Organismal appearances are shaped by selection from both biotic and abiotic drivers. For example, Gloger’s rule describes the pervasive pattern that more pigmented populations are found in more humid areas. However, species may also converge on nearly identical colours and patterns in sympatry, often to avoid predation by mimicking noxious species. Here we leverage a massive global citizen-science database to determine how biotic and abiotic factors act in concert to shape plumage in the world’s 230 species of woodpeckers. We find that habitat and climate profoundly influence woodpecker plumage, and we recover support for the generality of Gloger’s rule. However, many species exhibit remarkable convergence explained neither by these factors nor by shared ancestry. Instead, this convergence is associated with geographic overlap between species, suggesting occasional strong selection for interspecific mimicry.
The coloration and patterning of organisms is shaped over evolutionary timescales by a variety of factors, both biotic and abiotic, including temperature and humidity\textsuperscript{1–5}. Gloger’s rule, for example, describes the prominent ecological pattern wherein more pigmented populations are found in more humid areas\textsuperscript{1,6–8}. Sexual selection can push organisms to become conspicuous, whilst the risk of predation can select for inconspicuous visual signals\textsuperscript{9–11}.

The external appearances of animals are subject to frequent study because such work has the power to shape our understanding of phenotypic evolution. Yet, our understanding of how factors such as climate and biotic interactions with predators, competitors, and mates combine to influence evolutionary outcomes across large radiations remains rudimentary. This is true even for birds, regular subjects of research on phenotypic evolution\textsuperscript{12,13}. Here, we employ a 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 community composition on plumage pattern and colour evolution in woodpeckers (Picidae). This diverse avian clade of 230 bird species is an excellent group in which to examine the evolution of external appearances because they occupy a broad range of climates across many habitats. Woodpeckers also display a wide range of plumages, from species with boldly pied patterns to others with large bright red patches, to still others that are entirely dull olive (Fig. 1).

Furthermore, woodpeckers exhibit several cases of ostensible plumage mimicry\textsuperscript{14,15}, highlighted by a recent time-calibrated phylogeny\textsuperscript{16}. Although qualitatively compelling, it is unclear if these events can be explained simply as consequences of shared climate, habitat, and evolutionary history. Regardless of the answer to this question, these purported mimicry events and the impressive variation in plumage among woodpecker species provide the raw variation that we examine here to disentangle the contribution of the various abiotic and biotic factors that drive plumage evolution.

We find that climate and habitat exert strong influences on woodpecker plumage. Species from humid areas, for example, tend to be darker and less boldly patterned than those from drier regions, and thus offer compelling support of Gloger’s rule. These factors and shared evolutionary history explain some of the variation in woodpecker plumage, but they are insufficient to explain some of the dramatic convergence seen between various sympatric woodpecker species. Instead, sympatry in and of itself appears to drive certain species pairs to converge in plumage,

\begin{itemize}
  \item Picoides pubescens
  \item Picoides villosus
  \item Picoides fumigatus
  \item Veniliornis mixtus
  \item Veniliornis cassini
\end{itemize}

\textbf{Legend}

\begin{itemize}
  \item 0.5 Plumage dissimilarity
  \item 0.5 Million years
  \item Large seasonal shifts in temperature
  \item Minimal variation in temperature
\end{itemize}

Fig. 1 Evolutionary relationships and plumage similarity among exemplar species. 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. These species shared a common ancestor ~ 6.5 mya. 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. \textit{Veniliornis mixtus}, long classified as a member of \textit{Picoides}, is inferred to have invaded seasonal climates in the southern hemisphere, and accordingly evolved bold black and white plumage. \textit{Picoides fumigatus}, long classified as a member of \textit{Veniliornis}, is inferred to have invaded warm climates near the equator, and accordingly evolved dark, subtly marked plumage. \textit{Picoides pubescens} and \textit{P. villosus} are rather distantly related but largely sympatric; they are inferred to have converged on one another in plumage above and beyond what would be expected based on shared climate, habitat, and evolutionary history. Traditional scientific names are used in this figure to aid explanation, but the illustrated species are currently all members of an expanded clade, \textit{Dryobates}. Illustrations © HBW Alive/Lynx Edicions, map by authors.
lending credence to the notion that these species are true avian plumage mimics.

Results
Multidimensional, distance-based approaches. To investigate how climate, habitat, social interactions, and evolutionary history determine woodpecker plumage outcomes, we used multidimensional-colour and pattern-quantification tools to measure species’ colouration and patterns, quantifying species’ plumages from a standardized source (Figs. 2 and 3)\textsuperscript{12,17,18}. Evidence suggests that pattern and colour are likely processed separately in vertebrate brains, with achromatic (i.e., luminance) channels used to process pattern information\textsuperscript{19}, and differential stimulation of cones used to encode chromatic information\textsuperscript{20}. While both plumage colour and pattern are inherently multivariate, we reduced this complexity into a composite matrix of pairwise species differences to address whether purported convergences were a mere by-product of shared evolutionary history or, if not, whether shared climate, habitat, or geographic overlap could explain these events. We incorporated the potential for interactions between pairs of species into the analysis by quantifying pairwise geographic range overlap using millions of globally crowd-sourced citizen science observations from eBird\textsuperscript{21}. Species in complete allopatry have no chance of interacting, while increasing degrees of sympatry should correlate with the probability of evolutionarily meaningful interactions.

Variation in climate (multiple distance matrix regression, $r = 0.055$, $p = 0.006$), habitat ($r = 0.106$, $p = 0.007$) and, to a lesser degree, phylogenetic relationships ($r = 0.001$, $p = 0.015$) were all correlated with woodpecker plumage similarity scores. These results were robust to phylogenetic uncertainty (Supplementary Fig. 1). In short, woodpecker species in similar climates and habitats tend to look alike, even after accounting for shared ancestry. However, beyond the influences of habitat, climate, and evolutionary relatedness, we also found that close sympatry was a strong predictor of plumage similarity for the most similar-looking species pairs (Fig. 4). We interpret this result as evidence for multiple instances of plumage mimicry per se, transcending broader patterns of plumage convergence driven by similar environmental conditions. Following this result, we developed a method (see ‘Identification of putative plumage mimics’ in the Methods) to identify the species pairs that powered this result.

Using this method, we validated many previously qualitatively identified mimicry complexes, including the Downy-Hairy Woodpecker system (Fig. 1)\textsuperscript{22}, repeated convergences between members of Veniliornis and Piculus\textsuperscript{23}, Dinopium and Chrysocolaptes, Dryocopus and Campephilus\textsuperscript{24}, and the remarkable convergence of Celeus galeatus on Dryocopus and Campephilus\textsuperscript{15}. Collectively, these distance matrix-based analyses provide a powerful tool to identify and understand the various factors that drive evolutionary patterns of convergence and divergence.

These previous analyses focused on the whole-body phenotype; however, it is possible that environmental and social drivers of plumage operate in unique ways on different plumage patches\textsuperscript{12}. To investigate this possibility, we ran additional analyses for each of three different body segments: (1) the back, wings, and tail; (2) the head; and (3) the breast, belly and vent.

The whole-body results were largely recapitulated by these body-region-specific results, with subtle but notable differences. In particular, range overlap was particularly strongly associated with driving convergence in back plumage similarity, while genetic and climate similarity were not implicated, and genetic similarity was particularly closely associated with belly and head plumage similarity, while habitat (belly and head) and climate (belly) were not involved. To gain further insight into the evolutionary drivers of particular colours and patterns, we subsequently employed species-level phylogenetic comparative approaches.

Species-level phylogenetic comparative approaches. Considering the full-body plumage phenotype, we found that precipitation drives global patterns of pigmentation and patterning in woodpeckers. In particular, darker species tend to inhabit areas of higher annual precipitation (phylogenetic generalized least squares [PGLS] $r^2 = 0.084$, $p < 0.001$, Fig. 5a), supporting Gloger’s rule\textsuperscript{1,8}. In addition, high precipitation is also associated with reduced patterning (PGLS $r^2 = 0.170$, $p < 0.001$, Fig. 5c), augmenting the generality of Gloger’s rule. While this pattern of high precipitation occurring in areas of high precipitation is so well known as to be considered a “rule”, few large-scale comparative studies have quantitatively assessed this across a large radiation\textsuperscript{8}. The mechanism underlying Gloger’s rule remains debated, but proposed drivers include improved background matching\textsuperscript{25} in response to increased predation pressure in humid environments\textsuperscript{26}, and defence against feather-degrading parasites\textsuperscript{27}. There are some boldly marked woodpecker species in humid areas, but they invariably achieve these conspicuous phenotypes with minimal use of white plumage. This hints at the existence of an evolutionary trade-off wherein Gloger’s rule is due to the ability of melanin to forestall feather wear (e.g., by inhibiting parasites prevalent in humid areas\textsuperscript{27}), which subsequently narrows the breadth of means by which humid forest-inhabiting woodpeckers can achieve bold plumage phenotypes. Alternatively, unconcealed large white plumage patches might simply subject humid forest-dwelling birds to evolutionarily unacceptable levels of predation (the abundance and preferences of predators such as Accipiter hawks would shed more light on this issue, given that increasing body mass is associated with increasingly bold plumage patches in woodpecker, Fig. 5c). While additional research is necessary to delineate 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.

Seasonality, in addition to average annual precipitation and temperature, 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 considerable precipitation throughout the year (PGLS $r^2 = 0.084$, $p < 0.001$, Fig. 5a). The gradient from red to green plumaged woodpeckers (colorPC2) was best explained by a model that included variation in temperature seasonality, and that 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 $r^2 = 0.073$, $p < 0.001$, Fig. 5b). Seasonality also drives woodpecker patterning, and boldly marked birds (patternPC1) tend to be found in seasonal climates, open habitats, and temperate forests (PGLS $r^2 = 0.170$, $p < 0.001$, Fig. 5c).

We had suspected that variation along the gradient from species with large plumage elements to those with barring and spotting (patternPC2) might be associated with sexual selection, but after accounting for body mass, patternPC2 was not associated with sexual size dimorphism; instead, more finely marked birds tend to be smaller and found in lower reflectance habitats such as rainforests (PGLS $r^2 = 0.043$, $p = 0.025$, Fig. 5d). Like those results from the multiple distance matrix regressions, these results were robust to phylogenetic uncertainty (Supplementary Figs. 3–6).

Results were largely similar when considering the drivers of plumage variation for specific body parts, particularly for back plumage coloration and patterning (Supplementary Fig. 7). Yet these body-part-specific analyses did provide additional insights and investigating the mechanistic bases for these relationships should prove fruitful future research grounds. For example, red-headed species tend to be found in closed habitats, whereas black-, white-, and grey-headed species tend to be found in open habitats (Supplementary Fig. 8). In dark-headed species, including those with red heads, females tended to be heavier than males, whereas species with yellow and pale heads tend to have heavier males. Additionally, red-bellied species are most often found in forested habitats, species with boldly patterned bellies tend to have males that are heavier than females, and species with bellies patterned with large plumage patches (as opposed to fine barring) tend to be heavier and live in open habitats (Supplementary Fig. 9).

**Discussion**

Although climate and habitat appear responsible for some of the convergence in external appearance in woodpeckers, our analyses confirmed the decades-old suggestions that 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 (Fig. 4). We interpret this finding as evidence that the pattern of convergence we document is true mimicry, i.e., phenotypic evolution by one or both parties in response to a shared signal receiver. Indeed, our study almost certainly underestimates the degree to which close sympathy leads to mimicry in woodpeckers, since some postulated mimetic dyads are well known to track one another at the subspecific level, which we could not account for.
supported hypothesis in birds, but experimental work is needed to adequately quantify the selective advantage mimicry might confer. Relatedly, it remains unknown how distantly related lineages achieve plumage convergence genomically. Are multiple mutations required, each of which increases the degree of plumage convergence? Or might selection act on genetic modules controlled by a few loci shared across woodpeckers? Or might rare hybridization events between sympatric species have resulted in adaptive introgression of relevant plumage control loci? 

In summary, habitat and climate are strong determinants of woodpecker plumage. Shared evolutionary history shapes plumage phenotypes, but selective factors have driven plumage divergence far beyond that expected of simple evolutionary drift. Perhaps most notably, the plumage similarity predicted by shared climate, habitat, and evolutionary history is insufficient to explain the large number of cases we detected of closely sympatric but distantly related woodpecker species converging in colour and pattern. Woodpeckers appear to be involved in globally replicated mimicry complexes similar to those in well-studied groups such as butterflies, and while woodpeckers among the most conspicuous avian plumage mimics, others such as toucans exhibit qualitatively similar patterns. Assessing how these evolutionary constraints and selective pressures have operated in concert is a research question that has only recently become more tractable with the advent of large, time-calibrated molecular phylogenies, massive distributional databases such as eBird, and powerful computing techniques like pattern analysis. It seems likely that different clades have been more or less influenced by factors such as climate, habitat, and social interactions, and understanding how and why these factors differ among clades should be a particularly fertile line of enquiry.

**Methods**

**Taxonomic reconciliation and creation of complete phylogenies.** A time-dated phylogeny containing nearly all known woodpecker species was recently published by Shyaka and colleagues. As described below, we used (and verified the use of) illustrations from the Handbook of the Birds of the World (HBW) to quantify woodpecker plumage, and we used eBird, a massively crowd-sourced bird observation 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 as our final classification system.

To reconcile these three taxonomies (HBW, Shyaka et al., and eBird/Clements), we obtained a set of 10,000 credible trees, kindly provided by Shyaka. We checked to ensure that each tree contained no polytomies, was ultrametric, and included the same set of tip labels as the other trees. After passing these checks, we discarded the first 30% of trees as burn-in, then sampled 1000 of the remaining trees. We extracted a list of the tip labels from the first tree, then determined to which eBird taxon this label was best applied. Across the set of 1000 credible trees we then swapped out the original tip labels for their eBird taxonomic identities. For each credible tree, we then randomly dropped all but one of any taxon represented by more than one terminal. We then worked in the opposite direction and identified all woodpecker taxa according to eBird. This process made it clear which species, as recognized by eBird, were missing from the Shyaka tree.

Twenty-one such missing taxa were identified: Picumnus fuscus, P. ilmae, P. fulvescens, P. granadensis, P. cinnamomeus, Dinopium everetti, Geocolius viridis, Mulleripicus fulvus, Piculus simplex, Dryocopus hodgei, Melanerpes pulcher, Xiphidiopteran perucca, Veniliornis maculifrons, Dendrocopos analis, Dendrocopos ramsayi, Colaptes femernandiae, Chrysocolaptes festivus, C. xanthochalpos, C. strictus, C. guttacristatus, and C. stricklandi. We added these using the R package addTaxa, and taxonomic hypotheses outlined in previous work (reviewed in Shyaka et al.) were found to be largely corroborated. 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. javanensis, so it was simply added as sister to the latter species. The precise phylogenetic positions of the remaining three taxa are less well known. For these, we first added C. femernandiae as sister to Colaptes sensu stricto (as previously found), then added Piculus simplex into the clade Piculus + Colaptes, as previous work showed some members of the former genus to actually belong to the latter. We added X. perucca as sister to Melanerpes stritsatus and we added P. cinnamomeus into Picumnus while ensuring that the Old World P. nominatus remained sister to the rest of the genus (it is very likely the New World Picumnus form a clade). Each of the 1000 resulting trees contained 230 species. As described
below, most analyses were run across this set of complete credible trees. However, for other analyses, and particularly for visualization purposes, we also derived a maximum clade credibility tree from this set of complete trees. Finally, for each taxon in the complete tree, 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*. 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 to sample the red (R), green (G), and blue (B) pixel values for each of the following variables: climate principal component analysis (PCA), habitat principal component analysis (PCA), body mass, sexual size dimorphism, and latitude and longitude. Model-averaged parameter estimates and variable importance scores are shown in Fig. 5a–d. 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.

**Fig. 5** 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 climates. b Greenish (as opposed to reddish) birds are found in more open habitats. c Less-patterned birds are found in aseasonal climates, open habitats, and temperate forests. d Birds patterned in large plumage elements, such as large colour patches, tend to be larger in body size. e Climate PCA results, illustrating the distribution of woodpeckers in climate space, with qualitative descriptions of the first two PC axes. f Habitat PCA results, showing the distribution of woodpeckers across global habitats, with qualitative descriptions of the first two PC axes. Illustrations © HBW Alive/Lynx Edicions.
of the avian double-cone, responsible for luminance detection.48,49, because this photoreceptor type is assumed to be involved in processing pattern information from visual scenes. Additionally, because relative similarities in plumage do not generate perceptually-uniform colour spaces,59,61 we implemented visual models61 to generate Cartesian coordinates for the colour values from each of 1000 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 pairwise Mahalanobis distances28 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 new distance calculated as the Euclidean distance in a 3D space whose axes are floral and colour. 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 (Supplementary Table 9). 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 close correlations between colour dissimilarity (measured from specimens vs. measured from illustrations; Mantel test, r = 0.74, p < 0.001) and overall plumage dissimilarity (measured from specimens vs. measured from illustrations, Mantel test, 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 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 less than 5 km in length. Because eBird has grown exponentially in recent years, we connected directly to the database to ensure infrequent data coverage. In other words, we initially inflated the number of records by adding our 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 oversampled species in a spatially stratified manner. Specifically, for each of the specimens, we laid a grid of 100 cells over the species range, 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 (Supplementary Data 1). In sum, this process reduced the original data from 13,513,441 to 1,662,628 records.

We used the R package hypervolume62 to create pseudo-range maps across 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, e.g., minimum convex polygons.65 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 sympathy (complete overlap in geographic distributions). We then used this dissimilarity matrix to create a new hypervolume for the species pair and then compared this hypervolume to the hypervolumes of the species individually, to determine whether their overlap was driven by each species being hypothesised to occupy a similar climate space, rather than by sympatry.

We used the raster package to match each species’ point locations to climatic values using WorldClim bioclimatic data63. These data describe the annual and seasonal climatic conditions around the globe. After querying species’ climatic data, we bounded the resulting files together and ran a single large correlation matrix PCA across all of the variables except elevation, which we retained because bioclim6 and bio10. 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 generally warm throughout the year, to areas that show a substantial variation in temperature and large diurnal shifts in temperature. The second axis described a gradient from areas that receive precipitation in seasonal pulses, with 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.

Photographic quantification of plumage colour and pattern. To validate the use of colour plates for quantifying meaningful interspecific variation in plumage colour and pattern between woodpeckers, we employed digital photographic visual ecology methods to quantify the appearance of museum specimens and compared these results to those obtained using the whole-body 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 spaces. 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 photographs (one visible, one UV) under full-spectrum light (eyeColor arc lamps, Iwasaki: Tokyo, Japan, with UV filter). We then converted these image stacks into visual space using data from Dendrocyopus major and average visual sensitivities for other violet-sensitive bird species.56 The inferred peak-sensitivity (λmax) for the short-wavelength sensitive 1 (SWS1) cone of Great Spotted Woodpeckers, based on opsin sequence, is 405 nm57. After generating images corresponding to the stimulation filters, we then employed different photoreceptors to perform granularity-based pattern analyses with the Image Calibration and Analysis Toolbox58 in ImageJ44 using the image corresponding to the stimulation filters (one transmitting only UV light, one transmitting both UV and blue light). We found close correlations between colour dissimilarity (measured from specimens vs. measured from illustrations; Mantel test, r = 0.74, p < 0.001) and overall plumage dissimilarity (measured from specimens vs. measured from illustrations, Mantel test, r = 0.72, p < 0.001).

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Querying habitat data. We used ebird, which harnesses GDAL (http://www.gdal.org), to bind species’ point locations into ~50 MB-sized tables, then converted the resulting files into Google Earth Engine format 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 values44 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, which may produce “spectral differences of up to 500 m 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. We then 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. ebird contains functions to automatically combine and process these files from Google Earth Engine (although the functions currently employ Google Fusion Tables, which will be discontinued in December 2019). We then ran a single large correlation matrix PCA across all 7 MODIS bands. Before doing so, we naturally log-transformed bands 1, 3, and 4, as a few extreme values among 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, reflecting the greater infrared reflectance produced there, and described a gradient between low and high infrared reflectance to those with low visible and high infrared reflectance. This dichotomy is used to identify snuf in MODIS snow product (https://modis.gsfc.nasa.gov/data/atbd/atbd_mod10.pdf). Thus, at the species-average level, the second PC axis described the vegetation between the temperate snow-covered (temperate) forests and tropical woodland. Again, for each dyadic comparison, we calculated a Serenon similarity index, and then converted the resulting matrix to a dissimilarity matrix.

Multiple distance matrix regression. After the steps described above, we had data from 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 plumage colour and the plumage pattern dissimilarity matrices into a single matrix by repeatedly derived models with the same intercorrelations among them as our observed dependent (plumage dissimilarity) and four independent matrices (genetic, habitat, climate, and range dissimilarity). When input into the multiple distance matrix regression described above, the resulting matrix-specific coefficients and overall power of the simulated independent matrices to explain variation in the simulated woodpecker plumage dissimilarity matrix was identical to that in the observed matrices. By using these same matrices in the modified Mantel corregogram approach described above, we were able to test whether the pattern observed in Fig. 4 (red line) could result by chance alone. After 200 iterations of the simulation, we calculated the standardized effect size of the correlation coefficient of each thresholded plumage dissimilarity matrix with range dissimilarity as the difference between the observed value and the mean of the simulations, divided by the standard deviation of the simulated correlation coefficients. Standardized effect sizes greater than $\pm 0.196$ reflect observed correlation coefficients that deviated more than 95% of simulated values. These simulations strongly support our finding that close sympathy—above and beyond evolutionary relatedness, shared climate, and shared habitat preferences—drives otherwise unexpectedly high levels of plumage convergence in woodpeckers. In short, close sympathy appears to be associated with occasional plumage mimicry in woodpeckers. We recognize that Mantel tests, and presumably by extension variations such as that described here, can suffer from inflated type I error rates70,71. Future work should seek to further establish the relevance of sympathy to driving plumage mimicry in birds with alternative approaches.

Identification of putative plumage mimics. We developed a method to identify high-level dyadic correlations 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 $r$ of a thresholded plumage dissimilarity matrix (values from 0.0 – 0.92 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 and geographic range dissimilarity. 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 a uniform distribution. (B) The value in the PCA 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
Phylogenetic least squares regression. We derived species’ average scores along the first two axes of a plumage colour PCA (Fig. 2), a plumage pattern PCA (Fig. 3), the climatic 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 Dunning19. For those species for which mass was listed separately for males and females, we calculated sexual size dimorphism sensu Miles et al.72. These authors additionally reported dimorphism measures from a number of species not available in Dunning72. We then combined these datasets, resulting in sexual size dimorphism measures for 94 of 230 species. Sexual size dimorphism in woodpeckers is generally small compared to other avian groups such as the Icteridae, and they have not traditionally been considered a clade characterized by strong sexual selection pressures. During the process of combining datasets, 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 notably larger than females—and we replaced the values with the midpoint of ranges given in ref. 17. We used Rphylopars74 to impute missing body mass and size dimorphism data, which we did using a Browian motion model and the observed variance-covariance matrix between 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 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 corrplot75 (Supplementary Fig. 2). We used a model averaging approach to determine which explanatory variables strongly influenced plumage (Fig. 3). To test the robustness of our conclusions to phylogenetic uncertainty, for each dependent variable (colourPCA, colourPC2, patternPC1, and patternPC2), we identified all explaining explanatory variables with an adjacency coefficient that did not overlap zero. We then fit a series of 1000 PGLS regressions per dependent variable to the identified variables where, for each regression, we used a different one of the complete phylogenies. Variation in the coefficient estimations was small, as shown in Supplementary Figs. 3–6. In the main text, when reporting pseudo- R^{2} and values for the PGLS regressions, we report the median values from these 1000 models.

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

Data availability
All data supporting the findings of this study are available within the paper and its supplementary information files.

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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Author contributions
E.T.M., G.M.L., R.A.L. and A.C.L. were responsible for conceptualization and writing of the manuscript. E.T.M. and R.A.L. were responsible for analysis and visualization.

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