`charisma`: An R package to perform reproducible color characterization of digital images for biological studies

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Abstract

1. Advances in digital imaging and software tools have provided increasingly accessible datasets and methods for analyzing color evolution. Despite the variety of computational packages available, most rely on color classification before running analyses. Previous methods limit the ability to analyze large-scale image databases, decreases the accuracy of downstream analyses, and is not always representative of biologically relevant color classes.

2. Here, we present `charisma`, an R package designed to characterize the distribution of distinct color classes in images suitable for large-scale studies of biological organisms. Here, we demonstrate the utility of our package through an analysis of color evolution in a sample of diverse and charismatic birds, tanagers, in the subfamily Thraupinae.

3. We show that `charisma` can quickly and accurately classify every pixel in an image and validate these results using pre-identified, canonical color swatches. We find that `charisma` color classifications are consistent with those made by color-pattern experts in the field. Applying `charisma` to tanager color evolution, we find that `charisma` outputs seamlessly integrate with downstream evolutionary analyses.

4. Our results demonstrate that using `charisma` to manually curate and characterize colors in images provides a standardized, reliable, and reproducible framework for high-throughput color classification.

Keywords: automation · color · color classification · color pattern · macroevolution · R · reproducibility · software package

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1 Introduction

For well over a century, biologists have documented and been intrigued by the charismatic coloration and patterning of earths organisms (Darwin, 1981; Mayr et al., 1963; Santangeli et al., 2023). Animal colors and patterns have been shown to have ecologically important functions such as intra- and inter-specific communication in the form of sexual or social signaling, which includes crypsis, advertisement, or mimicry (Cooney et al., 2019; Feller et al., 2017; Håstad et al., 2005; Irwin, 1994; Rabosky et al., 2016). The evolution of conspicuous coloration and patterning has historically been studied using genetic and observational approaches (Andersson and Amundsen, 1997; Barlow et al., 2018; Ehrlich et al., 1977; McMillan et al., 1999; Neudecker, 1989; Stoddard et al., 2020). However, innovations in digital imaging and novel software tools have provided increasingly accessible datasets and reproducible methods for quantitative ecological and evolutionary investigations of color and pattern (Chan et al., 2019; Endler, 2012; Endler et al., 2018; Hemingson et al., 2024; Maia et al., 2013; Valvo et al., 2020; Van Belleghem et al., 2018; van den Berg et al., 2020; Weller and Westneat, 2019). To date, these approaches have advanced the field's understanding of the evolution of sexual dichromatism (i.e., males and females differing in color) and the factors influencing why some species have more cryptic, conspicuous, or diverse colors (Cooney et al., 2022; Dale et al., 2015; Shultz and Burns, 2013, 2017; Yu et al., 2024).

Despite this progress, eco-evolutionary explanations for why species display specific colors over others (e.g., blue vs. green) have been lacking. The ability to characterize discrete color classes in organisms is important to understand the drivers of color evolution and specifically address questions like: Does habitat influence the colors birds evolve? Which colors provide crypsis or conspicuousness? Do specific colors play a role in sexual or social signaling? Given the multi-dimensional, continuous nature of color and color space, it is both conceptually and technically challenging to carve up the color spectrum into discrete bins, limiting the number of studies (and software utilities) that use color categorization (Delhey et al., 2023; Ibáñez-Álamo et al., 2025). Additionally, many color analysis packages require users to input the number of color classes (`k`) *a priori* to compute various downstream color metrics, which means images must first undergo color profiling such that `k` meaningfully captures the specific dominant color classes of each organism (Maia et al., 2019; Van Belleghem et al., 2018; Weller and Westneat, 2019). Previous analyses have

been limited to small clades with low color variation across species (Alfaro et al., 2019; Hemingson et al., 2019; Weller and Westneat, 2019). A large-scale color class analysis in birds used a bespoke method for color categorization to analyze bird illustrations (Delhey et al., 2023). While this allowed for broad analyses of color evolution in birds, illustrators understandably exhibit artistic license in their renderings. Color analysis based on images of organisms can reduce these inherent biases. These small datasets and custom methods limit reproducibility and the breadth of organisms that can be studied using this approach.

To fill this gap, we introduce `charisma`, an R package designed to automatically determine the presence or absence of key human-visible color categories in images that can be used in studies of organisms across the tree of life. We provide a flexible and reproducible framework to efficiently characterize discrete color classes in images. The `charisma` package is suitable for large-scale studies of color and color pattern evolution and can be seamlessly integrated into popular downstream quantitative analysis workflows in R (e.g., `geiger`, `patternize`, `pavo`, etc.). We first describe the workflows for the `charisma` pipeline and then demonstrate the efficacy of our software by (*i*) validating `charisma`'s color-classification performance using images comprised of predetermined color classes, (*ii*) applying `charisma` to a small set of standardized, museum specimen images of *Tangara* species and allies in the subfamily Thraupinae and comparing the color classification performance of `charisma` to those made by an expert, and (*iii*) demonstrating how color classification labels produced by `charisma` can be leveraged within a trait-based macroevolutionary analysis of color evolution.

2 Methods

2.1 The `charisma` pipeline

The primary function of `charisma` is to characterize the distribution of human-visible color classes that are present in an image (**Figure 1**). The `charisma` package was intentionally designed with efficiency and reproducibility in mind, facilitating a standardized and extensible workflow for fully- and semi-automated color classification. To accurately profile the distribution of colors present in an image, we created a biologically inspired color look-up-table (CLUT), which contains hue, saturation, and value (HSV) boundaries for each of 10 human-visible color classes (black, blue,

brown, green, grey, orange, purple, red, white, and yellow). Segmentation of continuous color space into useful categories has previously been done and provides a means to investigate colors and color types in evolutionary biology Delhey et al. (2023); He et al. (2022); Ibáñez-Álamo et al. (2025). We determined HSV color space as the best option for the CLUT for a variety of reasons. (*i*) HSV color space provides an intuitive space to separate human-visible color categories. (*ii*) There is a simple calculation to convert between HSV and red, green, blue (RGB) color spaces, which is useful because most digital images are stored in RGB color space and color distance and complexity are easily calculated in RGB color space. In practice, this conversion can be performed directly using R's built-in `rgb2hsv()` function, which returns hue, saturation, and value in normalized units that can then be scaled (e.g., hue $\times$ 360°, saturation $\times$ 100%, value $\times$ 100%) for downstream analyses in `charisma`. (*iii*) An alternative color space is CIELab which was defined by the International Commission on Illumination in 1976 and provides a perceptually uniform color space representative of how the human eye perceives color (Commission Internationale de l'Éclairage (CIE), 2004). However, working in CIELab space is biased towards human visual perception, computationally intensive and requires information about lighting conditions, which limits its utility for large scale analyses of images taken in varying light environments or from different sources.

To determine the boundaries for each color across the HSV color space, we iteratively developed a schema for defining non-overlapping ranges of hue, saturation, and value triplets for each of the 10 color labels. For each color category, there are distinct HSV ranges that do not overlap and can be validated using the command `charisma::validate()`. These non-overlapping boundaries were tuned leveraging standardized, color-calibrated, research quality photos of bird museum specimens. The CLUT shipped with `charisma` out-of-the-box is open-source and editable (see `charisma::CLUT`). We also provide users the flexibility to define and test their own custom CLUTs (e.g., optimizing classification boundaries for different image sets including non-biological applications) for use within `charisma`.

Before applying the CLUT-based classification in `charisma`, images are pre-processed using the `recolorize2(bins = 4, cutoff = 20)` function from the `R` package `recolorize` (Weller et al., 2024). The `recolorize2()` function provides a flexible tool for human-visible color classification, which results in a spatially 'smoothed' version of the input image by removing stray or noisy pixels that may negatively influence the downstream `charisma` color-label classification (for an example,

see **Figure 1b**). The `recolorize` package primarily accomplishes this by performing a spatial-color binning procedure using the RGB 'histogram' method (Weller et al., 2024; Weller and Westneat, 2019), which bins each image pixel into a fixed number of color bins. This down-sampled representation of the dominant image colors enables faster color classification by passing each bin's RGB triplet (i.e., the average color of all pixels assigned to each color bin) into `charisma::color2label(r, g, b)`. The `charisma::color2label(r, g, b)` function tests for the union of the supplied RGB triplet within the non-overlapping HSV ranges for each color class in the CLUT and returns the matching color label from the set of 10 color classes. This approach is computationally efficient because only a fixed number of bins need to be classified (i.e., 4 bins for each of 3 channels; $4^3 = 64$ cluster centers using the histogram method; cluster centers with a Euclidean distance less than a default cutoff of 20 are combined). The alternative approach classifies every single pixel within the image, which could incorrectly classify shadows or image artifacts and becomes a computationally intensive procedure as the size and resolution of the image scales.

The entire `charisma` workflow can be run either autonomously or with minimal-to-maximal user-intervention to accommodate a wide range of use cases. This is accomplished by manually merging the color categories, replacing particular colors, and/or using a threshold cutoff to remove colors with low proportions of pixels that fall below the specified threshold. We develop a custom implementation that draws on the `recolorize` binning procedure with interactive prompts for color replacement and merging (Weller et al., 2024), empowering users to check the color classification at each stage of the `charisma` pipeline in an iterative and flexible fashion. The final `charisma` output (**Figure 1c**) for each image includes the number of colors present ($k = 1...10$), a table with presence and absence data for each color class, a log of all manual interventions performed, and R objects that can easily be passed through existing evolutionary analysis pipelines, like those in the R package `pavo` (Maia et al., 2013, 2019) or analyses of evolutionary models and rates (e.g., Harmon et al., 2008; Pennell et al., 2014; Revell, 2012, 2024). Overall, `charisma` facilitates a highly standardized and reproducible pipeline to characterize color class data from images of organisms for downstream analyses. By carefully designing the package to handle a spectrum of fully automated to completely manual workflows, users are equipped to adapt the precision of `charisma`-derived color label classifications to their particular research needs while enjoying automated data and image processing provenance out-of-the-box.

2.2 Validating `charisma`'s color classification performance

We validated the performance of `charisma` and the accuracy of our CLUT by first testing known color datasets. We obtained color grids for each of our 10 colors from the images on the Wikipedia "Shades of [Color]" pages (**Table S1**). These images contain grids of 9-25 color squares representative of each color, which we used as input in the automated `charisma` pipeline.

2.3 Imaging bird museum specimens

We then illustrate the utility of `charisma` for evolutionary color analyses with images of tanagers in the subfamily Thraupinae (Family Thraupidae). Tanagers in this subfamily have been well studied in terms of molecular phylogenetics and color evolution (Burns et al., 2014, 2016; Price-Waldman et al., 2020; Shultz and Burns, 2017). Previous work has found that lineages within Thraupinae have the highest evolutionary rates of plumage complexity in tanagers (Price-Waldman et al., 2020). The subfamily Thraupinae also contains the notably colorful genus *Tangara* (and allied genera that have been split from the traditional *Tangara* genus), an ideal clade for testing `charisma`. We photographed 32 bird museum specimens at the Natural History Museum of Los Angeles County (**Table 3**). This testing dataset consists of incomplete sampling within the subfamily and contains mostly male specimens with a few female specimens that exhibit minimal sexual dichromatism in the human visible spectrum. Specimens were photographed under consistent conditions using a Nikon D70s with Novoflex 35mm lens and Natural LightingNaturesSunlite 30-W full spectrum fluorescent bulbs. Each image included a color standard and RAW image files were white-balanced before `charisma` processing. The images were segmented manually by annotating the pixel coordinates to create precise polygonal mask contours directly around the boundary of each bird body (à la Schwartz and Alfaro, 2021) to remove the background. To focus our analyses on plumage coloration, we removed the bill, leg, tag, and cotton eye pixels of the specimen images prior to characterizing color metrics using `charisma`.

2.4 Bird coloration datasets

To classify color in our bird museum specimen images, we ran both the fully automated `charisma` pipeline and a modified version where we manually reduced pixel color noise (Figure 1b). For

the fully automated datasets, we tested threshold values of 5%, 7.5%, and 10%, where any color with a proportion of pixels lower than these threshold values would be removed from the color classification. We implemented these thresholds to automatically remove colors that may have been misclassified due to image artifacts like shadows or feather overlap. To ground-truth our `charisma` classifications, we extracted color classifications for our species from a dataset of color classifications for all members of the Thraupidae (true tanager) family determined by an expert in tanager coloration (A.J.S.). `charisma` color classification performance was evaluated by comparing the categorical classifications derived from the automatic and manual color datasets against our expert dataset using a binary contingency table (Powers, 2020). We used our expert color dataset as the true colors of the birds and classified each `charisma`-identified color classification as a true positive (i.e., 'hit'), false negative (i.e., 'miss'), false positive (i.e., 'false alarm'), or true negative (i.e., 'correct rejection').

2.5 Evolutionary analyses

We used our datasets and a previously published tanager phylogeny (Burns et al., 2014) to explore variation in the rates of color evolution and reconstruct ancestral color states. Additionally, because the color-producing mechanisms and structures are well known in birds (Hill, 2006; Mason and Bowie, 2020; Stoddard and Osorio, 2019; Stoddard and Prum, 2011), we also estimated rates and reconstructed ancestral states for color-producing mechanisms. We transformed our color data by grouping discrete colors by avian color-producing mechanism. We designated melanin-based colors as black, brown, and grey, carotenoid-based colors as red, orange, and yellow, and structural colors (produced by feather nanostructure, including those with pigment overlays) as green, blue, and purple (Hill, 2006). For purposes of this study, we have oversimplified the color producing mechanisms, specifically for green (includes carotenoids and nanostructure), blue, and purple (both include melanin and nanostructure). We removed white from the color mechanism analysis because it has two potential mechanisms: a lack of pigment or feather nanostructure. For each color and mechanism, we used the `fitDiscrete()` function in the R package `geiger` to test the fit of two models of evolution: the equal rates (ER) model, which assumes the rates of gains and losses of a color are equal, and the all rates different (ARD) model, which assumes gains and losses of a color occur at different rates. We compared transition rates for every color in our datasets to

determine the potential effects of automated, expert, and manual classifications on evolutionary analyses. We used the sample-size corrected Akaike Information Criterion (AICc) to select the best model for each color and mechanism for our manual dataset. We then leveraged the best-fitting model to reconstruct ancestral states for our manual dataset. Using the R package `phytools`, we estimated maximum-likelihood probabilities for each color and mapped them on the tanager phylogeny (Burnham et al., 1998; Burns et al., 2014; Huelsenbeck et al., 2003; Paradis et al., 2004; Revell, 2012).

3 Results and Discussion

3.1 Validation

Figure 2 demonstrates `charisma`'s ability to characterize the colors in an image. Here, we find that the majority of *charisma* color classifications identify the pre-assigned color class of the input grid. The highest variation in color classifications was present in the red and orange grids with four different colors being called for each. Brown had the second highest proportion of calls for both red and orange grids, which highlights the general difficulty of delineating between the boundaries of these three colors in HSV color space.

3.2 Comparison of color datasets

We found that the manual color dataset outperformed automatic color datasets when compared to the expert color dataset (**Table 4** and **Tables S2, S3, S4**). Black was well-classified in all datasets and brown and grey had high false alarm rates in automatic datasets (**Table 4** and **Tables S2, S3, S4**). The bases and tips of bird feathers, especially contour feathers, are often different colors, with the base generally being black, brown, grey, or white and the tip containing more highly pigmented or structural coloration (Price-Waldman et al., 2025; Terrill and Shultz, 2023). In bird museum specimens, overlapping feathers can be misaligned to create grey or brown patches where the base of feathers show (**Figure 1c**). These color artifacts may contribute to the over-representation of brown and grey in the automatic color datasets. For our analyses, these patches represented unwanted image artifacts, however, depending on the goal of the user, the classification of such subtle variation could be a benefit.

Red and orange had high miss rates in the automatic datasets (**Table 4** and **Tables S2, S3, S4**). Red ($n = 2$) and orange ($n = 1$) are rare in our dataset, but when present, they are represented by very small patches. As expected, the automatic thresholding procedure removed colors with a small proportion of pixels, making underrepresented color categories difficult to classify using the automatic pipeline. Together, the small sample size and small patch size of red and orange in these birds contribute to the high miss rates in the automatic datasets. The classifications derived from the manual `charisma` pipeline show an almost identical color profile to the expert color dataset as evidenced by the near-100% hit and correct rejection rate (**Table 4**). As such, signal-to-noise ratio (SNR) can be further improved by running `charisma` without the thresholding procedure and manually correcting both underrepresented color patches to reduce misses and color patches sitting at the boundary of the CLUT color class boundaries to reduce false alarm identifications.

3.3 Evolutionary analyses

To understand how classifying color in different ways (i.e., automatic vs. manual datasets) impacts evolutionary rates analyses, we compared evolutionary rates estimated for the expert, manual, and automatic datasets (**Figure 3** and **Table 1**). We found that the automatic datasets elevated the rate of evolution of grey across all models providing evidence that uncorrected color artifacts in bird museum specimens, likely due to misaligned feathers, impact downstream evolutionary analyses. We also found slower evolutionary rates for blue and green in the automatic datasets, which may be due to the higher miss rates of `charisma`-identified blue and green color classes (**Table 4** and **Tables S2, S3, S4**). As predicted, we see high congruence in evolutionary rates between our expert and manual color datasets.

Given the similarity between our expert and manual color datasets, we present the results of our evolutionary analyses using the best-performing `charisma` classification (i.e., the manual color dataset). We note that these results and interpretations are based on incomplete sampling of a subfamily of tanagers and they are presented as an example of the utility of `charisma` for these types of evolutionary analyses. Additionally, we have categorized highly complicated color-producing mechanisms into two simple mechanisms. Any biological interpretations of the data should be taken with caution. We tested two models of evolution on discrete color categories and colors grouped by color-producing mechanism (see **Figure 4**, **Table 1**, and **Table 2**). We

excluded purple and the melanin mechanism from our analyses because purple was not present in any species and melanin was ubiquitous across all species. When comparing the evolution of the melanin color using the ER model, brown showed an elevated rate compared to all other color classes, and black showed the slowest rate (**Figure 3**). Melanin molecules are structurally robust and are often deposited in the primary wing and tail feathers of birds to increase durability and resist abrasion in these high-use feathers (Bonser, 1995). This aligns with our finding that melanin coloration is highly conserved and indicates the need for structural integrity in bird feathers.

For color-producing mechanisms, carotenoid coloration showed a higher rate of evolution than structural coloration (**Figure 4**). Pigment-based color is more widespread across the avian tree of life than structural color (Hill and McGraw, 2006). However, across our tanager dataset, structural colors (green and blue), are present in more species than carotenoid colors (red, orange, and yellow), which may be contributing to the faster rate of evolution for carotenoid coloration. The structural color, blue, best fit the ARD model of evolution and showed elevated gain and loss rates compared to all other colors (**Figure 3** and **Table 2**). Where structural color is present, there is evidence that color diversity accumulates faster than pigment-based color because of the modularity of layering pigments and structure (Eliason et al., 2015; Maia et al., 2016). These subtle structural changes at the nanometer level may result in the production of significantly different colors allowing for rapid evolution and accumulation of color diversity.

Lastly, we found the ER model of evolution to be the best-fitting model for every color and color-producing mechanism except for blue and orange (**Table 1**). Using the best-fitting model for each color and mechanism, we reconstructed ancestral states and mapped them across the tanager phylogeny (**Figure 5**). We found that most ancestral nodes had black, brown, yellow, green, and blue color states, which were also the most common colors in our dataset. Black, white, brown, and grey have been shown to be the most common colors across the bird tree of life (Delhey et al., 2023) and differences in our findings are likely due to the uniquely colorful nature of birds in the subfamily Thraupinae. The ancestral state reconstructions demonstrate that rates of evolution are largely driven by losses of colors across internal branches of the tree. Orange fit the ARD model best with a slightly elevated rate of gain of orange than loss (**Figure 3**). However, orange is only present in one species in our dataset and this result is driven mainly by the uncertainty of the presence of orange at the root of the phylogeny (see **Figures 3 and 5**).

4 Conclusions

Here, we present `charisma`, an R package we developed to provide a standardized, reproducible, and flexible framework for characterizing and classifying color categories from digital images. To demonstrate its utility, we used color-calibrated images of bird museum specimens and found that a hybrid approach using both the built-in automated and manual clean-up pipelines provided the most accurate color profiling. Artifacts from misaligned feathers in our bird museum specimen image dataset led to over representation of brown and grey in the fully-automatic `charisma`-derived color classification. While these artifacts might not generalize to all image datasets, we recommend using `charisma` in two-stages: first, automatically characterize the color profile for each image; then, manually adjust the outputs using `charisma`'s built-in utilities for classification clean-up to best fit the biology of your system. Critically, `charisma` is built with a fully open source design philosophy where flexibility and customization are both welcomed and encouraged. One example is the built-in functionality to adjust the default CLUT based on user needs and their specific image dataset. Cases where this might be most useful are when fine-tuning is needed for standardized datasets of other organisms, like J.E. Randall's images of fish (http://pbs.bishopmuseum.org/images/JER/), or for extant datasets comprised of non-standardized images, like those culled from iNaturalist (Matheson, 2014; https://www.inaturalist.org) or eBird (Sullivan et al., 2009). Furthermore, we demonstrate that the outputs of `charisma` enable seamless transition to downstream evolutionary analyses, which we showcased in a vignette on tanagers in the subfamily Thraupinae. Ultimately, we present `charisma` as a solution for high-throughput organismal color analyses, but also do not restrict `charisma`'s utility to evolutionary biology applications.

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Competing Interests

We declare that there are no conflicts of interest with respect to the authorship or publication of this article.

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Authors' Contributions

- **S.T.S.:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Resources, Software, Supervision, Validation, Visualization, Writing - Original Draft Preparation, Writing - Review & Editing

- **W.L.E.T.:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Resources, Supervision, Validation, Visualization, Writing - Original Draft Preparation, Writing - Review & Editing
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- **J.E.M.:** Resources, Writing - Review & Editing
- **T.B.S.:** Methodology, Writing - Review & Editing
- **M.E.A.:** Conceptualization, Methodology, Writing - Review & Editing

Code Accessibility

CRAN: https://cran.r-project.org/package=charisma
`charisma` package GitHub repo: https://github.com/shawntz/charisma
`charisma` package docs and interactive tutorials: https://shawnschwartz.com/charisma

Data Accessibility

Analytic data/code for this manuscript can be found on the following Open Science Framework repo: https://osf.io/cqg59

Table 1. Rates of color evolution and ancestral state reconstruction model selection for all datasets.

		Equal Rates Model			All Rates Different Model			
	Color	**Rate of gain and loss**	**AICc**	**AICc weight**	**Rate of gain**	**Rate of loss**	**AICc**	**AICc weight**
Expert	Black	0.00226*	10.16	0.755	0	0.00226	12.41	0.245
	White	0.0248*	38.98	0.554	0.00859	0.0505	39.42	0.446
	Grey	0.00749*	23.75	0.565	0.0241	0.227	24.27	0.435
	Brown	0.159*	46.21	0.75	0.169	0.152	48.41	0.25
	Red	0.00466*	18.48	0.608	0.0252	0.374	19.36	0.392
	Orange	0.00475	21.4	0.266	0.0499*	0.747*	19.37	0.734
	Yellow	0.0327*	41.28	0.616	0	0.0283	42.23	0.384
	Green	0.0380*	44.87	0.589	5.61	2.94	45.6	0.411
	Blue	0.0111	32.8	0.42	6.99*	1.29*	32.15	0.58
Manual	Black	0.00226*	10.16	0.755	0	0.0026	12.41	0.245
	White	0.0248*	38.98	0.554	0.00859	0.0505	39.42	0.446
	Grey	0.00749*	23.75	0.565	0.0241	0.227	24.27	0.435
	Brown	0.159*	46.21	0.75	0.169	0.152	48.41	0.25
	Red	0.00466*	18.48	0.608	0.0252	0.374	19.36	0.392
	Orange	0.00475	21.4	0.266	0.0499*	0.747*	19.37	0.734
	Yellow	0.0326*	41.28	0.616	0.028	0	42.23	0.384
	Green	0.0317*	44.06	0.514	5.6	2.5	44.16	0.486
	Blue	0.0152	37.3	0.591	6.39*	1.79*	38.03	0.409
Auto Thresh - 5%	Black	0.00226*	10.16	0.755	0	0.0026	12.41	0.245
	White	0.01*	27.84	0.569	0.0278	0.188	28.4	0.431
	Grey	4.1*	46.49	0.64	4.55	3.11	47.64	0.36
	Brown	0.0282	42.59	0.409	0.144*	0.0563*	41.85	0.591
	Red	NA	NA	NA	NA	NA	NA	NA
	Orange	0.00743	24.55	0.467	0.0345*	0.33*	24.29	0.533
	Yellow	0.0243	41.845	0.486	0.0462*	0.12*	41.74	0.514
	Green	0.0359*	44.87	0.72	4.86	2.92	46.75	0.28
	Blue	0.0472*	44.92	0.747	0.055	0.046	47.09	0.253
Auto Thresh - 7.5%	Black	0.00464*	15.63	0.749	0	0.00463	17.82	0.251
	White	0.00747*	23.61	0.579	0.0223	0.209	24.25	0.421
	Grey	4.15*	46.49	0.709	3.58	4.6	48.27	0.291
	Brown	0.0434	45	0.5	0.123	0.0648	45	0.5
	Red	NA	NA	NA	NA	NA	NA	
	Orange	0.00478*	18.34	0.619	0.0141	0.205	19.31	0.381
	Yellow	0.0152*	34.74	0.534	0.0131	0.0769	36.02	0.466
	Green	0.0441*	45.36	0.741	0.0582	0.0453	47.46	0.259
	Blue	0.0544*	45.25	0.757	0.0537	0.0567	47.51	0.243
Auto Thresh - 10%	Black	0.00464*	15.63	0.749	0	0.00429	17.82	0.251
	White	0.00482*	18.94	0.551	0.0198	0.292	19.35	0.449
	Grey	3.17*	46.49	0.532	8.21	13.69	46.75	0.468
	Brown	0.107*	45.8	0.659	0.136	0.0948	47.12	0.341
	Red	NA	NA	NA	NA	NA	NA	NA
	Orange	0.00229*	11.83	0.675	0.00876	0.267	13.29	0.325
	Yellow	0.0111	29.32	0.475	0.00748*	0.0347*	29.12	0.525
	Green	0.0317*	40.99	0.63	0.00318	0	42.05	0.37
	Blue	0.0486*	44.85	0.706	0.0484	0.0687	46.61	0.294

Note. Asterisks (*) indicate best fit model for each color category.

Table 2. Rates of color-producing mechanism evolution and ancestral state reconstruction model selection for the manual dataset.

	Equal Rates Model			All Rates Different Model			
Mechanism	**Rate of gain and loss**	**AICc**	**AICc weight**	**Rate of gain**	**Rate of loss**	**AICc**	**AICc weight**
Carotenoid	0.0326*	41.28	0.616	0	0.0283	42.23	0.384
Structural	0.00468*	17.35	0.725	0.201	0.0138	19.29	0.275

Note. Asterisks (*) indicate best fit model for each color category.

Table 3. Bird museum specimens.

Catalog Number	Genus	Species	Common Name
LACM 34880	*Chalcothraupis*	*ruficervix*	Golden-naped Tanager
LACM 4843	*Ixothraupis*	*guttata*	Speckled Tanager
LACM 43685	*Ixothraupis*	*punctata*	Spotted Tanager
LACM 16611	*Ixothraupis*	*rufigula*	Rufous-throated Tanager
LACM 50758	*Ixothraupis*	*xanthogastra*	Yellow-bellied Tanager
LACM 37481	*Poecilostreptus*	*palmeri*	Gray-and-gold Tanager
LACM 39216	*Stilpnia*	*cayana*	Burnished-buff Tanager
LACM 37716	*Stilpnia*	*cyanoptera*	Black-headed Tanager
LACM 29385	*Stilpnia*	*heinei*	Black-capped Tanager
LACM 4841	*Stilpnia*	*larvata*	Golden-headed Tanager
LACM 53462	*Stilpnia*	*preciosa*	Chestnut-backed Tanager
LACM 36850	*Stilpnia*	*vitriolina*	Scrub Tanager
LACM 59610	*Tangara*	*arthus*	Golden Tanager
LACM 59272	*Tangara*	*chilensis*	Paradise Tanager
LACM 59652	*Tangara*	*cyanocephala*	Red-necked Tanager
LACM 27866	*Tangara*	*cyanoventris*	Gilt-edged Tanager
LACM 28775	*Tangara*	*desmaresti*	Brassy-breasted Tanager
LACM 16290	*Tangara*	*dowii*	Spangle-cheeked Tanager
LACM 60421	*Tangara*	*fastuosa*	Seven-colored Tanager
LACM 60422	*Tangara*	*florida*	Emerald Tanager
LACM 43661	*Tangara*	*gyrola*	Bay-headed Tanager
LACM 30414	*Tangara*	*inornata*	Plain-colored Tanager
LACM 37463	*Tangara*	*johannae*	Blue-whiskered Tanager
LACM 59219	*Tangara*	*labradorides*	Metallic-green Tanager
LACM 32721	*Tangara*	*mexicana*	Turquoise Tanager
LACM 40998	*Tangara*	*nigroviridis*	Beryl-spangled Tanager
LACM 29400	*Tangara*	*parzudakii*	Flame-faced Tanager
LACM 50757	*Tangara*	*schrankii*	Green-and-gold Tanager
LACM 53515	*Tangara*	*seledon*	Green-headed Tanager
LACM 29453	*Tangara*	*vassori*	Blue-and-black Tanager
LACM 43655	*Tangara*	*velia*	Opal-rumped Tanager
LACM 33255	*Tangara*	*xanthocephala*	Saffron-crowned Tanager

Table 4. Performance comparison between the *automated* `charisma` classification workflow (with manual adjustments) and expert classification across color categories. Each column reports the total number of hits (true positives), misses (false negatives), false alarms (false positives), and correct rejections (true negatives) in the `charisma` dataset. The percentage of correct hits (parentheses) are calculated as the number of hits divided by the total number of color targets (hits + misses) in the expert dataset. The percentage of correct rejections (parentheses) are calculated as the number of correct rejections divided by the total number of non-targets (correct rejections + false alarms) in the expert dataset.

Color	**Hits**	**Misses**	**Correct Rejections**	**False Alarms**
Black	31 (100%)	0	1 (100%)	0
Blue	25 (93%)	2	5 (100%)	0
Brown	17 (100%)	0	15 (100%)	0
Green	21 (100%)	0	10 (91%)	1
Grey	3 (100%)	0	29 (100%)	0
Orange	2 (100%)	0	30 (100%)	0
Purple	0 (100%)	0	32 (100%)	0
Red	2 (100%)	0	30 (100%)	0
White	9 (100%)	0	23 (100%)	0
Yellow	19 (100%)	0	13 (100%)	0

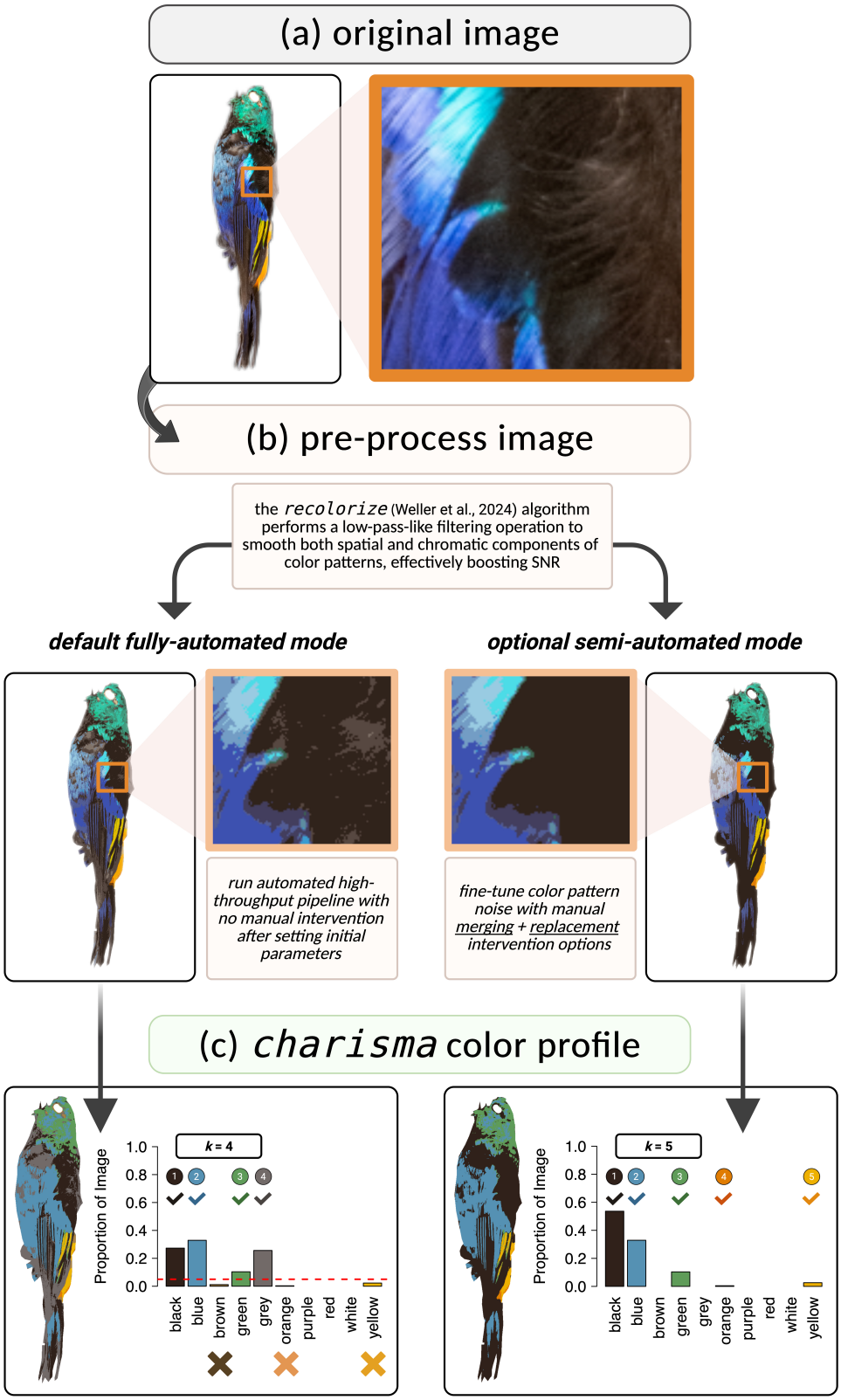

Fig. 1. Overview of the *charisma* workflow. ***a,*** Original digitized specimen image, *Tangara fastuosa*, passed into *charisma* for processing. ***b,*** The *recolorize* algorithm (see Weller et al., 2024) is used to boost SNR by effectively performing a low-pass-like filter. Then, users are prompted with an option to make manual adjustments to further fine-tune image noise (e.g., biologically irrelevant colors) with interactive color merging and replacement operations (adapted from the `recolorize` R package, see above). ***c,*** Lastly, users receive the *charisma* "color profile", which provides a count of the number of discrete color class labels (out of the 10 shown here; k) as well as the proportion of pixels in the image that fall into each of the 10 possible color categories. On the left, the dashed red horizontal line indicates a 5% user-specified threshold to perform automated rejection of low frequency color classes. The fully-automated workflow yielded $k = 4$ (i.e., black, blue, green, and grey). On the right, manual adjustments further reduced noise to eliminate the brown and grey artifacts and correctly call orange and yellow with a 0% threshold. Created in BioRender (Schwartz and Tsai, 2025a). https://BioRender.com/bccv8xm

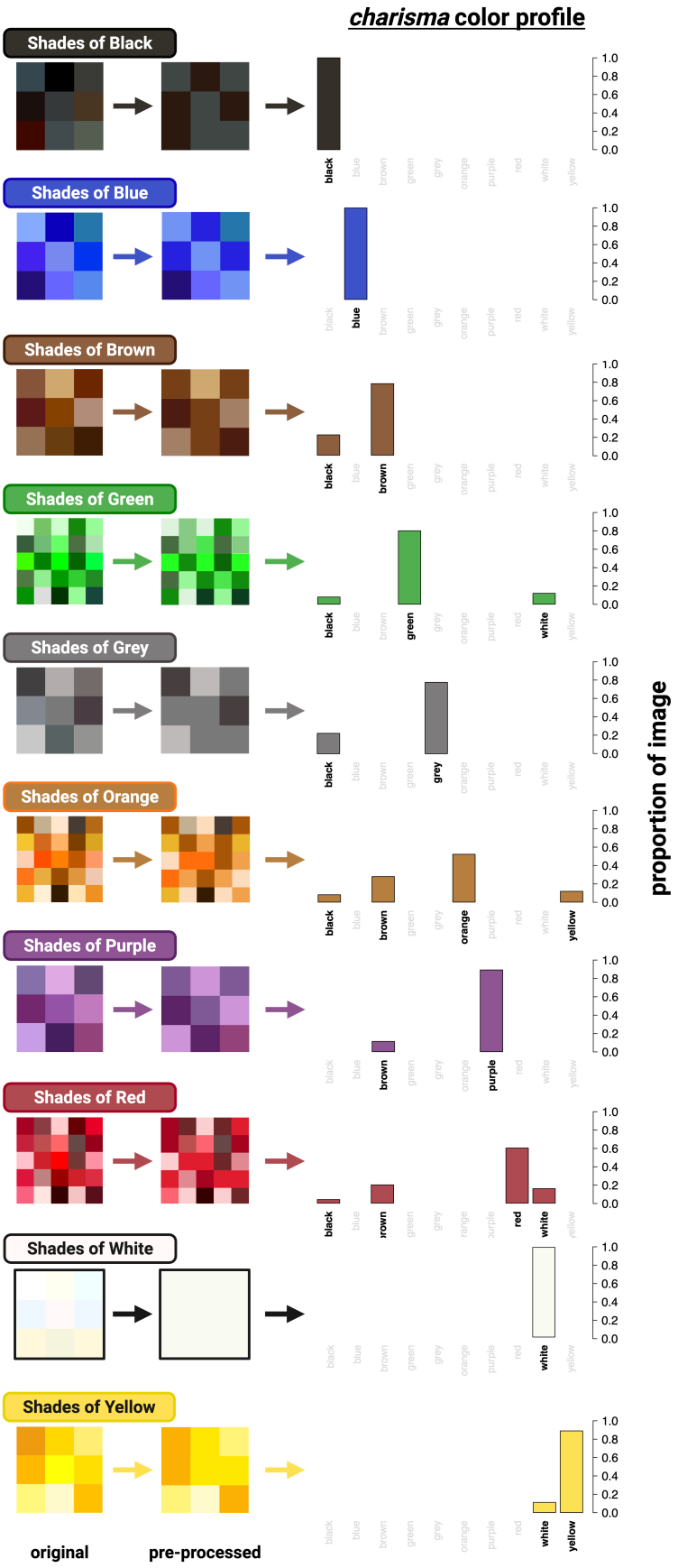

Fig. 2. Validating `charisma` color category classifications. Swatches each containing shades of one of nine color categories (white not shown) were obtained from Wikipedia (see **Table S1**) and were then submitted directly to the `charisma` fully-automated pipeline. `charisma` performed well-above chance at identifying each of the nine color categories (see *charisma color profile*). Created in BioRender (Schwartz and Tsai, 2025b). https://BioRender.com/ds5tav2

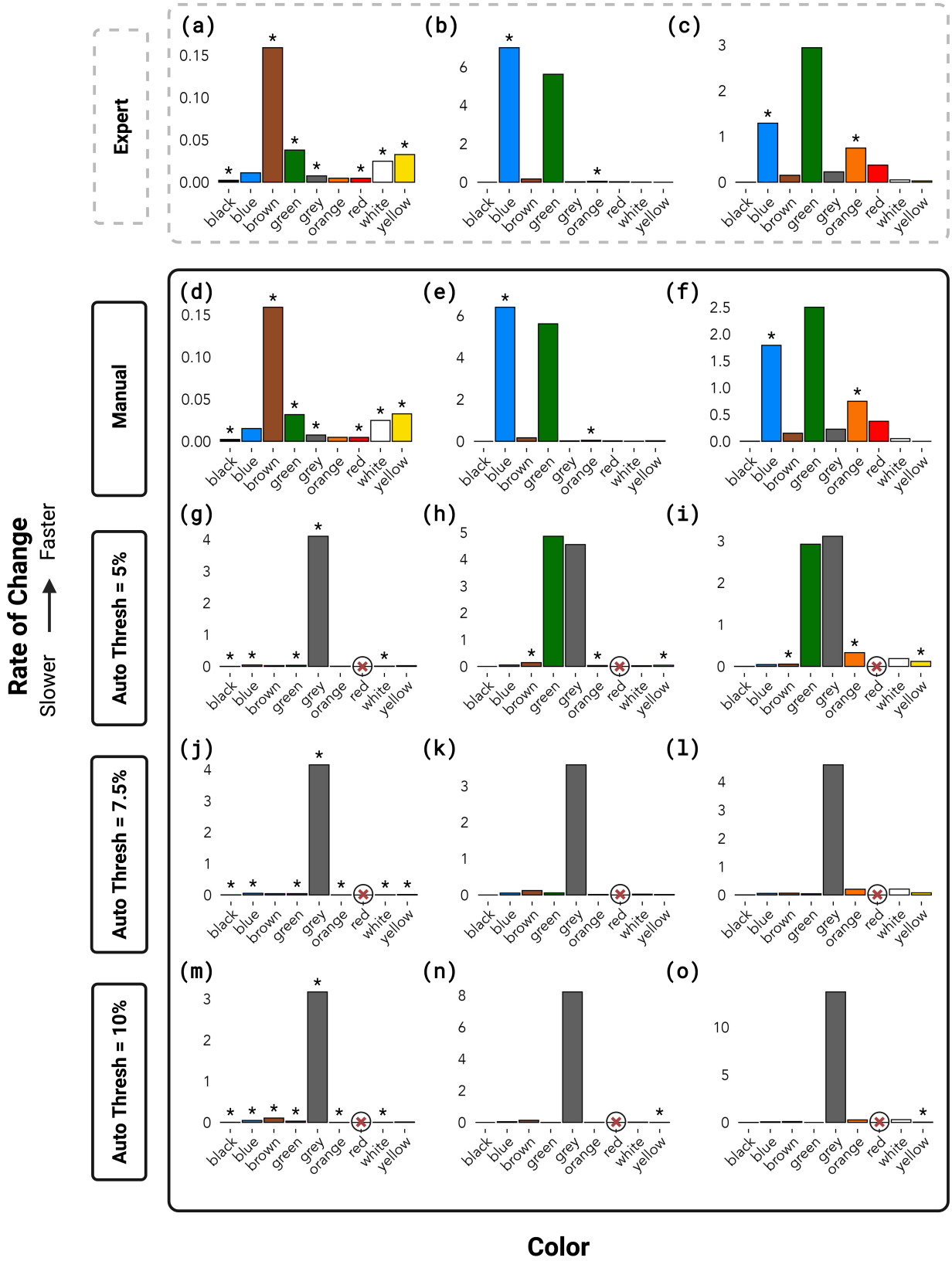

Fig. 3. Evolutionary rates of change for each color and evolutionary model as classified in our expert dataset (A.J.S.) – top-dashed – versus `charisma`-based classifications – **"Manual":** hybrid classification using a threshold = 0% with manual adjustments (W.L.E.T.); the three remaining classifications were derived from the fully-automated `charisma` pipeline with no manual editing, using increasingly conservative color-proportion thresholds from top-to-bottom. Red ⊗ indicates the color was not called by the `charisma` analysis; asterisks (*) indicate best fit model for each color category (rates and model selection can be found in **Table 1**). Each plot shows the relative rate of evolutionary change proportional to the highest rate on each plot. Each column represents the following rates: ***left,*** Equal Rates (ER), ***middle,*** All Rates Different (ARD) gain, ***right,*** ARD loss. Note that for the automated dataset with threshold 7.5% (j, k, l), the ER and ARD model selection was inconclusive with an AICc weight of 0.5 for each model. Created in BioRender (Schwartz and Tsai, 2025c). https://BioRender.com/w6sx1dx

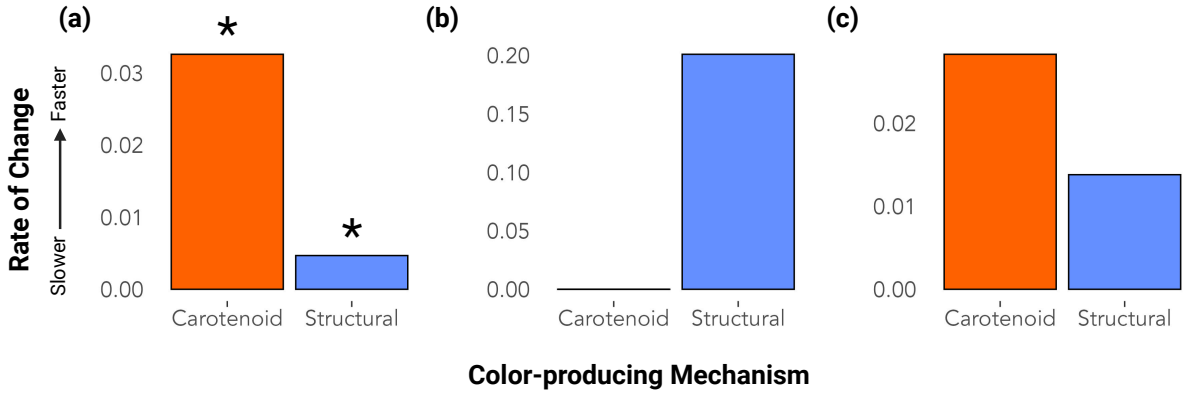

Fig. 4. Evolutionary rates for each color-producing mechanism and evolutionary model for the manual dataset: ***a,*** Equal Rates (ER) rate, ***b,*** All Rates Different (ARD) gain rate, ***c,*** ARD loss rate. Asterisks (*) indicate best fit model for each color-producing mechanism (rates and model selection can be found in **Table 2**). Created in BioRender (Schwartz and Tsai, 2025d). https://BioRender.com/8uliuti

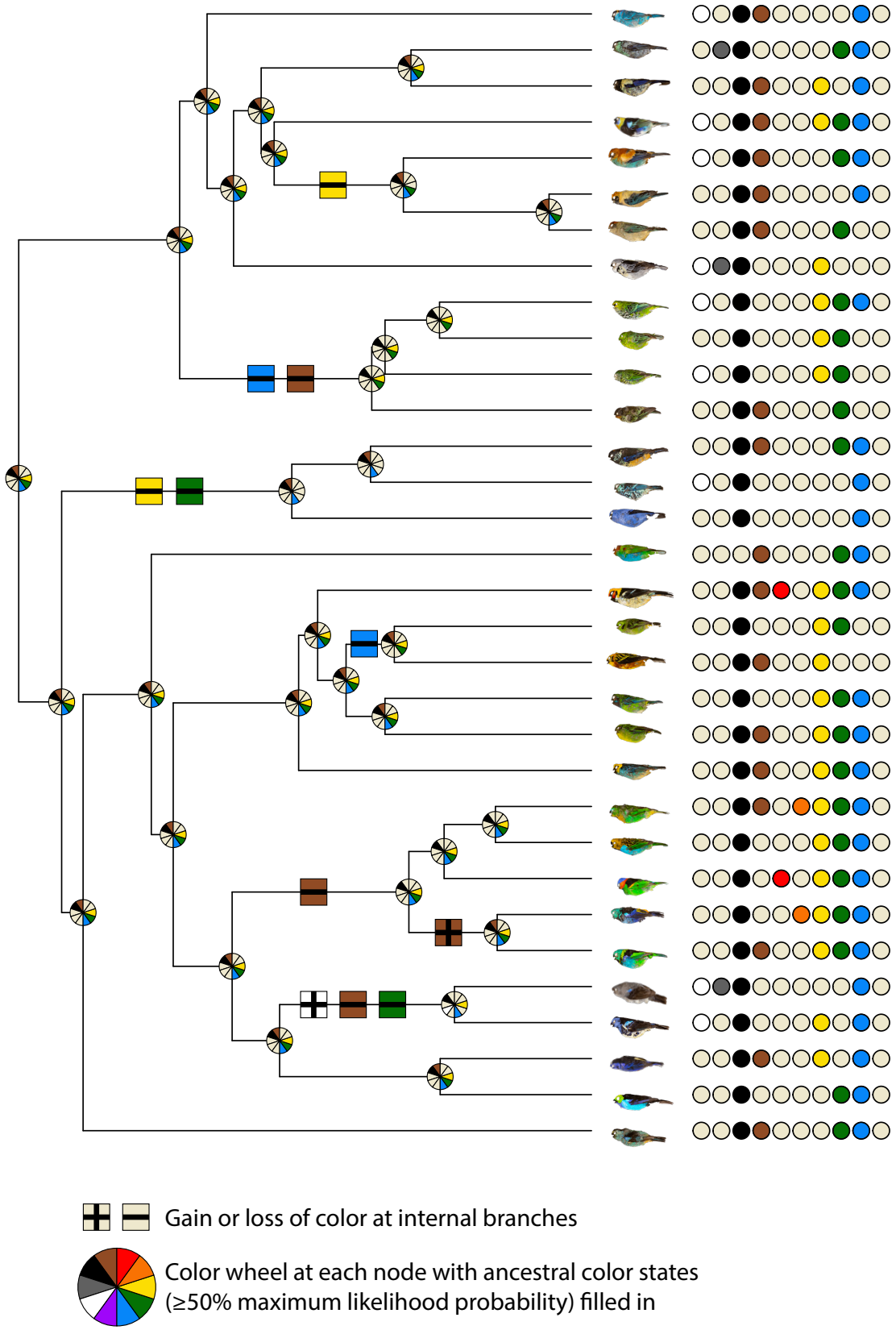

Fig. 5. `charisma` color classifications mapped on the tanager phylogeny. For each species, colored dots represent the colors present in the image. Color wheels at each node indicate estimated colors with greater than or equal to 50% maximum likelihood probability. Internal branches are marked with gains or losses of colors. Species order (top to bottom): *Chalcothraupis ruficervix, Stilpnia heinei, S. cyanoptera, S. larvata, S. preciosa, S. cayana, S. vitriolina, Poecilostreptus palmeri, Ixothraupis guttata, I. xanthogastra, I. punctata, I. rufigula, Tangara dowii, T. nigroviridis, T. vassorii, T. gyrola, T. parzudakii, T. florida, T. arthus, T. johannae, T. schrankii, T. xanthocephala, T. desmaresti, T. cyanoventris, T. cyanocephala, T. fastuosa, T. seledon, T. chlornata, T. mexicana, T. velia, T. chilensis, T. labradorides.*

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Table S1. Sources images for Wikipedia-based shades of color swatch validation.

Color	Author	Source
Black	Tony Mach	https://w.wiki/EghT
Blue	Booyabazooka	https://w.wiki/EghU
Brown	Booyabazooka, Mizunoryu, Badseed, Jacobolus	https://w.wiki/6TtW
Green	Booyabazooka	https://w.wiki/d6j
Grey	Mizunoryu, Badseed, Jacobolus	https://w.wiki/EghW
Orange	Booyabazooka	https://w.wiki/EghX
Purple	Mizunoryu, Badseed, Jacobolus	https://w.wiki/AGiB
Red	ThunderBrine	https://w.wiki/A9QR
White	Badseed	https://w.wiki/EghZ
Yellow	Badseed	https://w.wiki/Egha

Table S2. Performance comparison between the *automated* `charisma` classification workflow (with a 5% color-proportion threshold) and expert classification across color categories. Each column reports the total number of hits (true positives), misses (false negatives), false alarms (false positives), and correct rejections (true negatives) in the `charisma` dataset. The percentage of correct hits (parentheses) are calculated as the number of hits divided by the total number of color targets (hits + misses) in the expert dataset. The percentage of correct rejections (parentheses) are calculated as the number of correct rejections divided by the total number of non-targets (correct rejections + false alarms) in the expert dataset.

Color	**Hits**	**Misses**	**Correct Rejections**	**False Alarms**
Black	31 (100%)	0	1 (100%)	0
Blue	17 (63%)	10	5 (100%)	0
Brown	14 (82%)	3	6 (40%)	9
Green	19 (90%)	2	10 (91%)	1
Grey	3 (100%)	0	13 (45%)	16
Orange	0 (0%)	2	27 (90%)	3
Purple	0 (100%)	0	32 (100%)	0
Red	0 (0%)	2	30 (100%)	0
White	3 (33%)	6	22 (96%)	1
Yellow	9 (47%)	10	13 (100%)	0

Table S3. Performance comparison between the *automated* `charisma` classification workflow (with a 7.5% color-proportion threshold) and expert classification across color categories. Each column reports the total number of hits (true positives), misses (false negatives), false alarms (false positives), and correct rejections (true negatives) in the `charisma` dataset. The percentage of correct hits (parentheses) are calculated as the number of hits divided by the total number of color targets (hits + misses) in the expert dataset. The percentage of correct rejections (parentheses) are calculated as the number of correct rejections divided by the total number of non-targets (correct rejections + false alarms) in the expert dataset.

Color	**Hits**	**Misses**	**Correct Rejections**	**False Alarms**
Black	30 (97%)	1	1 (100%)	0
Blue	15 (60%)	10	7 (100%)	0
Brown	13 (76%)	4	7 (47%)	8
Green	19 (86%)	3	10 (100%)	0
Grey	3 (100%)	0	18 (62%)	11
Orange	0 (0%)	2	28 (93%)	2
Purple	0 (100%)	0	32 (100%)	0
Red	0 (0%)	2	30 (100%)	0
White	3 (33%)	6	23 (100%)	0
Yellow	7 (37%)	12	13 (100%)	0

Table S4. Performance comparison between the *automated* `charisma` classification workflow (with a 10% color-proportion threshold) and expert classification across color categories. Each column reports the total number of hits (true positives), misses (false negatives), false alarms (false positives), and correct rejections (true negatives) in the `charisma` dataset. The percentage of correct hits (parentheses) are calculated as the number of hits divided by the total number of color targets (hits + misses) in the expert dataset. The percentage of correct rejections (parentheses) are calculated as the number of correct rejections divided by the total number of non-targets (correct rejections + false alarms) in the expert dataset.

Color	**Hits**	**Misses**	**Correct Rejections**	**False Alarms**
Black	30 (97%)	1	1 (100%)	0
Blue	13 (52%)	12	7 (100%)	0
Brown	13 (76%)	4	9 (60%)	6
Green	17 (77%)	5	10 (100%)	0
Grey	3 (100%)	0	20 (69%)	9
Orange	0 (0%)	2	29 (97%)	1
Purple	0 (100%)	0	32 (100%)	0
Red	0 (0%)	2	30 (100%)	0
White	2 (22%)	7	23 (100%)	0
Yellow	5 (26%)	14	13 (100%)	0