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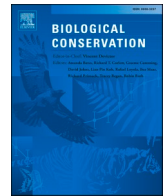
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Colourful Brazilian anurans are preferentially targeted by wildlife trade

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ABSTRACT

The global wildlife trade is a multi-billion-dollar industry, that when poorly managed, can threaten all major terrestrial taxa. Amphibians are currently the most threatened terrestrial vertebrate taxa, due in part to exploitation. Humans place a high value on the aesthetics of nature, with distinctive morphology often a key driver of wildlife trade. Here, we explore the association of colour on the trade of anuran species traded as both pets (traded alive) and products (traded dead) in Brazil, a hotspot of anuran diversity. We collected colour data on all 64 traded Brazilian anurans plus an additional 216 control species not in trade. Our results highlighted more vibrant colours in traded than non-traded species and that the probability of trade increases with the number of colours present. The presence of blue had the strongest effect on trade probability, followed by orange, black, then yellow, with the remaining colours having no effect on the likelihood of trade. Anurans displaying rarer colours are more likely to be traded and more colours increase the likelihood of trade for pets but not for products. Our results provide crucial evidence that colour diversity in amphibians influences the risk of trade and adds to the growing weight of evidence that colour is a key correlate of trade. This points to the need to focus monitoring and protection efforts on colourful species that are at-risk from unsustainable exploitation.

1. Introduction

Over the last 40-years, the volume of traded wildlife has vastly increased. On average, over 100 million plants and animals were internationally traded annually between 2005 and 2014 (Harfoot et al., 2018). The legal wildlife trade industry alone is estimated to be worth up to USD 220 billion per year (CITES Secretariat, 2022) with estimates of the value of illegal wildlife trade being inherently unreliable and often varying in magnitude (t Sas-Rolfes et al., 2019). Almost a quarter of the world's terrestrial vertebrates are traded, spanning across 75 % of terrestrial vertebrate families (Scheffers et al., 2019). This major global industry is driven by a diverse consumer demand for pets, and products such as luxury goods and food, ornamental purposes, research and education, traditional medicine, and cultural purposes (Baker et al., 2013; Nellemann et al., 2014; Thomas-Walters et al., 2020). For many taxa, poorly managed trade can trigger significant population declines (Symes et al., 2017; IPBES, 2020), yet considering the diversity of species traded, we have a poor evidence base for the scale of this impact for many taxa (Carpenter et al., 2014; Maxwell et al., 2016; Morton et al.,

2021).

Amphibians are undergoing a major extinction crisis (Stuart et al., 2004; Gascon et al., 2007; Wake and Vredenburg, 2008; Warkentin et al., 2009) with 41 % of amphibians threatened with extinction, the highest of all vertebrate taxa (IUCN, 2023). This amphibian decline is also occurring at a faster rate than that of both birds and mammals (Stuart et al., 2004). Although the causes of global amphibian decline are diverse (Sodhi et al., 2008), one major driver of their decline is Chytridiomycosis (Palomar et al., 2022), a disease caused by chytrid fungi. Trade of amphibians is linked with exacerbating the spread of this disease across the globe (Scheele et al., 2019; Fisher and Garner, 2020). Furthermore, amphibian trade is potentially linked with the global extinction of the Pass Stubfoot Toad (*Atelopus senex*) and two other amphibian species undergoing local extinctions (Hinsley et al., 2023). Scheffers et al. (2019) estimated that of the 6484 amphibian species globally, 8 % are traded. However, Hughes et al. (2021) suggest that the trade in un-/under-regulated species could double this estimate.

Amphibians are internationally traded predominantly for meat and as live individuals destined for the pet market, but also for their eggs,

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skins, and skeletons (Carpenter et al., 2014). National trade of amphibians has significance for culture and food security. For example, the Mountain Chicken (*Leptodactylus fallax*) was once the unofficial national dish of Dominica (Nicholson et al., 2020), and in Cameroon, tadpoles of the Mountain Egg Frog (*Leptodactylodon bicolor*), Hairy Frog (*Trichobatrachus robustus*), and other species can be important sources of protein when bushmeat availability is poor (Garner et al., 2009).

Humans value aesthetics in nature (Chang et al., 2020), and this tendency can carry over to become a driver of live wildlife trade (Su et al., 2015; Vall-Ilosera and Cassey, 2017). Existing studies on how colouration drives aesthetic attraction largely focus on birds. Senior et al. (2022) found that the pet trade targeted uniquely coloured passerines (perching birds), while Su et al. (2015) showed that bird prices in Taiwanese markets are driven by plumage colour, with more vibrant birds with yellow colouration fetching higher prices than birds with grey colouration. Furthermore, Santangeli et al. (2023) show that vivid colours, particularly blue and red, are associated with attractiveness in birds. Rarity also factors into demand, with Militz et al. (2018) demonstrating that rare colour morphs of clownfishes have an increased risk of exploitation. In amphibians, Mohanty and Measey (2019) highlighted that larger-bodied species are preferentially traded and that a few amphibian families with high species diversity – and high levels of colour diversity – (e.g. Dendrobatidae) are disproportionately targeted for trade. However, quantifying and examining colour's role in this targeted use remain under-researched across taxa, particularly in amphibians.

Amphibians possess a wide range of both vibrant and dull colours with colouration playing major ecological and biological roles (Rudh and Qvarnström, 2013). Most notably, amphibian colouration is important for reducing predation risk. While some species are cryptic (e.g., camouflage) to remain undetected by predators, other taxa, such as Dendrobatidae (known as poison frogs), have evolved vibrant colour hues contrasting with their environment (aposematism) as a warning signal to signify toxicity (Rojas, 2016; Toledo and Haddad, 2009). Amphibians face numerous environmental stressors beyond predators, where colouration is important. Differences in colour lightness in anurans influence thermoregulation, and pathogen and UV-B protection (Laumeier et al., 2023). Darker bodies protect individuals from UV-B-induced damages and absorb more heat from sunlight, whereas lighter bodies may aid with overheating (Rudh and Qvarnström, 2013). Furthermore, studies have linked anuran colouration with mate attraction, mating success (Vásquez and Pfennig, 2007; Hettyey et al., 2009), and even offspring survival (Sheldon et al., 2003). Thus, protecting this colour diversity is critical for conserving key ecological and biological roles in anurans.

The western and central Amazon (predominantly in Brazil) are a particular epicentre of traded amphibian richness (Scheffers et al., 2019). Similarly, the rate of amphibian population decline in Brazil is the fastest in South America, attributable to habitat loss and infectious disease, often facilitated by trade (Scheele et al., 2019). In April 2021, the Brazilian Ministry of Agriculture published legislation that aided the trade of animal products across its states (Brazilian Ministry of Agriculture and Livestock, 2021). Amphibians (and reptiles) were added to the list that permits the capture of fish, crustaceans, molluscs, echinoderms, and other aquatic animals used for human consumption, which will likely increase the trade of amphibians and potentially aggravate the spread of lethal pathogens (Ruggeri and Forti, 2021). Such changes to regulation risk triggering or exacerbating the unsustainable use of amphibians (Hughes et al., 2021).

This study aims to quantify how colour covaries with the trade of anurans (the largest order of Amphibia, dominating amphibian trade; Hughes et al., 2021) in Brazil. Bringing together large-scale data on species presence in trade and novel data on species colouration, we focused on four key questions: i) are traded anuran species more colourful than species not in trade; ii) are specific colours preferentially traded; iii) does increasing colour rarity increase the likelihood of trade;

and iv) are these patterns consistent in both the pet and product trade? We hypothesize that colour is a key driver of anuran trade in Brazil and will be particularly associated with the pet trade. We hypothesize that species with more colour diversity, and rarer colours (Militz et al., 2018; Senior et al., 2022) will be targeted in trade. We also hypothesize that vibrant colours (departing from brown-grey) are associated with attractiveness (Santangeli et al., 2023) and will increase the probability that a species is traded, whereas drabber colours (brown, black, white, and grey) will decrease the odds of being traded. Such hypotheses are grounded in existing literature on other taxa but remain unexplored in amphibians.

2. Methods

2.1. Data collection and sampling

2.1.1. Trade data

The trade data for this study was taken from Scheffers et al. (2019) who used databases from the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List), the United States Fish and Wildlife Service (USFWS) LEMIS data base, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to compile data on the trade status of each species. Species traded internationally, nationally, and locally were all classified as traded. This dataset also included information on the type of trade for each species. Species traded alive, e.g., for expositions, circus, or zoological gardens, were classified as pets. In contrast, species traded dead (e.g., for meat or clothing) were defined as products. Species can be traded as both. We then filtered this dataset to include only anuran species that are native to Brazil (including species whose distribution only partly overlaps with Brazil) using IUCN Red List species range maps. A review of the legal international trade of anurans from Brazil highlighted that no legal anuran exports from Brazil have been reported (<https://tradeview.cites.org/>), with the majority of trade therefore being at a local and national scale (or illegal).

2.1.2. Sampling methods

Of the 869 anuran species native to Brazil, 64 species were classified as traded and were all sampled. As controls, we randomly selected 216 non-traded species from the dataset, generating a total of 280 anuran species sampled. We ensured that all anuran families native to Brazil were included in the sample (excluding Ceuthomantidae, which has one native species, as no images could be sourced). To help control for phylogenetic non-independence, we stratified the sample by family. Where possible we ensured that all families in trade had at least 4 times as many non-traded than traded species sampled. Methods for collecting colour data and details of how rater agreement was confirmed are detailed in the supplementary materials. In brief, colour was visually assessed using representative images where species IDs were verified.

2.1.3. Measuring colour rarity

To assess colour rarity within the dataset, an average rarity score was calculated for each sampled species using the following equation:

$$Q = 1 - \frac{\sum \left(\frac{n}{N} \right) [\text{of colours present on a species}]}{C}$$

Q = Species average colour rarity

n = Total amount of a particular colour recorded in the sample

N = Total number of species sampled.

C = Colour richness of a species

This metric gave each species a unique rarity score by averaging the rarities of each colour present on the anuran species. Rarity is at its lowest when the index is near 0 and at its highest when the index is near

1.

2.2. Statistical analysis

All analyses were conducted using R version 4.3.2 (R Core Team, 2023). All assumptions for the statistical analyses were met following the appropriate data checks and no data transformations were deemed to be necessary. For spatial visualisation, we superimposed IUCN Red List species range maps of the traded Brazilian anurans. Species whose distribution only partly overlaps with Brazil were included.

2.2.1. Colour richness

To assess the difference in the mean colour richness of traded and non-traded species, we performed a two-sample *t*-test. To analyse whether increasing colour richness is associated with the probability of being traded, we fit a hierarchical logistic regression with the likelihood of being traded (1 = traded, 0 = non-traded) as the response variable and colour richness as the predictor variable. We included taxonomic family as a random effect to account for phylogenetic non-independence between species. Snout-vent length (SVL) was also included as a predictor variable within the model to account for body size, SVL data was sourced from Oliveira et al. (2017).

2.2.2. Colours driving anuran trade

To assess how specific colours correlate with trade, we fit another hierarchical logistic regression. The response variable was the likelihood of being traded and each of the individual colours were used as the predictor variables (presence or absence of colour). If a specific colour was present on fewer than 10 species, it was omitted from the model. Only pink was removed for this analysis. SVL was also included as a predictor variable within the model. The model used the absence of a colour as a reference group. We initially included taxonomic family as a random effect, but the model failed to converge so this was excluded.

2.2.3. Colour rarity

To assess the effect of colour rarity on trade, we fit another hierarchical logistic regression whereby the likelihood of being traded was the response variable and average colour rarity (Q) was the predictor variable. We included taxonomic family as a random effect to account for some phylogenetic non-independence between species. SVL was also included as a predictor variable within the model.

2.2.4. Pet vs product

Before analysing the pet and product data, we created a second dataset that removed any species with an unknown trade type (3 species in our dataset had unknown trade types) and split all traded species into traded as pets or as products. Colour data for species that were traded as both types were represented in both categories.

All the above analyses were repeated and modified using our second dataset. Firstly, we performed a two-sample *t*-test comparing the means of the colour richness of pet and product anuran trade. We then fit hierarchical logistic regression models for colour richness, colours driving pet and product trade, and colour rarity with our second dataset.

3. Results

Traded species richness is greatest in the Amazon rainforest (Fig. 1A). The average number of colours per traded species is greatest in the Pantanal/Cerrado biomes of Brazil followed by parts of the Amazon rainforest (Fig. 1B). The average colour rarity per traded species is not as clearly localised as for colour richness, although there are particularly high values in the south-east Atlantic forests and Caatinga (Fig. 1C). Hotspots for all individual traded colours tend to be in the Amazon rainforest (Fig. S2). Red has the lowest richness, followed by blue then grey, whereas blue has the most limited spatial extent.

3.1. Colour richness

The mean colour richness of traded species is significantly greater than non-traded species (Welch's $t = -3.80$, d.f. = 92.9, $p < 0.001$; Fig. 2A), with mean colour richness's for non-traded and traded species of 2.88 and 3.41, respectively. Increasing colour richness also significantly increases the probability of being traded ($\beta = 0.516$, se = 0.231, $z = 2.231$, $p = 0.026$; Fig. 2B, Table S1). For every additional colour present on a species, the odds of being traded increase by 1.68. When colour richness increases from 1 to 6, the average probability of trade increases 9-fold.

3.2. Colours driving anuran trade

The presence of four colours significantly increases the probability that a species is traded (Fig. 2C; Table S2): blue increases the probability of being traded the most, followed by orange, black, and yellow. The presence of the remaining colours was not associated with an increase or decrease in the probability of trade.

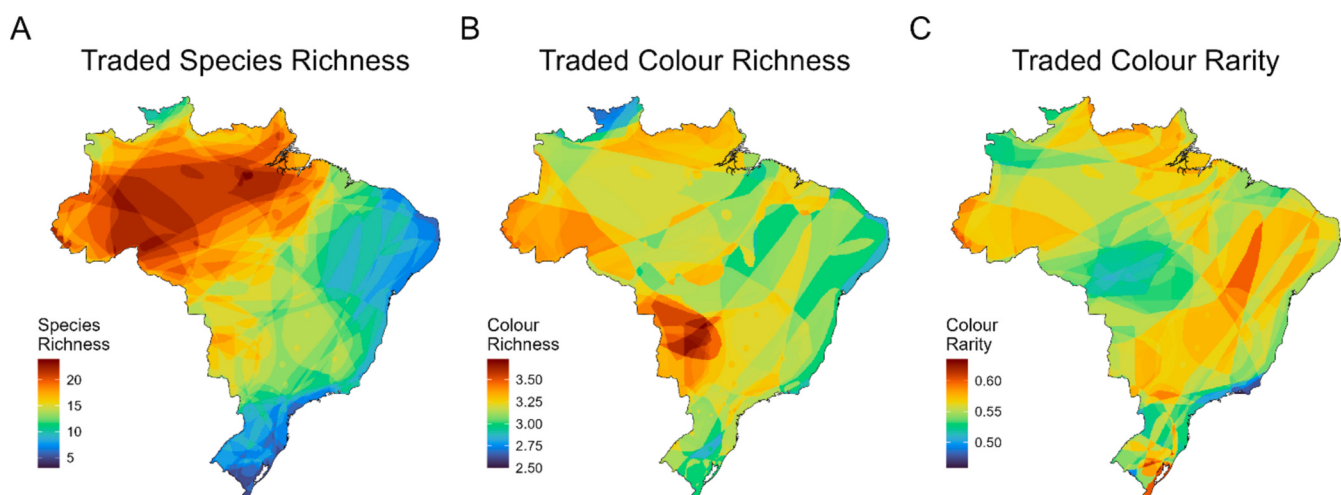


Fig. 1. Spatial distribution of anuran trade in Brazil.

Hotspots for A) traded species richness, B) the average number of colours per traded species, and C) the average colour rarity per traded species. See Fig. S2 for the geography of individual traded colours.

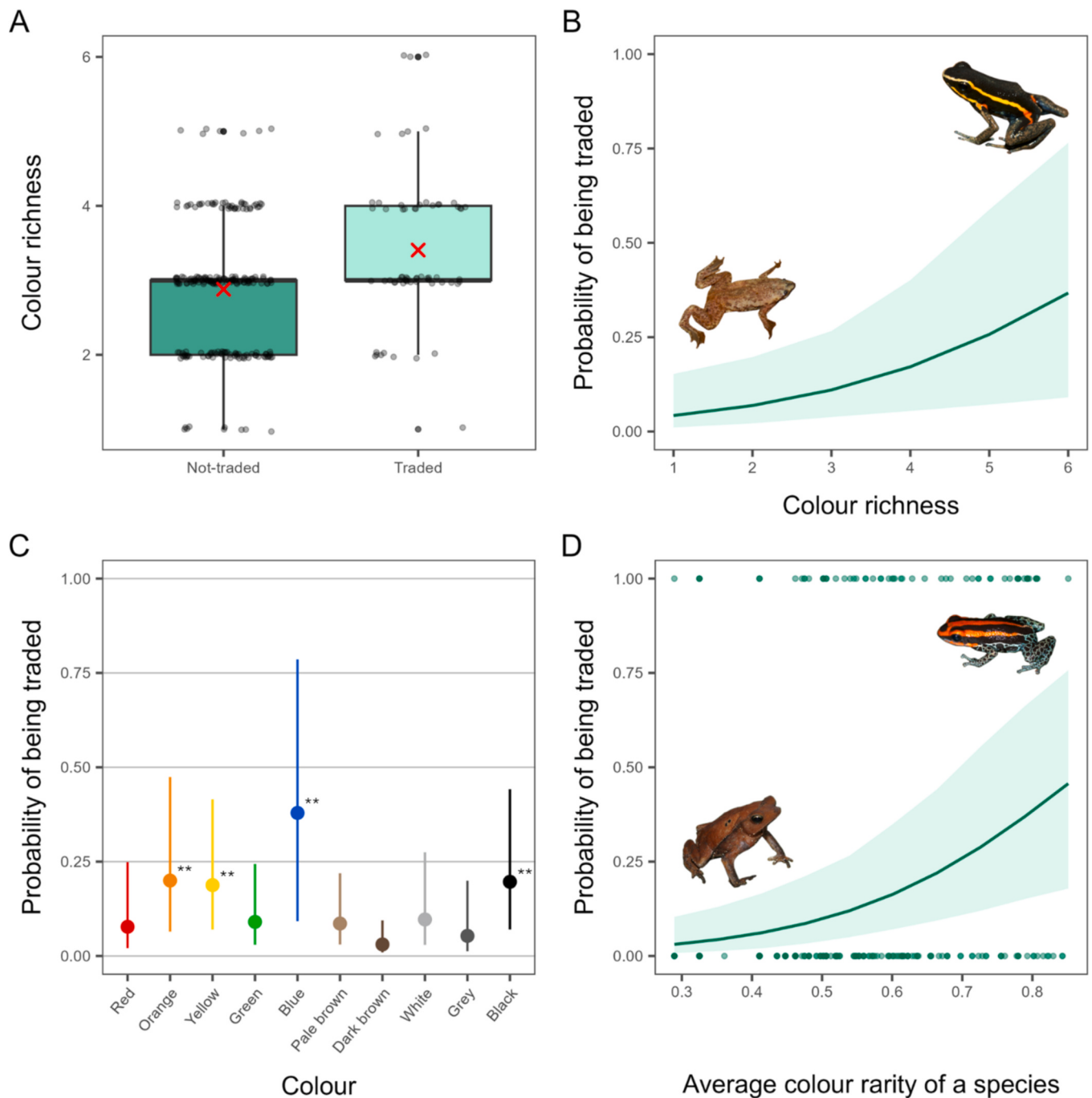


Fig. 2. Colour diversity and rarity correlate with presence in trade.

A) Colour richness in traded species and non-traded species. Boxplots show the first quartile, median and third quartile, while whiskers indicate maximum and minimum values, excluding outliers. Data points show the jittered distribution of the data. Red crosses denote the colour richness means of non-traded and traded species. B) Probability of being traded with increasing colour richness. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are the Arrabal's Suriname Toad (*Pipa arrabali*) (image credit: www.inaturalist.org/observations/136828619) and the Spot-legged Poison Frog (*Ameerega picta*) (image credit: Todd Pierson), two species with respectively the lowest and highest colour richness. C) Individual colours specific probability of being traded. SVL held fixed at the mean value. Bars show 95 % CIs and points the mean. Note: * indicates $p < 0.05$, ** indicates $p < 0.01$. D) Probability of being traded with increasing colour rarity. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are *Rhinella magnussoni* (image credit: Marco Aurelio de Sena) and the Amazonian Poison Frog (*Ranitomeya ventrimaculata*) (image credit: Felix Fleck), two species with respectively the lowest and highest colour rarity scores. See Fig. S3 for plots displaying individual family effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Colour rarity

Increasing average colour rarity is significantly associated with an increasing probability of being traded ($\beta = 5.926$, $se = 1.626$, $z = 3.645$, $p < 0.001$; Fig. 2D, Table S3), with greater average colour rarity

increasing the odds of being traded. Per 0.1 unit increase in average colour rarity, the odds of being traded increase by a factor of 1.81. From our sampled species pool the average probability of trade increases 15-fold from species with the lowest rarity score ($Q = 0.289$, 4 *Pipa* sp., *Chiasmocleis crucis*, *Hypodactylus nigrovittatus*, and *Rhinella magnussoni*)

and species with the highest rarity score ($Q = 0.851$, *Ranitomeya ventrimaculata*).

3.4. Pet vs product

The difference in mean colour richness between species traded as pets versus products is not significant (Welch's $t = 1.37$, d.f. = 25.7, $p = 0.184$; Fig. 3). Increasing colour richness significantly lowers the probability that a species is traded as a product ($\beta = -0.767$, se = 0.355, $z = -2.161$, $p = 0.031$, Fig. 4B, Table S4) but there is no significant association between colour richness and being traded as a pet ($\beta = 0.393$, se = 0.217, $z = 1.816$, $p = 0.069$; Fig. 4A, Table S5).

Being black, blue, orange, or yellow significantly increases the probability of a species being traded as a pet whereas dark brown significantly lowers this probability (Fig. 4C, Table S6). No colour significantly increases the probability of a species being traded as a product and, again, dark brown decreases the probability (Fig. 4D, Table S7).

Greater colour rarity significantly increases the probability of being traded both as a pet ($\beta = 6.559$, se = 1.621, $z = 4.047$, $p < 0.001$; Fig. 4E, Table S8) and as a product ($\beta = 8.486$, se = 3.119, $z = 2.720$, $p = 0.007$, Fig. 4F, Table S9). Per 0.1 unit increase in average colour rarity the odds of being traded as a pet or as a product increase by factors of 1.93 and 2.34, respectively.

4. Discussion

Attractiveness and colouration are commonly perceived drivers of trade, specifically for pets (Hughes et al., 2022), yet to date this has only been quantified and assessed for a limited number of taxa (Romero-Vidal et al., 2020; Senior et al., 2022). Our results add further support from Brazilian anurans, revealing that species with greater colour richness, higher average colour rarity, and more vibrant colours have higher probabilities of being traded even after accounting for taxonomic nestedness and body size. Furthermore, species traded as pets were more

colourful than those traded as products, further highlighting the key role of aesthetics in trade.

Amphibian trade richness and hotspots of amphibian trade are concentrated in the Amazon rainforest (Scheffers et al., 2019). Our results provide spatial context for the Brazilian amphibian trade in relation to colour. Regional differences exist between each metric, demonstrating areas that could hold species vulnerable to exploitation, which species richness maps alone would not display. While traded species richness dominates in the Amazon rainforest, average traded colour richness is greatest in the Pantanal/Cerrado biomes, and average traded colour rarity shows less distinct and localised hotspots across the country. The Amazon includes species with both high and low colour richness lowering the average colour richness in the region, even though the three species with the greatest colour richness (Brilliant-thighed Poison Frog, *Allobates femoralis*; Yurimaguas Poison Frog, *Ameerega hahnelti*; Spot-legged Poison Frog, *Ameerega picta*) all have geographic ranges within the Brazilian Amazon. Understanding the geography of where species are targeted in trade, or likely to be targeted in the future, can more effectively inform conservation management strategies (Scheffers et al., 2019). Future research should consider incorporating environmental factors into the research aims and analysis framework to better interpret the role of colour in trade across different biomes.

4.1. Colour richness is greater in traded species

Our results show that vibrant colours (particularly blue) increase the odds that an anuran species is traded, and that dark brown decreases the probability of trade. These support Su et al. (2015), who identified specific subsets of colours that influence avian trade, with vibrant yellow plumage a strong driver of traded species' value in Taiwan, but duller plumage tones (e.g. grey) reducing trade value. There appears to be no blanket rule on which colours drive wildlife trade with drivers of trade likely specific to each taxon (Scheffers et al., 2019), and further depending on socioeconomic (Toomes et al., 2022), regional (Corlett, 2007), and/or cultural (Gilbert et al., 2012; Tella and Hiraldo, 2014; Su et al., 2015) factors. Likewise, other ecological factors likely influence the commercial use of wildlife, such as body-size (Mohanty and Measey, 2019; Scheffers et al., 2019), abundance (Pires and Clarke, 2012; Scheffers et al., 2012), rarity (Palazy et al., 2012; Sung and Fong, 2018), and distinctive morphologies (Regueira and Bernard, 2012; Hinsley et al., 2015). Some reasons for the use and trade of species can be intrinsically difficult to study. Since access is often associated with exploitation (Morton et al., 2021; Hughes et al., 2022), some species may be too inaccessible for easy collection. Species-specific functional traits could also impact trade drive, for example, indigenous peoples may use the poison secreted by dendrobatids for hunting (de Oliveira Filho and Omori, 2015).

Interestingly, we found that black (a colour we classified as drab) increased the probability of trade, which could be due its co-occurrence with vibrant colours potentially creating an aesthetically pleasing tonal contrast. Future studies investigating how colour contrasts and combinations affect trade likelihood could provide additional valuable insights into the factors driving demand for certain species. Furthermore, social studies investigating human consumer preferences on anuran colour and contrasting patterning could complement the current study.

Our results on how colour influences the pet trade mirrored those of trade overall, with only orange no longer increasing the probability of being traded when only as a pet. In Brazil, two-thirds of the species traded as products are also traded as pets (Scheffers et al., 2019), which likely causes these similarities. Like Senior et al., 2022, our results show that colour plays less of a role for species traded as products. These results highlight that colour may hold greater significance for human attraction rather than as an inherent biological trait (Santangeli et al., 2023). South America has greater amphibian species richness in the pet trade, whereas east Asia is a hotspot for the product trade of amphibians (Scheffers et al., 2019). Meat is a large component of the product trade in

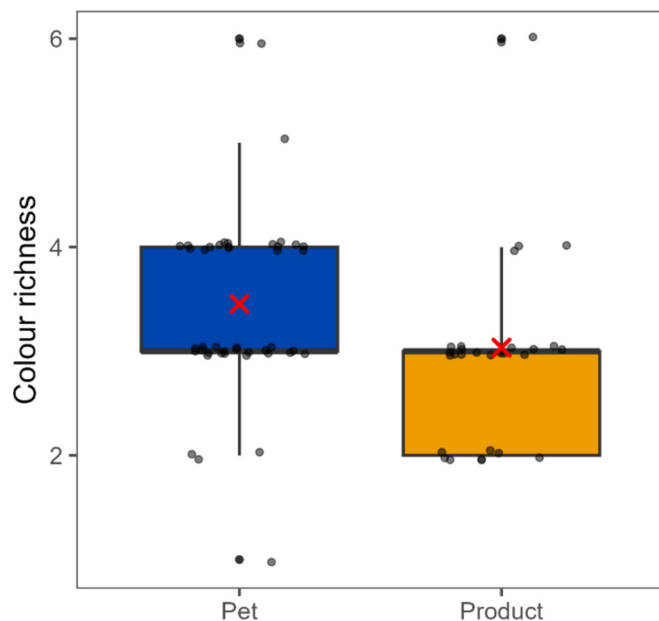
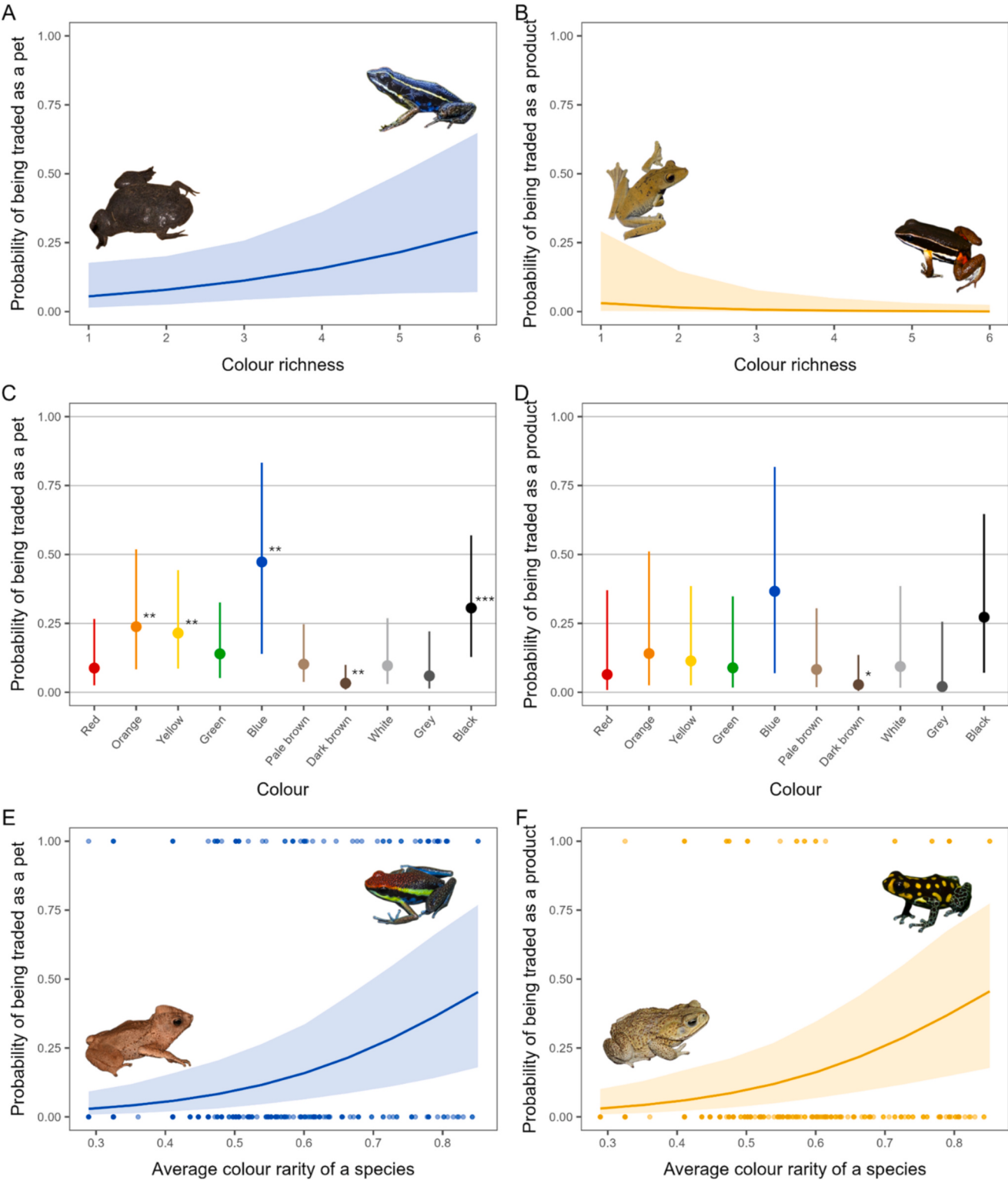


Fig. 3. Colour richness between pets and products.

Colour richness of anurans traded as pets and as products. Boxplots show the first quartile, median and third quartile, while whiskers indicate maximum and minimum values, excluding outliers. Data points show the jittered distribution of the data. The red crosses denote the colour richness means of species traded as pets and as products. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



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Fig. 4. Colour diversity and rarity correlate with presence in the pet and product trade.

A) Probability of being traded as a pet with increasing colour richness. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are the Utinga Surinam Toad (*Pipa snethlageae*) (image credit: Christian Marty) and the Yurimaguas Poison Frog (*Ameerega hahneli*) (image credit: Andrey Quiceno Rojas), two species in the pet trade with respectively low and high colour richness scores B) Probability of being traded as a product with increasing colour richness. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are the Rusty Treefrog (*Boana boans*) (image credit: Luis Enrique Calderón Franco) and the Brilliant-thighed Poison Frog (*Allobates femoralis*) (image credit: Pedro Ivo Simoes), two species in the product trade with respectively low and high colour richness scores C) Individual colours specific probability of being traded as a pet. SVL held fixed at the mean value. Bars show 95 % CIs and points the mean. Note: * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$. D) Individual colours specific probability of being traded as a product. SVL held fixed at the mean value. Bars show 95 % CIs and points the mean. Note: * indicates $p < 0.05$. E) Probability of being traded as a pet with increasing colour rarity. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are the South American Common Toad (*Rhinella margaritifera*) (image credit: Alex Castelein) and the Manu Poison Frog (*Ameerega macero*) (image credit: Tomaz Nascimento de Melo), two species in the pet trade with respectively low and high colour rarity scores F) Probability of being traded as a product with increasing colour rarity. The shaded area indicates a 95 % CI and the solid line the predicted mean. Inset images are the South American Cane Toad (*Rhinella marina*) (image credit: Nathan Vaughan) and the Brazilian Poison Frog (*Ranitomeya vanzolinii*) (image credit: www.inaturalist.org/observations/162385547), two species in the product trade with respectively low and high colour rarity scores. See Fig. S4 for plots displaying individual family effects.

amphibians (Carpenter et al., 2014; Auliya et al., 2023) and therefore we may expect colour to have little effect on the trade for amphibian products.

The preservation of amphibian specimens can cause discolouration over time (McDiarmid, 1994), therefore images of live specimens from verified sources must be obtained to collect data on anuran colouration. Some species are polymorphic (Hoffman and Blouin, 2000) and some exhibit rare morphological features such as in male Moor Frogs (*Rana arvalis*), which develop blue coloration maintained for just a few nights during peak reproductive activity (Hettyey et al., 2009). Relying on images can be problematic especially when considering different colour morphs, the quality and accuracy of the data are inherently limited by the availability of the images obtained.

4.2. Traded species display rarer colours

The trend in colour rarity is similar to the trend in colour richness. This indicates that rarer colours are perceived as more attractive and therefore are more valuable leading to greater demand in trade. These results align with those of Senior et al. (2022) who found that the pet trade targets uniquely coloured passerines. Furthermore, we show that some colours, such as blue, have a limited distribution, with many regions in Brazil lacking anurans displaying these hues, emphasising the general rareness of some colours. More broadly, several studies have shown that species rarity (e.g., VU, EN, and CR IUCN Red List statuses) influences species presence and desirability in trade (e.g., Sung and Fong, 2018; Krishna et al., 2019; Scheffers et al., 2019), risking positive feedback between rarity and price potentially leading to an anthropogenic allée effect (Hughes et al., 2022). Colour rarity could thus be interpreted as a further facet of rarity and be used to identify species likely to be at more intense risk of collection.

4.3. Ecological context

Colour can have important ecological function within a species, for example, in mate choice (Gomez et al., 2010). A single species of anuran can exhibit numerous colour morphs, for instance, the Splash-backed Poison Frog (*Adelphobates galactonotus*), a dendrobatid native to Brazil, can display black, blue, red, orange, yellow, cream, or white dorsal colouration (Hoogmoed and Avila-Pires, 2012). By targeting certain colours in trade, we risk exploiting key correlated ecological functions such as mate choice. Likewise, some anurans perform key ecological roles with many being important prey and predators for many species (Cortéz-Gómez et al., 2015). Anurans have a generalist diet that is largely composed of insects (Santos et al., 2004), therefore can serve a key ecological role within their environment in controlling insect populations (Spielman and Sullivan, 1974). Despite most anurans being carnivorous, da Silva et al. (1989) obtained the fruits and seeds of four different plants from the stomachs of the Izecksohn's Brazilian Tree Frog (*Xenohyla truncata*), a yellow anuran endemic to Brazil, suggesting

X. truncata is a potential seed disperser. Moreover, tadpoles of the yellow and black Cerro Campana Stubfoot Toad (*Atelopus zeteki*) shape the abundance and diversity of resources and primary consumers in tropical streams, influencing food web dynamics and energy flow (Ranvestel et al., 2004).

Species within Dendrobatidae (poison frogs) often display vibrant colours (Stynoski et al., 2015) highlighting their aposematism. Approximately 86 % of species displaying blue hues and half of the anurans with the highest colour richness in our dataset (5 or 6 colours) were part of this family. Dendrobatids lay terrestrial eggs and provide various forms of key parental care to their offspring (Grant et al., 2006) such as nest defence, clutch hydration, and tadpole transportation (da Rocha et al., 2021). In some species, parents provide their young with nutritive oocytes providing food but also supplying tadpoles with alkaloids to protect them from predators (Grant et al., 2006; Stynoski et al., 2015). Species in other families, such as the Brilliant-thighed Poison Frog (*Allobates femoralis*, part of Aromobatidae), one of the species with the highest colour richness in our dataset, also rely on similar parental care (Ursprung et al., 2011). Exploiting specific colour hues in wildlife trade may have major repercussions on entire families that display such unique ecological and reproductive behaviours that they rely on to facilitate the survival of their offspring.

By exploiting colouration, we may risk losing morphological and functional diversity. We propose that more extensive data collection is needed to achieve a higher resolution of colour data for all amphibians, rather than a subset of anurans. This is critical to safeguarding the key ecological roles and functions that these organisms and colours fulfil.

4.4. Implications and conclusions

Illegal wildlife trade continues to be a major issue both globally and in Brazil, which alone accounts for 10–15 % of the world's illegal animal trade (Pistoni and Toledo, 2010). International and domestic legislation exist (Auliya et al., 2016) to support the regulation of wildlife trade. This includes 44 protected Brazilian anuran species covered by CITES (<https://checklist.cites.org>; all are listed under appendix II). For species not protected by CITES, the demand and threats posed by trade vary. Some species, like Miranda's White-lipped Frog (*Leptodactylus macrosternum*), are abundant and widely distributed, and thus are not considered threatened by current harvesting levels. In contrast, species such as *Ranitomeya flavovittata*, which display vibrant and contrasting colour hues, have reports of illegal collection for the pet trade (IUCN, 2023). Further analysis to test if colour correlates with being CITES listed was constrained by the limited size of the database for listed Brazilian anuran species. The current study focuses on Brazilian anurans; however, there is recognition that colour influences wildlife trade globally (Su et al., 2015; Senior et al., 2022). Therefore, additional research with extensive colour data on traded anurans worldwide is necessary to better understand this correlation. The current study provides evidence to enforce and improve legislation so that nature's most

colourful amphibians can be protected, and their survival is not put at risk by commercial trade. Policy makers should use this knowledge to help conserve nature's aesthetic value.

In conclusion, wildlife trade is a major factor threatening amphibian species with extinction, making adequately identifying drivers of amphibian trade essential for the conservation of vulnerable species. Our study identifies how colouration and colour rarity correlates strongly with amphibian trade, highlighting that species with multiple colours, rare colours, and specific vibrant colours are more likely to be targeted. This underscores the need for better data on aesthetic traits for heavily traded taxa to guide policymakers in conserving both the aesthetic value and ecological functions of nature. Without understanding the nuanced drivers of use and demand creating effective legislation will remain out of reach, and the colour diversity of anurans in Brazil and beyond risks being forever diminished.

CRediT authorship contribution statement

Joseph L. Werling: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Oscar Morton:** Writing – review & editing, Validation, Supervision, Formal analysis. **David P. Edwards:** Writing – review & editing, Supervision, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110923>.

Data availability

All data will be freely available from a public repository upon publication.

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