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Ecology and Evolution of Melanism in Big Cats: Case Study with Black Leopards and Jaguars

Lucas Gonçalves da Silva

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Abstract

Variations in animal coloration have intrigued evolutionary biologists for a long time. Among the observed pigmentation polymorphisms, melanism has been reported in multiple organisms (influencing several biological factors), and classical hypothesis has suggested that such variant can present adaptive advantages under certain ecological conditions. In leopards (*Panthera pardus*) and jaguars (*Panthera onca*), melanism is caused by recessive and dominant mutations in the *ASIP* and *MC1R* genes, respectively. This chapter is focused on melanism in these two species, aiming to analyze its geographic pattern. About 623 leopard and 980 jaguar records that were used as baseline for modeling and statistical analyses were obtained. The frequency of melanism was 10% for both species. In leopards, melanism was present in five subspecies and strongly associated with moist forests, especially in Southeast Asia. In jaguars, melanism was totally absent from open and periodically flooded landscapes; in contrast, forests displayed a frequency that was similar to the expectations. The analyses of the environmental predictors suggest a relevant role for factors such as moisture and temperature. These observations support the hypothesis that melanism in big cats is not a neutral polymorphism (influenced by natural selection), leading to a nonrandom geographic distribution of this coloration phenotype.

Keywords: natural selection, geographic distribution, black panther, phenotypes, biomes

1. Introduction

The adaptive relevance of animal coloration has been explored and discussed for over a century (e.g., [1–4]). Pigmentation phenotypes have often been inferred to present adaptive roles in ecological, physiological, and/or behavioral processes such as camouflage, intra- and interspecific communication, and thermoregulation [3–6]. The broad phenotypic

variation of vertebrates observed in nature is one of the questions that have long intrigued evolutionary biologists, including its adaptive significance and genetic basis. Despite the interest in the subject, relatively few studies have addressed the association between phenotypes in natural populations and the environments in which organisms occur, aiming to investigate evolutionary processes involved in the generation and maintenance of coloration diversity and the environmental characteristics that influence the adaptive significance of phenotypes [7–9].

Melanism is a color polymorphism that is common in various groups of organisms, in which the skin/fur/plumage is darker than what would be considered the normal or "wild" phenotype. There are classical hypotheses that postulate an adaptive role of melanism in different species, involving many potential impacts on survival or reproduction [4–6, 10]. Several biological factors such as thermoregulation, susceptibility, or response to disease, camouflage, aposematism, sexual selection, and reproductive success could be directly influenced by melanism [5].

The occurrence of melanism is rather common in Felidae, having been documented in 13 of the 38 felid species, evolved independently at least eight times within the family [11–13], in some cases reaching very high frequencies in natural populations [14, 15]. In none of them has it reached fixation, but rather always exists as a polymorphic phenotype, and it is present only in two species of *Panthera*: the leopard (*P. pardus*) and the jaguar (*P. onca*) in contrast of the spotted wild phenotype present in these species. These observations support the hypothesis that melanism can provide an adaptive advantage in certain ecological conditions [6, 16], and exists the hypothesis of an association between darker individuals and wetter areas with dense vegetation (e.g., tropical forests) [1, 4, 10, 17]. In addition, there have also been suggestions of the potential for negative selection against dark individuals in open areas where the sunlight/radiation levels and mean temperatures are high [5, 10, 17, 18]. These hypotheses have been commonly mentioned in the technical literature as anecdotal postulates and also appeared in the popular culture for some time.

The leopard is the largest spotted cat in Africa and Asia [19] and an important extant representative of genus *Panthera* [19, 20]. Its historical distribution is the broadest among all felids (from the Russian far east to Africa), encompassing a diverse array of habitats, from deserts to rainforests, and from the humid tropics to temperate zones [19]. In contrast, the jaguar (*Panthera onca*) is the largest wild cat in the Americas, and the only extant representative of genus *Panthera* in the New World [19]. Its current distribution stretches over 18 nations, from the southern United States to Argentina [21].

Although variant pigmentation phenotypes in vertebrates are caused by several genes [5], in the case of leopards it has been shown that melanism is induced by a recessively inherited mutation in the *ASIP* (*agouti signaling protein*) gene, which leads to a nonsense mutation predicted completely ablate *ASIP* function and thus induce black pigmentation [12]. In other hand, melanism in jaguars is inherited as a dominant trait, caused by a 15-base-pair deletion in the *MC1R* gene that leads to a "gain of function" mutation favoring the production of dark melanin (eumelanin) in the background regions of the coat [11, 22]. Although the trait has been well known in these species for many years and easily identifiable in nature (e.g., [15, 17, 23–26]), its

geographic distributions, as well as the environmental factors that may influence its persistence in natural populations, are being discovered recently [26–29].

This chapter presents the geographic distribution of melanism in *P. pardus* and *P. onca* in nature, as well as the response to environmental predictors aiming to evaluate the adaptive relevance of this phenotype. There were considered and tested two alternative hypotheses: (1) melanism present throughout the species' distribution, occurring randomly across all environments (i.e., the absence of association with different landscape conformations) and (2) melanism distributed according to biogeographic constraints.

2. Methods

2.1. Species database

The data set comprised location records points from the entire historical range of leopards (**Figure 1**) and jaguars (**Figure 2**), encompassing various biomes (e.g., moist and dry forests, grasslands and desert areas). These records were obtained from five different sources: (1)
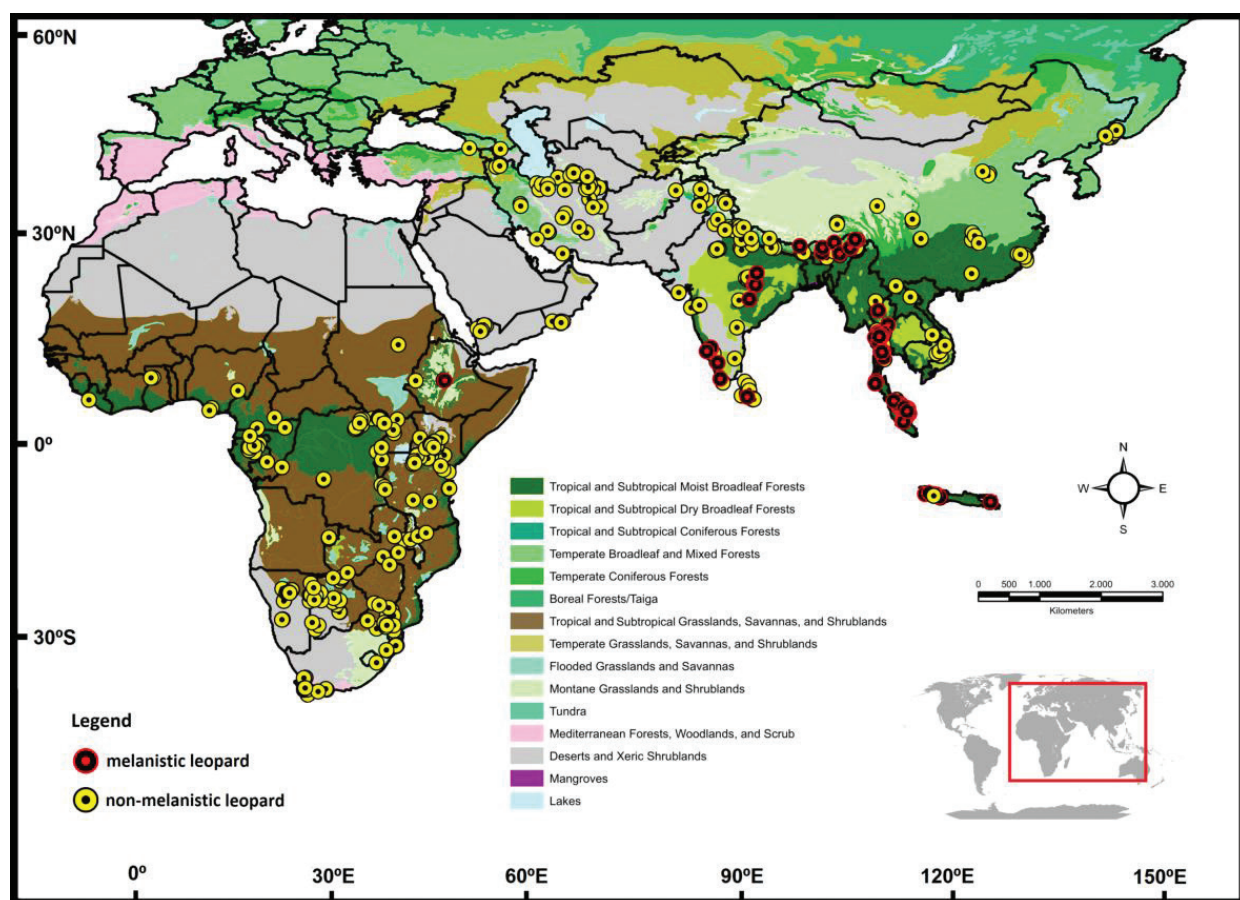

Figure 1. Location of melanistic and nonmelanistic leopard records, overlaid on a map of terrestrial biomes (based on Ref. [30]).
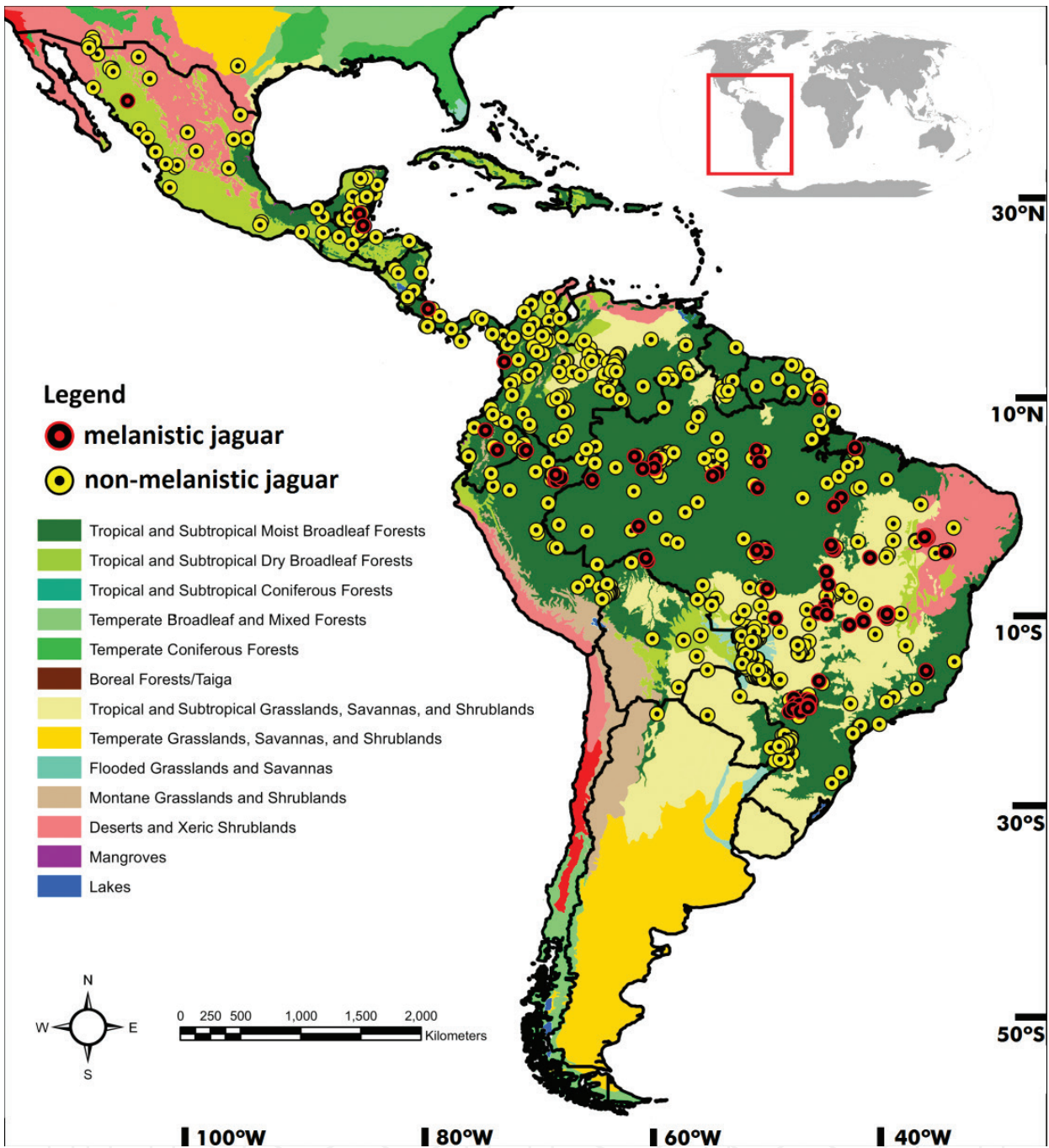
Figure 2. Location of melanistic and nonmelanistic jaguar records, overlaid on a map of terrestrial biomes (based on Ref. [30]).

individuals kept in scientific collections that possessed information on the geographic coordinates of the sampling location as well as on coat color (or, preferably, available skin for direct assessment and photographic documentation of coat color); (2) individuals captured or found dead during field ecology studies; (3) field-collected fecal samples whose melanism status could be confidently inferred using a molecular assay (following [22]); (4) camera trap records; and (5) samples available in online databases with precise geographic origin and available source information.

Location records of individuals confirmed to be melanistic or nonmelanistic were used in the statistical analyses based on the frequency of these phenotypes for both species. As there was no type of bias in our records with respect to coloration phenotype (i.e., sampling was random with regard to coat color), it was assumed that the frequency in which melanism appears in the total data set represents the overall frequency in the species, which provided a null hypothesis against which we tested potential deviations in different regions.

2.2. Environmental predictors

The occurrence of different phenotypes throughout leopard and jaguar distributions was mapped by building a database of location records of melanistic and nonmelanistic individuals. All the records were converted into degree coordinates, using the *WGS84* standard reference system. Additionally, biome and terrestrial ecoregion shapefiles [30] were used as mask layers to extract and analyze information about natural landscapes in which the phenotypes occur.

For modeling the potential distribution of melanism, in the initial analysis we considered 37 explanatory environmental predictors and landscape data that covered 100% of leopards and jaguars known distributions International Union for Conservation of Nature (IUCN) data. We used 35 environmental variables obtained from the Worldclim (http://www.worldclim.org) and Climond (http://www.climond.org) databases: annual mean temperature (Bio01), mean diurnal temperature range (Bio02), isothermality (Bio03), temperature seasonality (Bio04), max temperature of warmest week (Bio05), min temperature of coldest week (Bio06), temperature annual range (Bio07), mean temperature of wettest quarter (Bio08), mean temperature of driest quarter (Bio09), mean temperature of warmest quarter (Bio10), mean temperature of coldest quarter (Bio11), annual precipitation (Bio12), precipitation of wettest week (Bio13), precipitation of driest week (Bio14), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17), precipitation of warmest quarter (Bio18), precipitation of coldest quarter (Bio19), annual mean radiation (Bio20), highest weekly radiation (Bio21), lowest weekly radiation (Bio22), radiation seasonality (Bio23), radiation of wettest quarter (Bio24), radiation of driest quarter (Bio25), radiation of warmest quarter (Bio26), radiation of coldest quarter (Bio27), annual mean moisture index (Bio28), highest weekly moisture index (Bio29), lowest weekly moisture index (Bio30), moisture index seasonality (Bio31), mean moisture index of wettest quarter (Bio32), mean moisture index of driest quarter (Bio33), mean moisture index of warmest quarter (Bio34), and mean moisture index of coldest quarter (Bio35). In addition, we included data on altitude (obtained from the SRTM [http://www2.jpl.nasa.gov/srtm]) as well as on landscape surface cover (obtained from ESA GlobCover Project 2009 [http://due.esrin.esa.int/page_globcover.php]). All variables were used at a fine (~1 km) spatial resolution.

Since correlation among explanatory predictors can lead to model overfitting, we computed Pearson's correlation coefficient (*r*) between each pair of variables [31–33]. The correlation was assessed by extracting predictor information from 10,000 unique and randomly generated points within the present geographic distribution layer of both species (obtained from IUCN and complemented with our own database records). Then, the predictors that were not highly

correlated to each other were selected, using $r = 0.7$ as the cutoff value, assuming that they are sufficient for modeling the geographic distribution of these species, and the distribution of melanism within it.

2.3. Modeling procedures and statistical analyses

The models for the overall distribution of leopards and jaguars and the spatial distribution of melanism were generated using the maximum entropy algorithm implemented in the software Maxent [34] along with associated statistical tools [35–38]. The total set of location records divided by each phenotype for both species, 70% of which were used for training and 30% for testing the models, was employed. The data were sampled using the bootstrap routine of 10 random partitions with replacement [39]. All runs were configured in random seed, convergence threshold of 1E-5 with 500 iterations and 10,000 hidden background points [40]. Model performance was assessed by the AUC (area under curve) value for the receiver operating characteristic (ROC curve) and the binomial probability [39, 41], aiming to obtain models of continental-scale distribution of distinct phenotypes.

The statistical analysis of record distribution for each biome was performed using the chi-square test with Fisher correction [42]. The basic approach was to test differences between the observed and expected frequencies of melanism for each different ecoregion. As there was no detected bias with respect to the sampling of different phenotypes at any location (i.e., our sampling was random in regard to coat color), we used the overall frequency of melanism across the whole range to generate the expected number of melanistic records per biome.

3. Results

3.1. Leopards

About 623 leopard samples, comprising 556 nonmelanistic individuals and 67 melanistic individuals (**Figure 1**), providing a broad coverage of the known leopard current range, were obtained. Melanism presented a global frequency of 10.75% across the species' range, with regional frequencies varying among different landscapes (biomes and ecoregions). The confirmed presence of melanistic leopards was recorded only in five of the nine valid subspecies (**Figure 3**): Africa (*P. p. pardus*), Central India, Nepal, and Bhutan (*P. P. fusca*), Sri Lanka (*P. p. kotiya*), Southeast Asia (*P. p. delacouri*), and Java (*P. p. melas*). All of these regions contained new records for areas in which melanism had been previously described, as well as representation of additional areas. Melanism was absent in the leopard subspecies occurring in the Russian Far East (*P. p. orientalis*), Central China (*P. p. japonensis*), Arabian Peninsula (*P. p. nimr*), and Middle East (*P. p. saxicolor*).

Although leopards were found in more than 100 ecoregions, melanism was most common in tropical and subtropical moist forests (59 of 67 records), especially in the Indian Ghats, Javan forests, Kayah-Karen/Tenasserim forests (Southeast Asia), and Peninsular Malaysian rain forests (Southeast Asia). All of these records were consistent with high suitability of occurrence
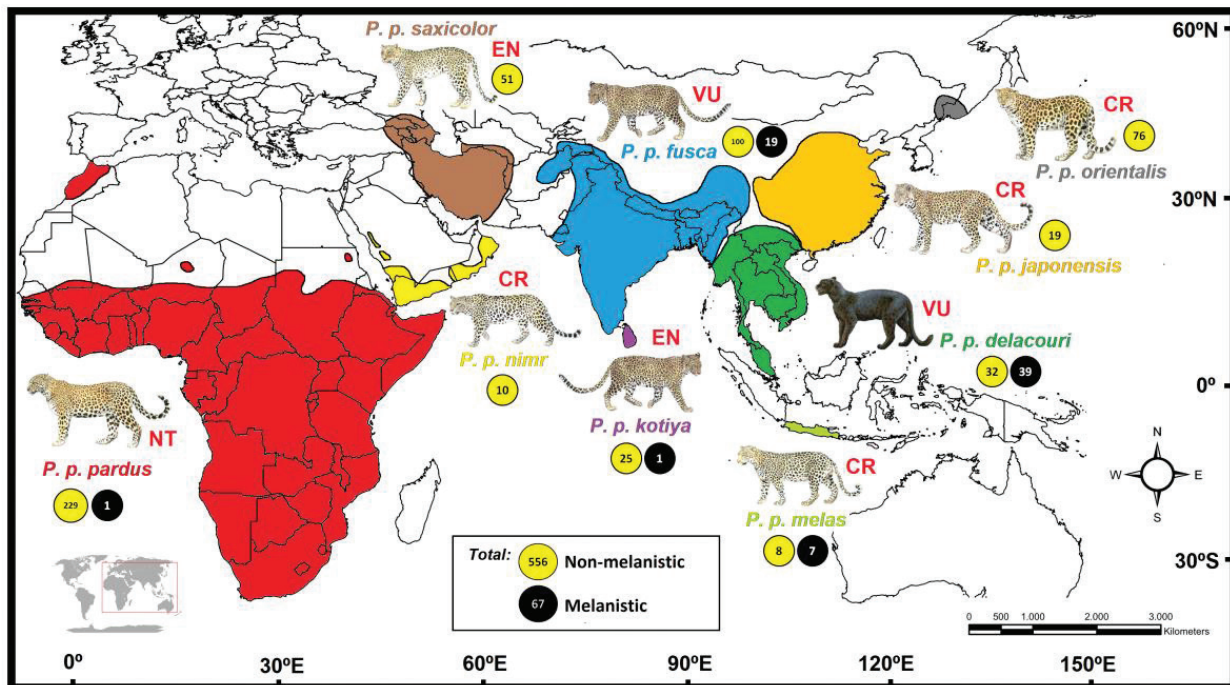
Figure 3. Location records database of leopards, divided by each valid subspecies (based on Uphyrkina et al. [55], with information about IUCN conservation status (NT = near threatened, VU = vulnerable, EN = endangered, and CR = critically endangered).

in the model for melanistic leopards (**Figure 4**). Differences among biomes were significant, especially in tropical and subtropical moist broadleaf forests, where 30% of the animals were black, which is almost three times more than expected if melanism were an evenly distributed neutral polymorphism. In contrast, the frequency of melanism was significantly lower than expected in deserts/xeric shrublands, temperate broadleaf and mixed forests, as well as tropical/subtropical grasslands, savannas, and shrublands.

Niche models were considered satisfactory (AUC ≥ 0.9): nonmelanistic model (AUC training = 0.926, test = 0.924) and melanism (AUC training = 0.976, test = 0.963). Control and melanism-predicted distributions generated through niche models are presented in **Figure 4A** and **B**. This assessment allowed a comparison between the overall range of leopards and the presence of melanistic animals, showing regional enrichment for this variant in some areas, as well as its absence in many others. When were analyzed the environmental variables that were most influential on the models, we observed that predictors related to moisture to have the largest effect.

3.2. Jaguars

About 980 jaguar samples, 884 of which were nonmelanistic individuals and 96 were melanistic animals, were obtained. The overall frequency of melanism was 9.80% across the species' range. Intriguingly, almost the same frequency expected for leopards. Most of the records of melanistic animals (92 in total) were located in South America. Moreover, all regions that had previously been reported as potential sites of melanistic jaguar occurrence in different biomes
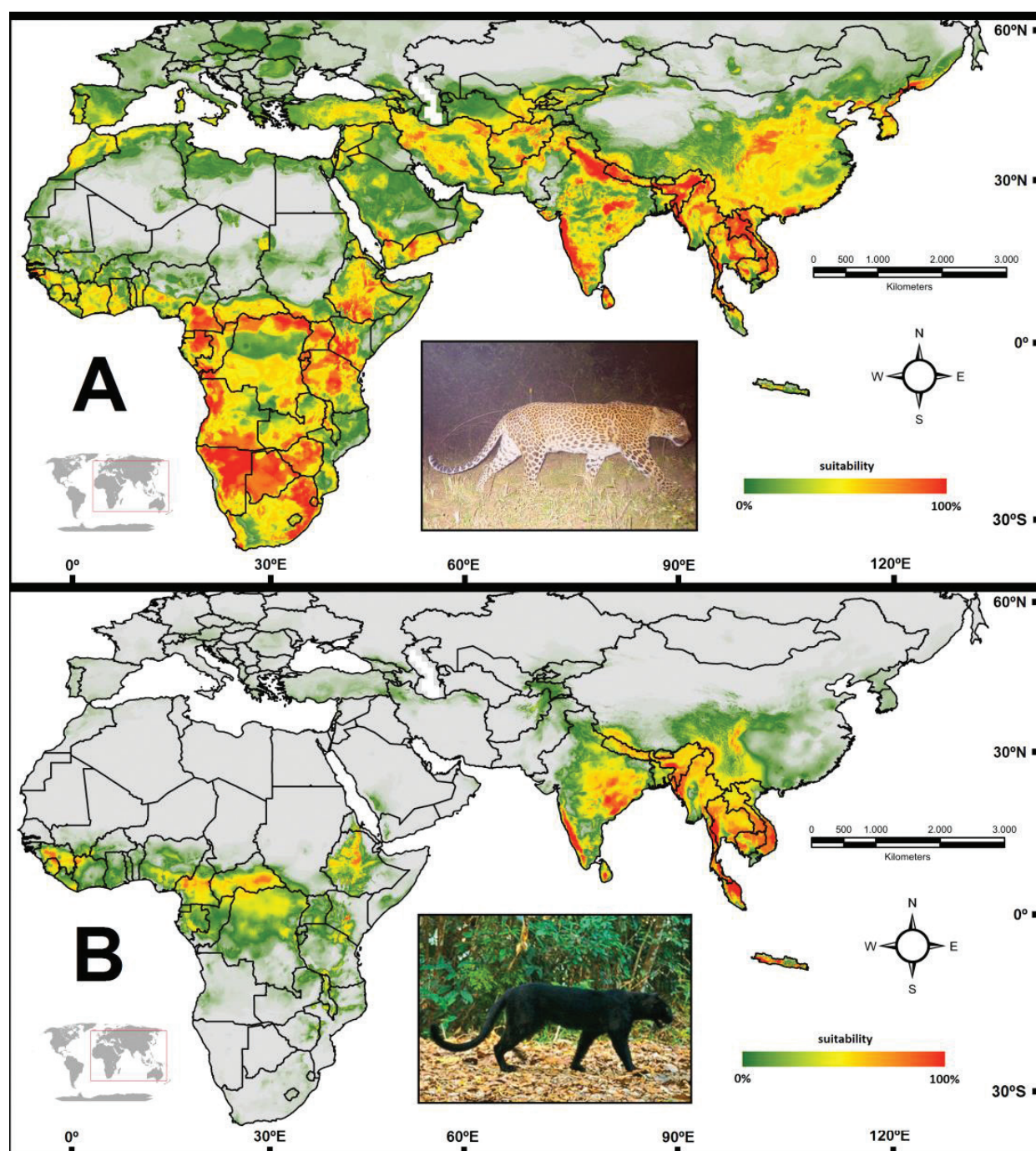
Figure 4. Potential distribution maps of the two coloration phenotypes analyzed in this study: (A) distribution of nonmelanistic leopards and (B) distribution of melanistic leopards. *Photos:* Andrew Stein and Bruce Kekule.

of Brazil were corroborated by this study, especially the Amazon and Cerrado areas (states of Amazonas, Pará, Mato Grosso, Goiás, and Minas Gerais; see Ref. [43]) and Caatinga (Serra da Capivara National Park [44, 45]). Additionally, new records were obtained for areas where there were no previous reports of melanistic animals (Colombia, Peru, Ecuador, and Costa Rica). When the presence of melanism across regions was assessed, we observed marked

differences in its frequency among distinct biomes and ecoregions. For example, melanism can reach high frequencies in a single ecoregion, such as the Alto Paraná Atlantic Forest, Cerrado, and Caatinga (inside the Brazilian territory), whereas can present a complete lack in the Pantanal and Llanos (implying a significantly lower frequency of this phenotype in these regions).

Niche models generated here were considered satisfactory (AUC ≥ 0.9): nonmelanistic model (AUC training = 0.949, test = 0.941) and melanistic model (AUC training = 0.978, test = 0.955). The nonmelanistic model provided a good fit to know the present broad distribution model for jaguars in the Americas, indicating that it provides a suitable baseline against which to compare the melanism model (**Figure 5A**). The melanism model showed some similarities with the control model, but also some important differences, especially the low suitable habitats for occurrence in the Pantanal and Llanos ecoregions (**Figure 3B**). When were analyzed the environmental variables that were most influential on the models, we observed that predictors related to mean temperatures have the largest effect.
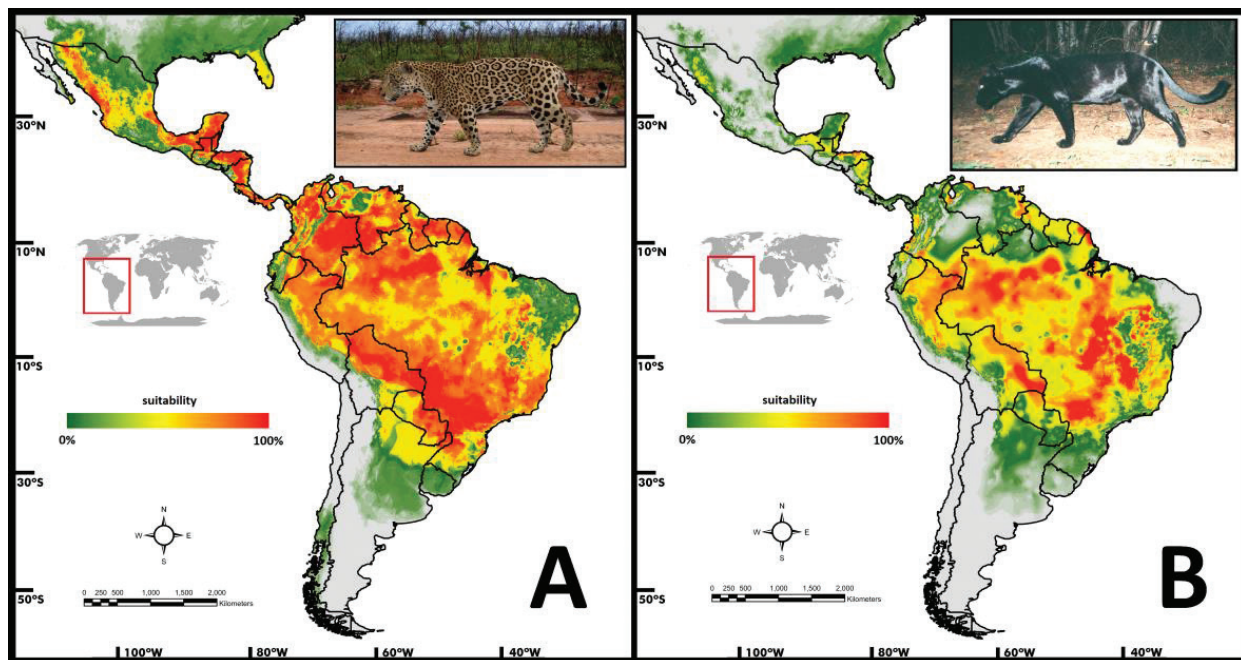

Figure 5. Potential distribution maps of the two coloration phenotypes analyzed in this study: (A) distribution of nonmelanistic jaguars and (B) distribution of melanistic jaguars. The species is considered almost as panmictic population [46] and near threatened by IUCN. *Photos:* Edsel Amorim Jr. and Leandro Silveira.

4. Discussion

The combination of statistical techniques associated with geoprocessing data has been used for some time in predictive models of ecology [47], especially in ecological niche models in the context of macroecological analysis [37, 41, 48, 49]. The models shown in **Figures 3** and **5** were

designed to provide an analysis of the relative influence of environmental predictors on the geographic distribution of melanism in big cats. The main differences between nonmelanistic and melanistic models were restricted to predictors (moisture and temperature) related to thermoregulation in natural habitats, suggesting that the presence (or frequency) of melanism in panthers may be regulated by climatic features.

For a character to be recognized as adaptive, it must be derived and involved in the response to a selective agent [50], and in this context, it is interesting to determine if a polymorphism deviates from equilibrium expectations [51]. To elucidate biological issues related to melanism in natural populations and assess the relevance of different adaptive phenotypes, it is necessary to consider the relative importance of genetic drift and natural selection on the dynamics of different phenotypes in distinct landscapes [33, 52]. A selectively neutral phenotype should show a random pattern of variation among populations, while nonrandom patterns suggest the occurrence of selection (if populations are demographically connected). In the case of a stable polymorphism (such as melanism), an important issue to be considered is the phenotype frequency across different landscapes [53] because in some cases ecological variables describing a species range can predict genetic patterns [33]. That is the exactly pattern observed in leopards and jaguars, where the frequency is almost the same for both species in natural populations, and the geographic distribution is nonrandom in the two cases. This scenario supports the hypothesis of natural selection acting under the frequency and occurrence of melanism in these animals.

In fact, this study has provided a characterization of the spatial distribution of melanism in leopards and jaguars and demonstrated that such distribution is nonrandom. Recent analyses have indicated that melanism can reach very high frequencies in some leopard populations (e.g., Southeast Asia reported by [14]). In addition, there have been confirmed reports of melanistic leopards in India, Abyssinia, and Ethiopian Highlands, Java and Malaysia, Aberdare Mount Kenya, Highlands of Nepal, as well as a doubtful occurrence in South Africa [19, 26, 28, 54]. These observations are restricted to some areas and may support the hypothesis that melanism can provide an adaptive advantage in certain ecological conditions [5, 18]. At least four of the nine currently recognized leopard subspecies (based on [55]) are already cited in the literature as having confirmed records of melanistic animals: *P. p. pardus, P. p. fusca, P. p. delacouri*, and *P. p. melas*. However, the exact geographic range of this coloration phenotype has never been mapped in leopards in general, or in any of its subspecies.

Moist forests (especially in Southeast Asia) presented very high frequencies of melanistic leopards (e.g., 39 of 71 individuals [55%] in Southeast Asia), and more than 80% of the black animals in our database, a fivefold increase relative to the expected number based on the overall number of records. Furthermore, we found no confirmed melanistic leopards in the Middle East, Arabian Peninsula, Central China, and Russian Far East (**Figure 1**), nor any mention in the literature as to the presence of melanism in these regions, indicating that this polymorphism is really absent from these areas. Overall, there was a significant reduction in the frequency of melanism in some biomes that consist of open habitats or temperate forests. There thus is a clear pattern in which melanism tends to increase in tropical/subtropical moist forests and decrease in open/dry or temperate habitats. Such a result supports the classical

hypothesis postulating an adaptive role for melanism, which would be favored in tropical and humid environments.

An alternative explanation is that variation in the melanism frequency could have been driven by demographic processes, including population structure and drift-induced differentiation. According to Ref. [55], significant geographic structure can be identified in leopards, indicating the existence of restricted historical gene flow among some portions of the range. This division formed the basis for currently recognized leopard subspecies, although in that study the authors noted that in some areas, such as African continent, Arabian Peninsula, Sri Lanka, and Java, the sampling was too sparse to identify clear-cut phylogeographic relationships. Nevertheless, the presence of demographic distinctiveness among at least the nine recognized species argues that such differentiation must be taken into account when comparing the frequency of melanism among regions. Although the possibility that demography has influenced the present-day frequency of melanism in leopards cannot be completely excluded, it is unlikely that it could explain most of the observed patterns, since each of the subspecies' ranges tends to contain a variety of habitats. Therefore, demographic effects caused by historical differentiation among subspecies would tend to obscure, rather than generate, the observed pattern of association between melanism and forested habitats.

Therefore, we consider that the most probable historical scenario for melanism in leopards is the emergence of the causative allele at a particular location and its dispersal throughout much of the species' distribution, suffering selection under the influence of varying environmental conditions in different landscapes, as well as genetic drift in some situations (e.g., founding of new populations during range expansion events). Since melanism in leopards is a recessive trait [12], it is plausible that its causative allele can disperse long distances over evolutionary time even across habitats where it could be selected against (e.g., deserts and grasslands). This is because the allele can remain "hidden" in heterozygosity for many generations when it is at low frequency, while at the same it could be lost in some areas due to an effect of genetic drift. Another possibility is that melanism arose in leopards more than once.

When the distribution of melanism in leopards is examined more closely, Southeast Asia emerges as a particularly interesting region. Our data support the findings reported by [14] and [15], showing that melanism is almost fixed in areas south of the Isthmus of Kra (Thailand/Malaysia). This study obtained only two records of nonmelanistic animals south of the Isthmus, while in more northerly areas both phenotypes appear at similar frequencies. This intriguing pattern may have been caused by some degree of demographic isolation across the Isthmus, which is consistent with the hypothesis that in the past (during the Last Glacial Maximum period, between 20,000 and 25,000 years ago, [56]) it operated as an effective ecological barrier restricting gene flow for several organisms. The fact that present-day landscapes appear to be similar on both sides of the Isthmus argue for a demographic, rather than selective explanation of the high frequency of melanism in the southern portion. However, the analysis of environmental predictors that influence the distribution of leopards in Southeast Asia revealed that moisture is the main factor that induces the presence of melanism, without correlations with landscape features (vegetation index). Given the observed

support for an increased frequency of melanism in moist forests areas, it is interesting to discuss its potential causes in the light of classical hypotheses suggesting a selective advantage related to thermoregulation [57] in leopards.

The most part of melanistic jaguars was recorded in South America, especially in Brazil, Ecuador, and Peru territories. The species potential distribution map and melanism distribution map indicate a high habitat suitability in moist areas. As we know, the Amazon region has a large size and high population density of jaguars and can be considered a core habitat for the species [58]. In addition, the Brazilian Atlantic Forest region, despite the recent population decline [59–61] and the local loss of genetic diversity in jaguars [62], still has remaining populations. The presence of melanism in Brazilian moist and dry forests and Cerrado areas had already been documented and can reach high local frequencies in some remnant areas [44, 63]. In contrast, flooded grasslands and savanas such as Pantanal (Brazil) and Llanos (Colombia/Venezuela) present no records of melanistic jaguars, indicating that this polymorphism is really absent in these areas.

Although jaguars are often documented in North and Central Americas [19], there were historically only four records of melanistic individuals in these regions. The only record of melanism from North America prior to this study was a black female photographed in 2004, in the El Fuerte River Valley, near Sinaloa, Mexico [64]. In Central America, there are two records of melanistic animals from Belize: Ek Balan and El Rancho Grande River (previously reported as possible by [43]), and one record from Costa Rica [65]. Remaining populations of the species have been recently identified in the northern portion of its distribution, in the southern United States [66, 67], but there has been no record of melanism in these areas. The generated models showed high suitability for melanism occurrence in Belize and Costa Rica and low suitability in Mexico.

Previous studies have shown that jaguars possess low levels of geographic structure on a wide range of scale [46]. Phylogeographic analyses indicated that there were no impassable historical barriers to gene flow throughout the species' range. Only a few historical barriers to dispersal were inferred at this scale, such as the Amazon River, whose influence was much stronger on the female-inherited mitochondrial DNA than on nuclear markers. These results suggested that the species has behaved historically almost as a panmictic population, which argues against the possibility that founder effects and/or high genetic drift at a regional scale could have induced the observed nonrandom patterns in the distribution of melanism. Moreover, there is so far no evidence of historical bottleneck events [46], which could have exacerbated genetic drift and thus lead to large scale increases in the frequency of melanism. In this context, it may be noted that melanism is present with high suitability on both sides of the Amazon River, suggesting that it has not been affected by the historical (albeit incomplete) restriction to gene flow inferred with molecular markers. Given these considerations, this study conclude that the most probable scenario is the jaguar melanism allele arose at a particular location and dispersed throughout the species' distribution, with its regional frequency being influenced at least partially by natural selection related to environmental predictors that vary across different landscapes. In conclusion, the geographic variation observed here provides evidence for the existence of natural selection in this system and provides some hints as to its nature.

5. Conclusions

Given the current genetic evidence indicating that population structures in leopards and jaguars have historically comprised a broadly connected population across its distributions, it would be expected to find a random distribution pattern of melanism throughout their ranges if this variant was selectively neutral. The results of this study indicate that this is not the case and demonstrate that its distributional pattern is nonrandom. Although the observed punctual cases of increased frequency of melanism may be indeed derived from recent drift-induced shifts in locally isolated populations, we do not find support for a drift-based explanation for the observed pattern, and thus favor a scenario implying an effect of natural selection under polymorphic phenotypes in big cats such as melanism. Moreover, the suitability maps generated here showed differences in the distribution of melanistic records relative to the ancestral phenotype (spotted) and suggested that at least some of the underlying differences could be related to environmental predictors, possibly to thermoregulation issues. Overall, this study contributed to address a question that has circulated anecdotally for almost 200 years in the scientific literature but remained blurred in zoology, particularly in wild felids. The results open up new avenues for investigating this polymorphism in other mammal species. In this context, it is relevant to note that the ecology of some species can drive genetic diversity, and phenotypes in natural populations can present spatial patterns of variation associated with adaptation to some environments, regulated by natural selection. By connecting coloration diversity to environmental information which may have a direct or indirect influence on the adaptive significance of coat color variants, it is possible to investigate evolutionary processes involved in the generation and maintenance of polymorphic phenotypes in nature.

Acknowledgements

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