilis</i>	15	15	0.00
<i>Dendrocopos atratus</i>	216	215	0.00
<i>Dendrocopos auriceps</i>	798	766	0.04
<i>Dendrocopos canicapillus</i>	7331	2517	0.66
<i>Dendrocopos cathpharius</i>	114	114	0.00
<i>Dendrocopos darjellensis</i>	115	115	0.00
<i>Dendrocopos doriae</i>	26	26	0.00
<i>Dendrocopos himalayensis</i>	683	600	0.12
<i>Dendrocopos hyperythrus</i>	440	423	0.04
<i>Dendrocopos kizuki</i>	1749	1447	0.17
<i>Dendrocopos leucopterus</i>	29	29	0.00
<i>Dendrocopos leucotos</i>	1025	897	0.12
<i>Dendrocopos macei</i>	1205	1105	0.08
<i>Dendrocopos maculatus</i>	874	789	0.10
<i>Dendrocopos mahrattensis</i>	1738	1704	0.02
<i>Dendrocopos major</i>	53357	16302	0.69
<i>Dendrocopos medius</i>	2090	1967	0.06

<i>Dendrocopos minor</i>	4803	4200	0.13
<i>Dendrocopos moluccensis</i>	1070	645	0.40
<i>Dendrocopos nanus</i>	2752	2576	0.06
<i>Dendrocopos noguchii</i>	78	78	0.00
<i>Dendrocopos obsoletus</i>	93	93	0.00
<i>Dendrocopos ramsayi</i>	5	5	0.00
<i>Dendrocopos syriacus</i>	3674	2846	0.23
<i>Dendrocopos temminckii</i>	101	100	0.01
<i>Dendropicos abyssinicus</i>	32	32	0.00
<i>Dendropicos elachus</i>	16	16	0.00
<i>Dendropicos fuscescens</i>	1747	1676	0.04
<i>Dendropicos gabonensis</i>	14	14	0.00
<i>Dendropicos lugubris</i>	66	65	0.02
<i>Dendropicos poecilolaemus</i>	20	20	0.00
<i>Dendropicos spodocephalus</i>	248	248	0.00
<i>Dendropicos stierlingi</i>	21	21	0.00
<i>Dinopium benghalense</i>	27462	10801	0.61
<i>Dinopium everetti</i>	129	129	0.00
<i>Dinopium javanense</i>	2432	1381	0.43
<i>Dinopium rafflesii</i>	75	74	0.01
<i>Dinopium shorii</i>	396	385	0.03
<i>Dryocopus galeatus</i>	113	113	0.00
<i>Dryocopus hodgei</i>	91	91	0.00
<i>Dryocopus javensis</i>	1284	1138	0.11
<i>Dryocopus lineatus</i>	25340	12456	0.51
<i>Dryocopus martius</i>	4085	3578	0.12
<i>Dryocopus pileatus</i>	880900	45878	0.95
<i>Dryocopus schulzi</i>	165	165	0.00
<i>Gecinulus grantia</i>	58	58	0.00
<i>Gecinulus viridis</i>	60	60	0.00
<i>Geocolaptes olivaceus</i>	132	132	0.00
<i>Hemicircus canente</i>	1764	1550	0.12
<i>Hemicircus concretus</i>	268	256	0.04
<i>Jynx ruficollis</i>	301	301	0.00
<i>Jynx torquilla</i>	5811	5000	0.14
<i>Meiglyptes jugularis</i>	80	80	0.00
<i>Meiglyptes tristis</i>	499	478	0.04
<i>Meiglyptes tukki</i>	359	352	0.02
<i>Melanerpes aurifrons</i>	152584	30289	0.80
<i>Melanerpes cactorum</i>	1361	1280	0.06

<i>Melanerpes candidus</i>	2751	2637	0.04
<i>Melanerpes carolinus</i>	2786073	118320	0.96
<i>Melanerpes chrysauchen</i>	1747	1398	0.20
<i>Melanerpes chrysogenys</i>	8174	3452	0.58
<i>Melanerpes cruentatus</i>	5156	4109	0.20
<i>Melanerpes erythrocephalus</i>	248530	32984	0.87
<i>Melanerpes flavifrons</i>	1255	1111	0.11
<i>Melanerpes formicivorus</i>	293995	13956	0.95
<i>Melanerpes herminieri</i>	614	614	0.00
<i>Melanerpes hoffmannii</i>	18129	10002	0.45
<i>Melanerpes hypopolius</i>	961	706	0.27
<i>Melanerpes lewis</i>	22697	12526	0.45
<i>Melanerpes portoricensis</i>	6677	5458	0.18
<i>Melanerpes pucherani</i>	15800	5399	0.66
<i>Melanerpes pulcher</i>	240	240	0.00
<i>Melanerpes pygmaeus</i>	3687	2880	0.22
<i>Melanerpes radiolatus</i>	2056	1779	0.13
<i>Melanerpes rubricapillus</i>	22707	10111	0.55
<i>Melanerpes striatus</i>	3312	2864	0.14
<i>Melanerpes superciliaris</i>	3282	2343	0.29
<i>Melanerpes uropygialis</i>	139724	16914	0.88
<i>Mesopicos elliotii</i>	60	60	0.00
<i>Mesopicos goertae</i>	749	549	0.27
<i>Mesopicos griseocephalus</i>	399	398	0.00
<i>Mulleripicus fuliginosus</i>	16	16	0.00
<i>Mulleripicus fulvus</i>	153	152	0.01
<i>Mulleripicus funebris</i>	142	110	0.23
<i>Mulleripicus pulverulentus</i>	591	586	0.01
<i>Nesocittes micromegas</i>	390	390	0.00
<i>Picoides albolarvatus</i>	18217	10103	0.45
<i>Picoides arcticus</i>	9981	7310	0.27
<i>Picoides arizonae</i>	13064	2013	0.85
<i>Picoides borealis</i>	6694	3953	0.41
<i>Picoides dorsalis</i>	8486	6648	0.22
<i>Picoides fumigatus</i>	7630	3959	0.48
<i>Picoides nuttallii</i>	227670	45396	0.80
<i>Picoides pubescens</i>	3522364	96162	0.97
<i>Picoides scalaris</i>	183953	33887	0.82
<i>Picoides stricklandi</i>	158	158	0.00
<i>Picoides tridactylus</i>	200	200	0.00

<i>Picoides villosus</i>	1301772	77338	0.94
<i>Piculus aurulentus</i>	540	540	0.00
<i>Piculus callopterus</i>	167	167	0.00
<i>Piculus chrysochloros</i>	844	844	0.00
<i>Piculus flavigula</i>	1121	1024	0.09
<i>Piculus leucolaemus</i>	265	264	0.00
<i>Piculus litae</i>	79	78	0.01
<i>Piculus simplex</i>	1620	1140	0.30
<i>Picumnus albosquamatus</i>	900	899	0.00
<i>Picumnus aurifrons</i>	381	359	0.06
<i>Picumnus castelnau</i>	115	114	0.01
<i>Picumnus cinnamomeus</i>	560	424	0.24
<i>Picumnus cirratus</i>	3573	2921	0.18
<i>Picumnus dorbignyanus</i>	274	206	0.25
<i>Picumnus exilis</i>	303	303	0.00
<i>Picumnus fulvescens</i>	108	108	0.00
<i>Picumnus fuscus</i>	3	3	0.00
<i>Picumnus granadensis</i>	1189	1061	0.11
<i>Picumnus innominatus</i>	927	927	0.00
<i>Picumnus lafresnayi</i>	684	619	0.10
<i>Picumnus limae</i>	302	291	0.04
<i>Picumnus minutissimus</i>	70	70	0.00
<i>Picumnus nebulosus</i>	162	162	0.00
<i>Picumnus olivaceus</i>	3279	2689	0.18
<i>Picumnus pumilus</i>	47	47	0.00
<i>Picumnus pygmaeus</i>	304	304	0.00
<i>Picumnus rufiventris</i>	112	111	0.01
<i>Picumnus sclateri</i>	444	387	0.13
<i>Picumnus spilogaster</i>	103	103	0.00
<i>Picumnus squamulatus</i>	805	724	0.10
<i>Picumnus steindachneri</i>	142	142	0.00
<i>Picumnus subtilis</i>	131	131	0.00
<i>Picumnus temminckii</i>	1785	1709	0.04
<i>Picumnus varzeae</i>	24	24	0.00
<i>Picus awokera</i>	231	231	0.00
<i>Picus canus</i>	4023	2922	0.27
<i>Picus chlorolophus</i>	2333	2071	0.11
<i>Picus erythropygius</i>	254	251	0.01
<i>Picus flavinucha</i>	1102	988	0.10
<i>Picus mentalis</i>	352	295	0.16

<i>Picus mineaceus</i>	1117	654	0.41
<i>Picus puniceus</i>	389	387	0.01
<i>Picus rabieri</i>	38	38	0.00
<i>Picus squamatus</i>	357	357	0.00
<i>Picus vaillantii</i>	157	157	0.00
<i>Picus viridanus</i>	147	145	0.01
<i>Picus viridis</i>	33902	19560	0.42
<i>Picus vittatus</i>	868	527	0.39
<i>Picus xanthopygaeus</i>	1494	1060	0.29
<i>Reinwardtipicus validus</i>	269	267	0.01
<i>Sasia abnormis</i>	355	347	0.02
<i>Sasia africana</i>	33	33	0.00
<i>Sasia ochracea</i>	254	253	0.00
<i>Sphyrapicus nuchalis</i>	48968	25419	0.48
<i>Sphyrapicus ruber</i>	78098	20374	0.74
<i>Sphyrapicus thyroideus</i>	14544	9938	0.32
<i>Sphyrapicus varius</i>	459645	58917	0.87
<i>Thripias namaquus</i>	419	418	0.00
<i>Thripias pyrrhogaster</i>	103	103	0.00
<i>Thripias xantholophus</i>	99	99	0.00
<i>Veniliornis affinis</i>	1136	1025	0.10
<i>Veniliornis callonotus</i>	1358	1124	0.17
<i>Veniliornis cassini</i>	206	206	0.00
<i>Veniliornis chocoensis</i>	32	31	0.03
<i>Veniliornis dignus</i>	435	434	0.00
<i>Veniliornis frontalis</i>	210	210	0.00
<i>Veniliornis kirkii</i>	1624	1511	0.07
<i>Veniliornis lignarius</i>	2417	1894	0.22
<i>Veniliornis maculifrons</i>	416	416	0.00
<i>Veniliornis mixtus</i>	2446	1375	0.44
<i>Veniliornis nigriceps</i>	357	342	0.04
<i>Veniliornis passerinus</i>	2832	2725	0.04
<i>Veniliornis sanguineus</i>	115	115	0.00
<i>Veniliornis spilogaster</i>	2097	2065	0.02
<i>Xiphidiopicus percussus</i>	1486	1373	0.08
TOTAL	13513441	1037628	0.92

Extended Data Fig. 1 | Illustration of the results of the modified Mantel correlogram approach. Plumage dissimilarity is positively associated with range dissimilarity for the most similar-looking, geographically overlapping species pairs. Additionally, this illustration of results from a modified Mantel correlogram approach reveals that the two variables are negatively associated with one another for species dyads of intermediate plumage similarity.

Extended Data Fig. 2 | Paneled correlation plot showing the relationships between all species-level averaged traits. Climate, habitat, latitude, and woodpecker body mass and plumage appearance exhibit a variety of intercorrelations. The lower triangle panels show the pairwise trait relationships. The diagonal panels contain histograms of the indicated variable. The upper triangle panels summarize the Pearson's correlation coefficient and the significance of the relationship, both numerically and in color, where bright red indicates a strong negative correlation, and bright blue indicates a strong positive correlation.