Biogeography of polymorphic phenotypes: Mapping and ecological modelling of coat colour variants in an elusive Neotropical cat, the jaguarundi (*Puma yagouaroundi*)

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Abstract

The jaguarundi *Puma yagouaroundi* is a small Neotropical cat that presents two main coloration phenotypes (grey/dark vs. reddish). Although these coat colour variants have been known for decades, and historically speculated to be associated with different habitats, their exact geographical distribution has never been mapped. Moreover, their association to different habitats has so far not been tested statistically, so that their ecological relevance with respect to varying environmental features remains unknown. Based on 566 location records encompassing the entire historical range of the species obtained from camera-traps, captures and skins held in scientific collections, we produced suitability models for both jaguarundi phenotypes using maximum entropy algorithms of niche modelling. The frequency of grey/dark jaguarundis is *c.* 80%, whereas reddish animals represent *c.* 20% of our overall sample set. However, there were marked differences in these frequencies across regions. Although the spatial distribution of grey/dark animals did not depart substantially from random expectations (as it encompassed the whole species range), the occurrence of the ancestral reddish form was strongly and significantly non-random. In spite of their broad distribution across multiple habitats, grey/dark animals were significantly associated with moist and dense forests, whereas reddish forms were associated with dry and open areas such as deserts and xeric landscapes. Furthermore, there were clear spatial differences in the suitability models generated for these coat colour phenotypes. We also employed the distribution models to investigate whether particular environmental predictors could explain these different distributions. Predictors related to moisture were especially influential on the differences between the grey/dark and reddish models, and demonstrate an effect of natural selection on coloration traits, suggesting that a complex interplay of different ecological processes regulates this system over evolutionary time.

Introduction

Polymorphic phenotypes observed in natural populations are often hypothesized to present behavioural or ecological relevance (e.g. Lande, 1976; West-Eberhard, 1989; Majerus, 1998). In vertebrates, coloration phenotypes are often polymorphic, and may represent adaptations to varying ecological conditions (e.g. Caro, 2005). A common example of pigmentation polymorphism is melanism (darkening in relation to

what would be considered the 'normal' or 'wild' phenotype), which has been classically associated with biological factors such as thermoregulation, aposematism, camouflage, susceptibility to disease and parasites, as well as sexual selection (Majerus, 1998; Majerus & Mundi, 2003). Putative associations between darkened colour and some types of environment have been mentioned in early studies of animal coloration, and used to propose the classical hypothesis that melanistic animals are favoured in wetter areas covered by

dense vegetation (e.g. tropical forests) (Gloger, 1833; Poulton, 1890; Beddard, 1895; Cott, 1940; Ulmer, 1941). However, up to now this hypothesis has been rarely tested statistically or rigorously investigated using spatially explicit approaches.

The occurrence of melanism is common in the Felidae (Mammalia, Carnivora), having been so far documented in 13 of the 38 species (Schneider *et al.*, 2012, 2015). The biological significance and even the geographical distribution of felid melanistic variants are still poorly understood, but recent analyses indicate that melanism in some cases can reach very high frequencies in regional populations (e.g. Kawanishi *et al.*, 2010; Hedges *et al.*, 2015). Such observations support the hypothesis that melanism can provide an adaptive advantage in certain ecological conditions (Eizirik & O'Brien, 2003; Eizirik *et al.*, 2003; Caro, 2005; Allen *et al.*, 2011).

The jaguarundi *Puma yagouaroundi* is a small Neotropical cat whose ecology is still poorly known (Grassman & Tewes, 2004; Maffei, Noss & Fiorello, 2007). Its range extends from the southern United States to Argentina (Sunquist & Sunquist, 2002; Almeida *et al.*, 2013; Caso *et al.*, 2015) and includes a wide variety of habitats, from semiarid and grassland areas to dense dry and wet forests (Oliveira, 1998; Sunquist & Sunquist, 2002). The species is listed as 'least concern' by the IUCN (Caso *et al.*, 2015) and vulnerable in regional lists (Almeida *et al.*, 2013). Habitat loss, fragmentation and human persecution are the most important threats to the species (Almeida *et al.*, 2013; Caso *et al.*, 2015).

The species is a unique felid in several respects. It has an elongated body and is the only felid whose pelage is almost completely unmarked (i.e. devoid of stripes or spots) throughout its life (Sunquist & Sunquist, 2002). In addition, there is a remarkable coloration polymorphism in this species, with two main forms (grey/dark and reddish) that can be easily recognized. The ancestral phenotype is the reddish form, and a semi-dominant mutation in the *MC1R* (*Melanocortin 1-Receptor*) gene induces the grey/dark phenotype, which can thus be considered a melanistic form (Eizirik *et al.*, 2003). Although these two main forms have been known for many years and anecdotally speculated to be associated with different habitats (e.g. Sunquist & Sunquist, 2002; Grassman & Tewes, 2004; Grigione *et al.*, 2007; Maffei *et al.*, 2007), their exact geographical distributions have never been mapped.

The goal of the present work was to conduct a survey of the distribution of the jaguarundi coloration phenotypes, and to test their association with different types of environments. We constructed range-wide spatial distribution models for both forms and tested two alternative hypotheses: (1) melanism occurs randomly across all environments (absence of association between melanism and different habitats); and (2) melanism presents a non-random distribution, and a significant association with particular biomes. Our results strongly supported the latter hypothesis, and opened up new avenues to investigate the evolutionary ecology of this intriguing coloration polymorphism.

Materials and methods

Data base construction

The database included location records from the entire range of the jaguarundi, from the southern United States to Argentina, in various different biomes and ecoregions. These occurrence points were obtained from five different sources: (1) specimens kept in scientific collections that presented geographical coordinates and photographic documentation of their coat colour; (2) captured individuals or those found dead (e.g. road-killed) during fieldwork; (3) camera trap records; (4) field observations made by the authors or by other experienced researchers; and (5) published bibliographical sources (Table S1).

We observed that some individuals had colour variants that could not easily be categorized into reddish or grey/dark (i.e. intermediate colours or heterogeneous patterns across different body regions), either due to the putative effect of additional genetic loci (i.e. modifier genes), or to differences in the lighting conditions (Fig. 1). These ambiguous animals were excluded from the dataset, and we therefore performed our analyses on a curated set of individuals whose colours could be confirmed and reliably classified into reddish or grey/dark (see Figs 1 and S1).

Mapping of jaguarundi phenotypes

We mapped the occurrence of different phenotypes throughout the species' distribution by inserting location records (Figs 1 and S2) into an ArcGis 9.3 database (ESRI, 2010). We used a shapefile of terrestrial biomes (Olson *et al.*, 2001; Hoekstra *et al.*, 2010) as a mask layer to extract and analyse information on the natural landscapes in which these phenotypes occur. Such mapping exercise allowed an initial assessment of potential relationships between jaguarundi coloration phenotypes and landscape conformations across the species' range.

Since our sampling of records was opportunistic and unbiased with respect to coloration phenotypes (i.e. different phenotypes had the same capture probability), we assumed that the observed proportion of each colour in the overall dataset corresponded to its species-wide frequency. Such overall frequencies were then used to generate expected values for use in chi-square tests of association performed for each biome.

We then tested whether the spatial distribution of the distinct phenotypes was random throughout the geographical range of the jaguarundi, using a complete spatial randomness (CSR) analysis. This was performed using our full record database and the nearest-neighbour method of multivariate kernel estimation (Fortin & Dale, 2005), employing the 'raster' and 'spatstat' packages in R software (Fischer & Wang, 2011). To conduct this test, we initially delimited the spatial scope of analysis by assigning a buffer around each of our sampled points (~200 km), and then merging all the included buffers into a single polygon to cover the effectively sampled area (Fig. S3). To test the null hypothesis that our location records were randomly distributed, we performed 500 simulations of random points within this global polygon, and compared their
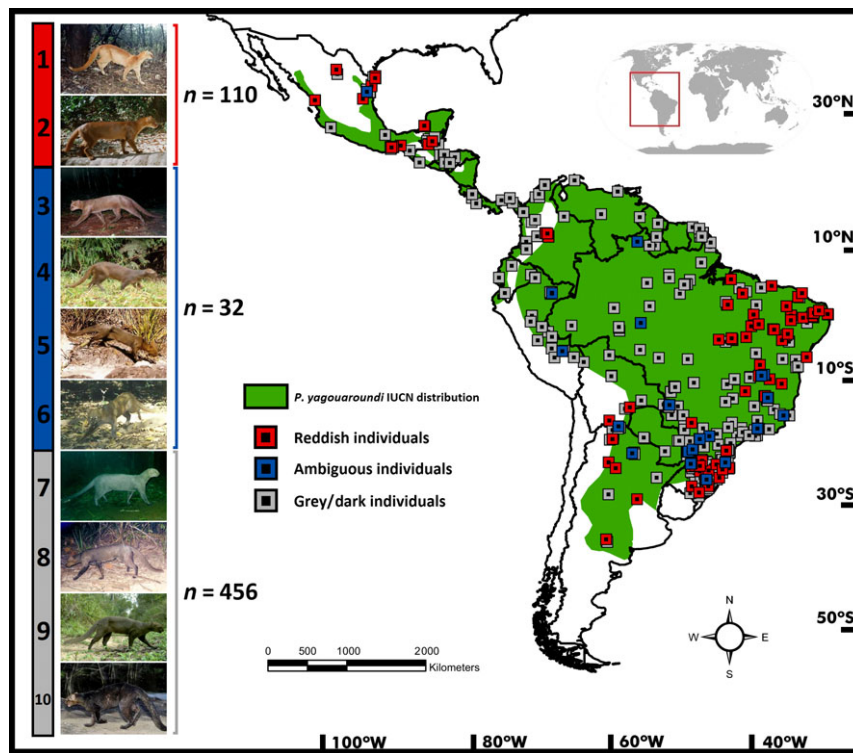
Figure 1 Coat colours of *Puma yagouaroundi* and location records used in this study, overlaid onto the IUCN distribution polygon.

distribution with the patterns observed for the grey/dark and reddish phenotypes.

Selection of environmental variables for modelling

To generate probabilistic distribution models, we initially considered 37 explanatory environmental variables and landscape data. We used 35 bioclimatic variables obtained from the Worldclim (http://www.worldclim.org) or Climond (http://www.climond.org) databases (Table S2). Altitudes were obtained from the SRTM database (http://www2.jpl.nasa.gov/srtm) and landcover information was obtained from the ESA GlobCover Project 2009 (http://due.esrin.esa.int/globcover). All variables were analysed using a ~1 km spatial resolution. After initial exploratory analyses, landcover information was removed from our modelling effort due to potential biases that might be introduced by the difference between the timeframe of its collection (recent) and that of the location records (especially museum specimens).

To avoid model overfitting induced by correlation among explanatory variables, we performed Pearson's correlation coefficient test (*r*) for each pair of quantitative variables (Kumar & Stohlgran, 2009; Raes *et al.*, 2009; Mukherjee *et al.*, 2010). The correlation was assessed by extracting variable information from 10 000 unique and randomly generated points inserted in the known present geographical distribution layer of jaguarundis (obtained from IUCN and complemented by our records)

using ArcGis 9.3. We selected 12 predictors that were not strongly correlated with the remaining variables, using $r = 0.7$ as the cut-off value, and employed them as ecological predictors for niche modelling. The selected variables were: annual mean temperature, temperature seasonality, temperature annual range, annual precipitation, precipitation of driest week, precipitation of wettest quarter, precipitation of driest quarter, annual mean radiation, annual mean moisture index, highest weekly moisture index, lowest weekly moisture index and altitude (see Table S2).

Spatial models

We modelled the spatial distribution of the distinct phenotypes of jaguarundis using the maximum entropy algorithm implemented in the software package Maxent 3.3.3k (Philips, Anderson & Schapired, 2006), a robust statistical method for predicting species distributions (Waltari *et al.*, 2007; Philips & Dudik, 2008; Elith *et al.*, 2010; Merow, Smith & Silander, 2013; Radosavljevic & Anderson, 2014). We ran and assessed two different models: (1) subset of records comprising only grey/dark animals; and (2) subset comprising only reddish animals. We defined the parameters and validated the models using standard procedures for Maxent analyses. For each of the sample sets, we used 70% of the included points for training and 30% for testing the models in each run independently, considering the mean values for the final map. The data were sampled using the bootstrap routine (Pearson, 2007). All runs

were configured to incorporate a random seed, a convergence threshold of 1E-5 with 500 iterations and 10 000 hidden background points (Ferraz *et al.*, 2012). Model performance was assessed by the area under curve (AUC) value for the receiver operating characteristic (ROC) curve based on sensitivity (omission rate) versus specificity (fractional predicted area) of the response between occurrence data and predictors, incorporating a binomial probability as a null model (Pearson, 2007; Tôrres *et al.*, 2012; Calabrese *et al.*, 2014). The Maxent modelling results were converted into ASCII format files and processed with ArcGis 9.3, yielding distribution maps for the two different phenotypes.

To assess potential differences in habitat association between the grey/dark and reddish individuals, we directly compared suitability values between the models generated for the two phenotypes. This was performed by extracting absolute values of habitat suitability for each of our location records (regardless of the coat colour of its individual) in each of the two models (i.e. each point yielded two values). The mean suitability values of the two models across all sampled points were then compared statistically using a t-test.

Finally, to investigate which environmental predictors most influenced the differential distribution of the two phenotypes, we analysed the relative importance (in the Maxent models), as well as the mean absolute values, of each of the 12 selected predictors. The relative importance was used to assess if any predictor behaved differently between the two models, and whether any consistent pattern could be discerned. Since this assessment did not allow an inference of directionality in the case of differences between the two models, the mean absolute values of the predictors were analysed. This was computed as the value of each predictor averaged across all sampled points for each phenotype.

Results

We obtained records of 566 individuals with confirmed coat colour (110 reddish, 456 grey/dark), and removed 32 location records of animals with ambiguous coloration (Fig. 1). Our database updates the current IUCN distribution map of the species, filling some geographical gaps where jaguarundis had not been recorded previously (Fig. S2). Considering all samples in our database, 80.6% of the animals were grey/dark and 19.4% were reddish (Table 1).

Grey/dark jaguarundis occurred in all biomes in which the species was recorded, whereas reddish individuals were totally or mostly absent from flooded grasslands and savannas respectively (Fig. 2; Table 1). In addition, the observed frequency of these phenotypes was quite different among biomes. Considering the proportion of distinct coat colour patterns in our global database as an overall standard for the entire species, and applying a chi-square test, we found no significant departures from the overall mean in tropical and temperate grasslands and savannas (71.4% grey/dark, 28.6% reddish; $P > 0.05$), nor in dry forests (77.3% grey/dark, 22.7% reddish; $P > 0.05$). However, in moist forests we found a significantly higher frequency of grey/dark jaguarundis (89.6% grey/dark, 10.4% reddish; $P < 0.05$), whereas in desert and xeric areas there was a

significantly higher proportion of the reddish form (31% grey/dark, 69% reddish; $P < 0.05$) (see Table 1).

The observation that reddish forms were not evenly distributed across the jaguarundi range was supported by the CSR analysis. The results obtained for the two sample sets (grey/dark and reddish) were quite different (Fig. S4). The grey/dark records presented a spatial distribution that did not depart substantially from randomness within our sampled polygon (although the departure was significant; $P = 0.013$). In contrast, the reddish records strongly deviated from the expected random pattern ($P = 0.003$).

Maxent models were considered satisfactory (mean AUC ≥ 0.9): grey/dark model: mean AUC = 0.972, (Fig. S5A); reddish model: mean AUC = 0.970 (Fig. S5B). The models provided a suitable and broad prediction of the distribution of jaguarundi phenotypes for the entire species' range. These niche models corroborated the inference that the geographical distribution of these different jaguarundi phenotypes is non-random (Fig. 3). There were marked differences between estimated models for grey/dark and reddish animals. Reddish animals showed low suitability (<0.5) in most of the Amazon basin, in the Pantanal and portions of the Cerrado, and an increased suitability in the Caatinga ecoregion in northeastern Brazil. These models also allowed us to compare statistically the habitat suitability between the two coloration phenotypes across the jaguarundi range, revealing a significant ($P < 0.01$) difference between them (Fig. S6).

When we assessed the relative importance of all the environmental predictors used to generate the different distribution models, we noticed some differences that may be relevant to explain the observed patterns (Fig. S7). The most influential predictors were 'temperature seasonality' for grey/dark and 'annual mean moisture index' for reddish animals. Interestingly, when we inspected the absolute values of each predictor in the two models, we observed consistent differences between the phenotypes (higher values in the dark/grey model) in eight of 12 predictors, seven of which were related to precipitation and moisture (see Fig. S7).

Discussion

The results from this study affirmed an extended the usual perception that the grey/dark coloration of jaguarundis is more common than the reddish form (Eizirik *et al.*, 2003). Furthermore, our analyses allowed an in-depth assessment of this pattern, and a quantitative spatial comparison of the distributions of these two forms. The grey/dark form [which is evolutionarily derived (Eizirik *et al.*, 2003)] was documented throughout the species' distribution (see Fig. 2), whereas the reddish phenotype (which is ancestral) was restricted to only four geographical regions (southern Brazil to Patagonia; northeastern Brazil; Colombia; and Yucatan peninsula to southern United States). This spatial distinctiveness between the two phenotypes was corroborated by the disparate results of the CSR test, which demonstrated a much stronger departure from randomness in the reddish form than in the grey/dark one (see Fig. S4).

Reddish jaguarundis were clearly more common in open habitats, whereas the frequency of grey/dark animals was higher

Table 1 Association test of biomes with groups of *Puma yagouaroundi* samples ('reddish' and 'grey/dark')

Biomes	Statistics	Phenotypes		Total
		Grey/Dark	Reddish	
Desert and xeric shrublands	Count	18	40	58
	Expected	46.7	11.3	58.0
	% within landscape	31.0%	69.0%	100.0%
	% within groups	3.9%	36.4%	10.2%
	% of total	3.2%	7.1%	10.2%
	Adjusted residual	−10.1	10.1	
Flooded grasslands and savannas	Count	14	0	14
	Expected	11.3	2.7	14.0
	% within landscape	100.0%	0%	100.0%
	% within groups	3.1%	0%	2.5%
	% of total	2.5%	0%	2.5%
	Adjusted residual	1.9	−1.9	
Temperate grasslands, savannas and shrublands	Count	5	2	7
	Expected	5.6	1.4	7.0
	% within landscape	71.4%	28.6%	100.0%
	% within groups	1.1%	1.8%	1.2%
	% of total	0.9%	0.4%	1.2%
	Adjusted residual	−0.6	0.6	
Tropical and subtropical dry broadleaf forest	Count	34	10	44
	Expected	35.4	8.6	44.0
	% within landscape	77.3%	22.7%	100.0%
	% within groups	7.5%	9.1%	7.8%
	% of total	6.0%	1.8%	7.8%
	Adjusted residual	−0.6	0.6	
Tropical and subtropical grasslands, savannas and shrublands	Count	83	23	106
	Expected	85.4	20.6	106.0
	% within landscape	78.3%	21.7%	100.0%
	% within groups	18.2%	20.9%	18.7%
	% of total	14.7%	4.1%	18.7%
	Adjusted residual	−0.7	0.7	
Tropical and subtropical moist broadleaf forest	Count	302	35	337
	Expected	271.5	65.5	337.0
	% within landscape	89.6%	10.4%	100.0%
	% within groups	66.2%	31.8%	59.5%
	% of total	53.4%	6.2%	59.5%
	Adjusted residual	6.6	−6.6	
Total	Count	456	110	566
	% of total	80.6%	19.4%	100.0%

Adjusted residuals <−2 or >2 indicate significant departure from the null hypothesis of no association, for alpha = 0.05.
Chi-square = 112 903; Likelihood ratio = 94 429; Linear-by-linear association = 91 737, with 566 valid cases.

in moist and dry forests (see Table 1). Ongoing field studies provide additional evidence supporting this pattern. For example a long-term study monitoring felids of the semi-arid scrub of the Brazilian Caatinga has found the reddish morph to be highly prevalent, representing 92% of records at a site in Paraíba state (T.G. Oliveira, unpubl. data). This pattern is reminiscent of the hypotheses put forth in the last two centuries by Gloger (1833); Poulton (1890); Cott (1940), suggesting that coloration variants may represent adaptations to particular environmental settings. Specifically, part of the trend that we observed here (higher frequency of darker animals in moist forests) fits Gloger's rule (Gloger, 1833), indicating some selective advantage of darker pelage in these areas. Interestingly, we have also observed significant differences in the

regional frequency of melanism in two other felid species, the leopard *Panthera pardus* and jaguar *P. onca*, with the leopard fitting the pattern expected under Gloger's rule (Silva, 2014). These comparative observations suggest that Gloger's rule may apply more generally in felids or even across mammals, highlighting the need for additional research addressing its mechanistic causes.

For a character to be recognized as adaptive, it must be derived (although the ancestral state may also present advantages in some cases) and involved in the response to a selective agent (Futuyma, 2009). It is therefore interesting to test whether a single-locus polymorphism displays an evolutionary dynamics that is contrary to neutral expectations (Kreitman, 2000). A random geographical distribution across connected
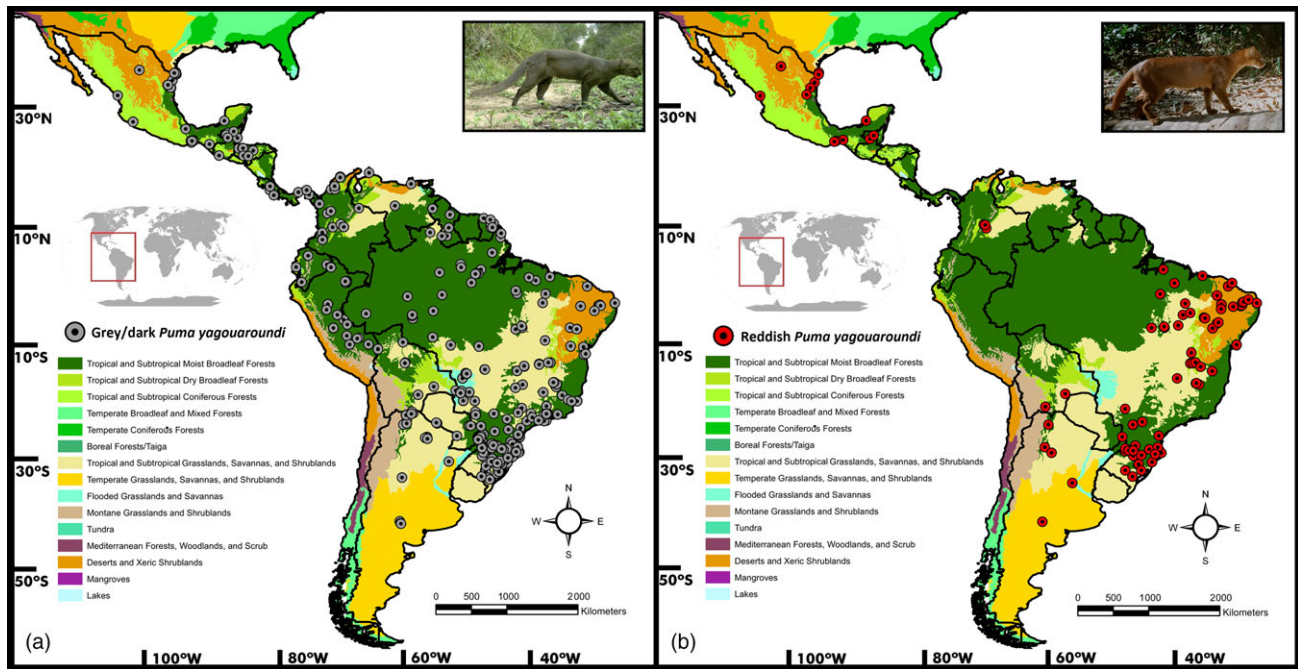
Figure 2 Maps depicting the location of jaguarundi records used in this study, overlaid onto the distribution of Neotropical biomes. (a) Grey/dark individuals; (b) reddish individuals.
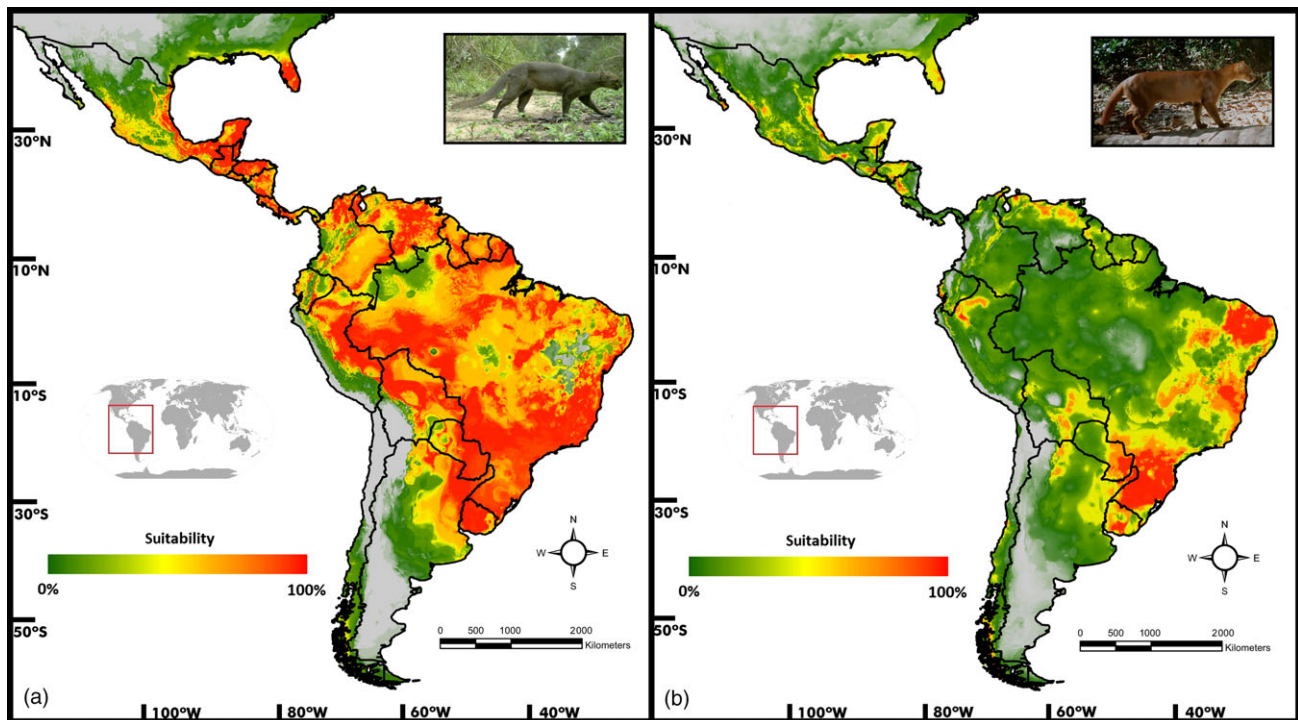

Figure 3 Suitability distribution map for *Puma yagouaroundi*: (a) Distribution of grey/dark animals (*n* = 456) and (b) distribution of reddish animals (*n* = 110).

natural populations would be expected for a neutral phenotype, whereas non-random patterns may indicate the occurrence of natural selection affecting the trait. To assess the adaptive relevance of a polymorphism such as melanism, it is therefore necessary to consider the phenotype frequency among different landscapes that are connected by historical gene flow.

The jaguarundi is an interesting system with which to test these predictions, since phylogeographic analyses have been performed with this species using mitochondrial DNA and microsatellite markers (Pires, 2012; Ruiz-Garcia & Pinedo-Castro, 2013). These studies indicated that there is no genetic structure in jaguarundi populations that might explain the spatial pattern of coat colour distribution described here. Although there were limitations in their sampling, these previous studies identified a single genetic unit south of the Amazon River, with a seemingly continuous distribution that includes northeastern Brazil and southern Brazil/Patagonia (which are areas where the reddish forms appear to be abundant). In addition, those studies supported the inference that there was historical gene flow in the recent past between the major groups located south and north of the Amazon River. These results argue against the hypothesis that population structure could have led to the observed patterns of phenotypic distribution. We therefore conclude that these patterns are caused by spatially heterogeneous natural selection. The most probable scenario is a single emergence of the dark/grey allele and its subsequent expansion throughout the jaguarundi distribution, driven by natural selection, whereas the ancestral allele coding for the reddish phenotypes maintained an adaptive advantage in some environments.

The models generated in our study (see Fig. 3) were found to be robust, with high AUC values and realistic occurrence probabilities compared with our initial dataset and the presently known distribution of the species. The two models were designed to allow an assessment of the relative influence of the included environmental predictors on the geographical distribution of distinct phenotypes. The main differences between them were related to precipitation and moisture (see Fig. S7). These predictors may have direct effects on coat-colour-related fitness [e.g. moisture affecting susceptibility to parasites (e.g. Burtt & Ichida, 2004)]. Alternatively, these variables may exert their influence indirectly by affecting landscape features (e.g. forest cover) that are themselves the selective agents on jaguarundis (e.g. related to camouflage efficacy).

Interestingly, jaguarundi coloration seems to represent a case in which balancing selection is taking place, as the two main forms are alternatively favoured in different regions, and ongoing gene flow maintains connectivity between these populations. We can thus hypothesize that there is a constant tension between divergent natural selection and unifying gene flow in this species, making it an attractive system for in-depth evolutionary analyses. Future studies on this species should therefore target both the investigation of the ecological mechanisms underlying selection (e.g. testing the relative roles of processes such thermoregulation, camouflage and parasite interactions) and the evolutionary genetic dynamics of this colour polymorphism through space and time.

The fact that this striking polymorphism has so far received little attention from scientists is noteworthy, and illustrates the fact that this species remains poorly known in multiple respects. It is often assumed to be a fairly common wild cat, likely due to frequent sightings because of its diurnal habits and the view that it can be tolerant to semi-altered and fragmented areas (Almeida *et al.*, 2013; Caso *et al.*, 2015). However, it has not been found to be particularly abundant anywhere, usually ranking third in order of abundance across all habitat types in Brazil (Oliveira *et al.*, 2010). We hope that this study will contribute to open up new avenues for the investigation of the evolutionary ecology of this elusive and unusual felid, and also to stimulate similar research focusing on other polymorphic phenotypes, aiming to better understand their adaptive relevance in different environments.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1: Example of the classification of jaguarundi (*Puma yagouaroundi*) museum specimens into two main coloration phenotypes ('dark/grey' vs. 'reddish').

Figure S2: New distributional map for *Puma yagouaroundi*. Location records comprising our full data base are indicated, and overlaid on the present IUCN range map along with additional areas of occurrence documented in this study.

Figure S3: Basemap for the Complete Spatial Randomness (CSR) test.

Figure S4: Results of the CSR test comparing random and observed distributions of location records in our database for each of the two main jaguarundi phenotypes: (A) dark/grey individuals ($P=0.013$) and (B) reddish individuals ($P=0.003$).

Figure S5: Graphs depicting receiver operating characteristic (ROC) curves that display average sensitivity vs. specificity in our two Maxent models: (a) grey/dark jaguarundis and (b) reddish jaguarundis.

Figure S6: Graphs depicting the results of the suitability test comparing the dark/grey and reddish models across all the location records in our database ($P < 0.01$).

Figure S7: Detailed assessment of the 12 bioclimatic predictors selected for inclusion in the Maxent modelling of the two coloration phenotypes, after removing the variables showing the most correlation relative to all others (see Methods and Table S2).

Table S1: Location records for *Puma yagouaroundi*.

Table S2: Environmental predictors used in the initial analysis and selected by Pearson's test (in red).