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Research Article

Research Article

Ecological niche modeling of the *Leopardus tigrinus* complex sheds light on its elusive evolutionary history

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Abstract

The evolutionary history and taxonomy of the *Leopardus tigrinus* species complex have been studied based on several approaches, mostly employing genetic and morphological data, leading to distinct classification schemes. We approached this problem from an ecological perspective, with 2 main goals: (i) to evaluate ecological niche differences among regional *L. tigrinus* populations to determine the extent of ecological divergence among them; and (ii) to identify environmental barriers to historical dispersal that could have driven differentiation among the proposed groups. We modeled the ecological niche of all taxonomic/geographic groups proposed so far to comprise the *L. tigrinus* complex using the Maximum Entropy algorithm, and evaluated geographic and ecological niche differences among them. Furthermore, we investigated possible environmental barriers to historical dispersal that could have driven differentiation among regional groups. We evaluated 4 hypothetical barriers across 3 time periods to assess their potential historical effect. We found high ecological divergence between northeastern tigrina populations and the northern Andean and Central American tigrinas. Other groups within the *L. tigrinus* complex are less divergent. In addition, the Guiana Shield tigrina, where the type locality of the species is located, seems to be ecologically similar to populations from northeastern Brazil while also showing some overlap with Andean populations. The Panama center, the Llanos of Colombia and Venezuela, and the Amazon region were identified as historical barriers for tigrina dispersal across all time periods. The inferred historical barriers and ecological divergence observed in this study contribute to the inference of evolutionary differentiation among geographic groups comprising the *L. tigrinus* complex, revealing areas of consistently low habitat suitability that have likely contributed to divergence among regional populations.

Key words: ecological divergence, geographical barriers, Neotropical, oncilla, tiger cat, tigrillo.

Modelado de nicho ecológico del complejo *Leopardus tigrinus* ilumina su elusiva historia evolutiva

Resumen

La historia evolutiva y la taxonomía del complejo de especies *Leopardus tigrinus* se han estudiado en base a varios enfoques, en su mayoría empleando datos genéticos y morfológicos, lo que ha llevado a distintos esquemas de clasificación. Abordamos este problema desde una perspectiva ecológica, con dos objetivos principales: (i) evaluar las diferencias del nicho ecológico entre las poblaciones regionales de *L. tigrinus* para determinar la existencia de divergencia ecológica entre ellas; e (ii) identificar las barreras ambientales para la dispersión histórica de estos organismos que podrían haber impulsado la diferenciación entre los grupos propuestos. Modelamos el nicho ecológico

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de todos los grupos taxonómicos/geográficos propuestos hasta ahora para comprender el complejo *L. tigrinus* utilizando el algoritmo de Máxima Entropía y evaluamos las diferencias geográficas y ecológicas de nicho entre ellos. Además, investigamos posibles barreras ambientales para la dispersión histórica de estos organismos que podrían haber impulsado la diferenciación entre estos grupos regionales. Evaluamos cuatro barreras hipotéticas en tres períodos de tiempo para determinar su posible efecto histórico. Encontramos una alta divergencia ecológica entre las poblaciones de tigrinas del noreste de Brazil y las tigrinas del norte de los andes y centroamericanas. Otros grupos dentro del complejo *L. tigrinus* son menos divergentes. Además, las tigrinas del Escudo Guayanés, donde se encuentra la localidad tipo de la especie, parece ser ecológicamente similar a las poblaciones del noreste de Brasil, mientras que también muestra cierta superposición con las poblaciones andinas. El centro de Panamá, los Llanos de Colombia y Venezuela y la región amazónica fueron identificados como barreras históricas para la dispersión de tigrinas en todos los períodos de tiempo. Las barreras históricas inferidas y la divergencia ecológica observada en este estudio contribuyen a la inferencia de la diferenciación evolutiva entre los grupos geográficos que comprenden el complejo *L. tigrinus*, revelando áreas de baja idoneidad para el hábitat que probablemente han contribuido a la divergencia entre estas poblaciones regionales.

Palabras clave: Divergencia ecológica, barreras geográficas, oncilla, tigrillo, gato tigre, neotropical.

The genus *Leopardus* Gray, 1842, which is endemic to the Neotropics and the most speciose within the cat family, comprises small to medium-sized felids that diverged from other cat genera ca. 8 million years ago (Johnson et al. 2006; Li et al. 2016). Considerable intraspecific diversity, occasional inter-species overlap in pelage features, and hybridization have historically posed challenges to accurate species-level delimitation and identification in this group (e.g., Johnson et al. 1999; Trigo et al. 2008, 2013; Breton and Sanderson 2011; Nascimento and Feijó 2017; Nascimento et al. 2020), which in turn has led to recalcitrant uncertainties affecting the geographic distribution and habitat association of some of these cats. One of the main foci of taxonomic discussion is the tigrina (or tiger cat), *Leopardus tigrinus* (Schreber 1775) species complex, whose type locality is in Cayenne, French Guiana (Allen 1919; Cabrera 1958) and whose distribution ranges from Costa Rica to northern Argentina (Macdonald et al. 2010).

Four subspecies were traditionally recognized for *L. tigrinus* (e.g., Wozencraft 2005): *L. t. oncilla* (Thomas 1903) in Central America; *L. t. pardinoides* (Gray, 1867) in the Andean region; *L. t. tigrinus* in northern Brazil and the Guiana shield; and *L. t. guttulus* (Hensel, 1872) in southern Brazil, Paraguay, and northeastern Argentina (Fig. 1). Johnson et al. (1999) reported a strong genetic divergence between *L. t. oncilla* and *L. t. guttulus* based on mitochondrial DNA (mtDNA) sequences, and presented a putative distribution of tigrina subspecies (Fig. 1a). However, there was uncertainty with respect to central Venezuela and the boundaries among these units were not clearly delimited. Later, Trigo et al. (2013) reported evidence for consistent genetic differentiation and lack of ongoing gene flow between populations of *L. tigrinus* from northeastern and southern/southeastern Brazil, leading them to recognize the latter as a distinct species, *L. guttulus*. Considering this taxonomic arrangement, the International Union for Conservation of Nature (IUCN) recognized *L. tigrinus* as being distributed from Costa Rica to Bolivia and central Brazil (Payan and de Oliveira 2016). In its turn, *L. guttulus* would be distributed in southern/southeastern Brazil, Paraguay, and northeastern Argentina (de Oliveira et al. 2016). Moreover, it is noteworthy that after the recognition of *L. guttulus* as a distinct species, the distribution of *L. tigrinus* in South America was provisionally delimited in an arbitrary fashion, as the 2 species were separated by an almost straight line due to insufficient information on their actual geographic limits (Fig. 1b).

Recently, Kitchener et al. (2017) also recognized *L. guttulus* as a distinct species and considered the existence of 2 subspecies within *L. tigrinus*—*L. t. oncilla* in Central America and *L. t. tigrinus* in South America—they followed the IUCN proposal with respect to the distribution of these species (Fig. 1). Those authors mentioned the possibility that Central American tigrinas might represent a distinct species, and that those from northwestern South America could also warrant recognition as *L. pardinoides*, but in both cases they concluded that additional analyses were required to settle these questions. In that same year, Nascimento and Feijó (2017) presented a morphological revision of this species complex and recognized 3 morphotypes that were equated to species (Fig. 1c): *L. tigrinus*—herein referred to as "*L. tigrinus* (m)"—in Central America, Andes, and northern South America including Amapá state (Brazil), with discontinuities in the Llanos of Colombia and Venezuela, in the Amazon region, and in the Panama center; *L. emiliae* (Thomas 1914) in central and northeastern Brazil, mainly in the Caatinga and Cerrado biomes; and *L. guttulus* in southern and southeastern South America, consistent with the results of Trigo et al. (2013). Finally, a recent genetic analysis using mtDNA data (Diana Buitrago-Torres, Pontificia Universidade Catolica de Rio Grande do Sul, Porto Alegre, RS, Brazil, personal communication, June 2023) revealed differences among samples from Central America (C. Am. tigrina), Colombia (N. Andean tigrina), and Peru (S. Andean tigrina), as well as between those and the eastern South American units (*L. guttulus* and samples from northeastern Brazil—herein referred to as "NE tigrina"). However, they did not include samples from the Guiana Shield, precluding an assessment with respect to the *L. tigrinus* type locality. In parallel, analyses of genome-wide markers identified a deep divergence between NE tigrina and *L. guttulus,* almost as old as that between *L. guigna* (Molina 1782) and *L. geoffroyi* (d'Orbigny and Gervais, 1844), further supporting their recognition as distinct species (Trindade et al. 2021; Lescroart et al. 2023). In addition, those studies revealed that the C. Am. and Colombian tigrina populations do not belong to the same monophyletic group as NE tigrina and *L. guttulus*, thus supporting species-level distinction between these geographic units in northwestern versus eastern South America. Taken together, these studies suggest that this complex may comprise up to 5 different evolutionary units, even allowing for uncertainty regarding the affinities of the Guiana Shield population (Fig. 1d). In this context, a recent biogeographic analysis suggested that populations from the Guiana Shield and those of northern/northeastern Brazil may be closely related (de Oliveira et al. 2022), adding another layer of complexity to the species distributional limits that can be further tested using additional approaches.

The complex is distributed across a broad diversity of environments, while some intervening areas have never been found to harbor these felids. It may be hypothesized that these areas represent habitat barriers that limit historical gene flow among regional populations, leading to potential evolutionary differentiation through time. In addition, there are areas with no recorded occurrence, but in which it is not clear if the complex is absent or difficult to detect (Fig. 1). In this context, 4 putative habitat barriers may be specifically hypothesized: the Panama center; the Llanos of Colombia and Venezuela; the Amazon region; and the Huancabamba depression

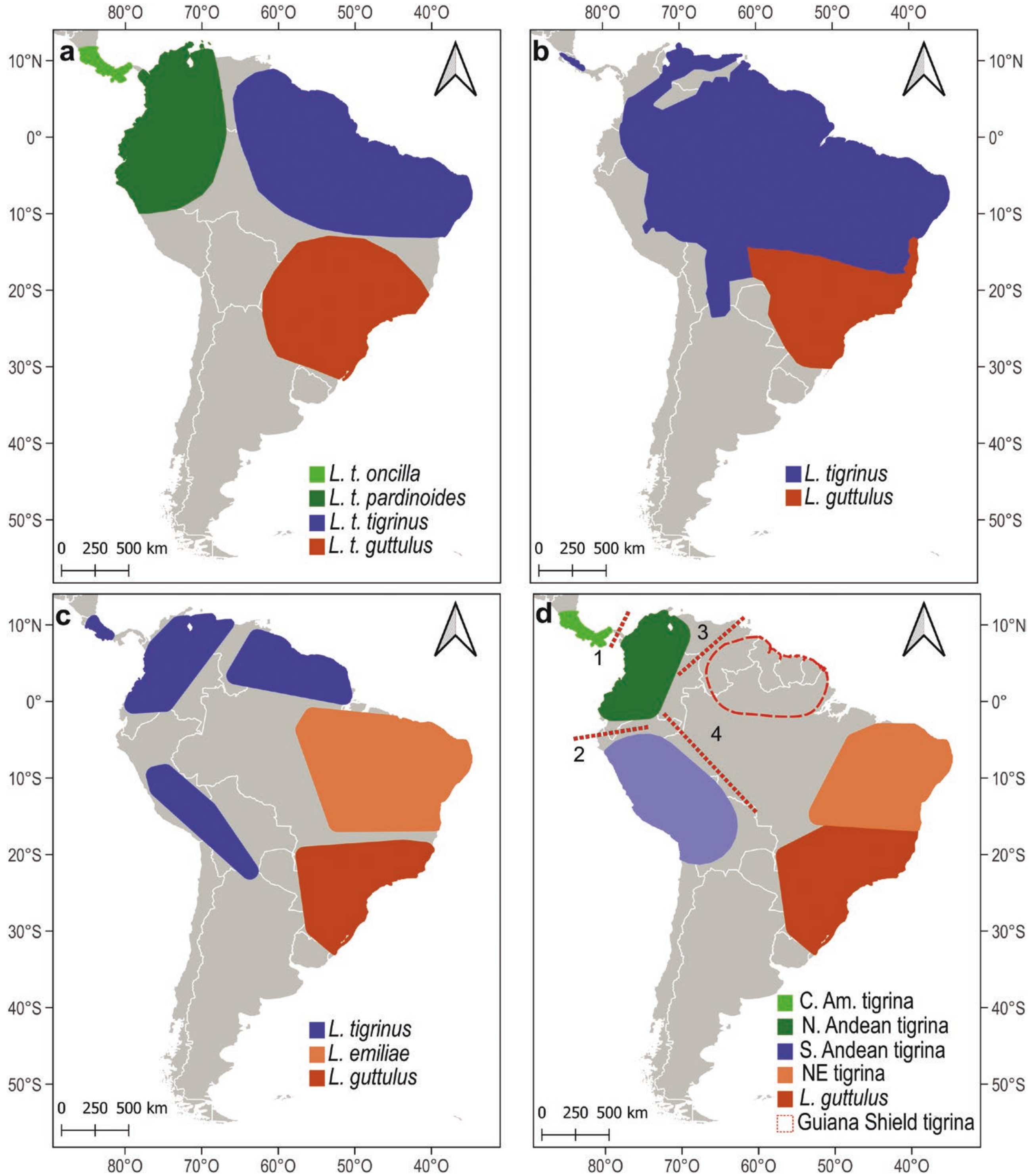

Fig. 1. Taxonomic composition and hypothetical distributions in Central and South America of the *Leopardus tigrinus* complex, according to different sources: (a) Johnson et al. (1999); (b) Kitchener et al. (2017), in which *L. guttulus* is treated as a separate species; (c) polygons created based on occurrence records compiled by Nascimento and Feijó (2017), who used morphological data to propose splitting the complex into 3 species—the *L. tigrinus* shown here is referred in text as *L. tigrinus* (*m*), as well as *L. emiliae* is referred in text as NE tigrina; (d) genetically identified evolutionary units comprising the complex according to Johnson et al. (1999), Trigo et al. (2013) (Diana Buitrago-Torres, Pontificia Universidade Catolica de Rio Grande do Sul, Porto Alegre, RS, Brazil, personal communication, June 2023); Trindade et al. (2021)—the Guiana Shield population (which includes the *L. tigrinus* type locality), delimited with a dashed line, has not yet been surveyed genetically. The potential barriers (shown in panel "d") to *L. tigrinus* complex distribution are indicated with the dotted, numbered lines: (1) Lowland forests in Panama center and Choco-Darien; (2) Huancabamba depression; (3) Llanos in Colombia and Venezuela; and (4) Amazon region. The detailed altitudinal gradient is presented in Supplementary Data SD1. Map projection: WGS84.

in northern Peru and southern Ecuador (Fig. 1d; Supplementary Data SD1). These barriers are identified as lowland areas that could limit the dispersion of populations mainly distributed in the highlands of the Andean region (Tirira 2001; Rodríguez and Rojas-Suarez 2008; Payán-Garrido and González-Maya 2011; SERFOR 2018) and the Talamanca Mountain range in Central America (Bagley and Johnson 2014; Payan and de Oliveira 2016). This isolation pattern between these highland regions has already been recorded in other taxonomic groups including amphibians and reptiles (Savage 1996; Myers et al. 2007). The Llanos have never been suggested as a suitable habitat for the species complex, and the IUCN distribution (Fig. 1b) does not include this area within its expected range. Elevation in the Llanos is extremely low for the highland population of Colombia and Venezuela and could limit their dispersion toward the east. Similarly, the Panama center—with a mean elevation of 200 m a.s.l. (Bagley and Johnson 2014)—and the lowland Choco-Darien Forest could jointly be a barrier between the highland-dwelling populations of Costa Rica/Panama—restricted to the Talamanca Mountain range (Payan and de Oliveira 2016)—and populations from Colombia which are restricted to the Andean region (Payán-Garrido and González-Maya 2011). The Huancabamba depression is a lower-elevation region between southern Ecuador and northern Peru in which the Andes range is partially interrupted by the Chamaya/Marañon river systems (Weigend 2002). This area has been suggested as a barrier for some plants in Peru (Weigend 2002) and could restrict gene flow between populations of Colombia and Peru. Finally, the interior regions of the Amazon could also be a barrier to the dispersal of populations, preventing contact between eastern and western areas (de Oliveira 2004; de Oliveira et al. 2022).

In addition to clarifying present-day distributional patterns of the *L. tigrinus* complex, it is important to understand the historical processes that have shaped them. In particular, it is relevant to assess the influence of glacial–interglacial dynamics, which have often driven the intermittent contact and isolation among regional populations (Barrantes 2009). These dynamics may have allowed the vegetation from nearby mountainous areas to become continuous during glacial periods (Bagley and Johnson 2014). Thus, it is possible to hypothesize that species adapted to high Andean climates could reach similar regions in Central America and then become isolated in the subsequent interglacial period (Barrantes 2009). These changes during the Pleistocene, for example, may provide an explanation for the apparent isolation of *L. tigrinus* in Central America relative to its distribution in South America. On the other hand, the Amazon Forest reduction and savanna expansions during glacial periods (Behling 2002) could have led to a historical connection between open biomes such as the Caatinga and Cerrado in Brazil and savannas that regionally replaced the forest at those times (de Oliveira et al. 2022).

These hypotheses (existence of historical barriers among tigrina units and their stability over time) can be tested using habitat suitability modeling based on climatic and topographic variables, an approach that allows assessment of geographic and ecological aspects of a given species (Tocchio et al. 2015). Although climate and topography are not the only factors that drive the distribution of a species—and in some cases biotic interactions (Eltonian Niche) can dramatically change its predicted distribution (Francis et al. 2021)—such information is not available for all species and can be very difficult or impossible to model for the past. Therefore, macroclimatic and topographic variables can provide sufficient information to predict distributions at a large scale such as the Neotropical region, and we assumed here that they would be informative to investigate differentiation among tigrina units. Indeed, the possibility of projecting niche models toward past climates has allowed scientists to test hypotheses related to the isolation or connectivity of different areas over time, leading to a better understanding of the processes likely underlying the present distribution of a species (Guevara et al. 2018). Therefore, comparing predictions of habitat suitability over time across putative barriers may help us understand the evolutionary history of the *L. tigrinus* complex. In this context, the objectives of this study were to: (i) determine the ecological divergence, in the geographical and environmental space, among the regional groups previously proposed (based on morphological and/or genetic data) to comprise the *L. tigrinus* complex; and (ii) employ ecological niche modeling to identify potential barriers across the overall distribution of this complex that may have induced the evolutionary differentiation among such regional groups.

Materials and methods.

Occurrence data.

Due to the taxonomic changes that have recently affected the complex, we used records assigned to *L. tigrinus*, *L. emiliae*, and *L. guttulus*. All records included in this study came from a data set comprising museum specimens, literature citations, and photographic records—all of which were verified by photo, video, and/or genetic analysis to guarantee their correct identification (Supplementary Data SD2). We filtered the data based on the maximum home range reported for *L. tigrinus* (de Oliveira et al. 2010) to have only 1 record within a 25-km radius to minimize overprediction in areas with a high concentration of points. The spatial filter was performed using the R package “SpThin” (Aiello-Lammens et al. 2015)—we created a maximum of 5 random record sets that adjust for this distance parameter and applied it to each group set that was modeled in this study.

Environmental data.

Environmental information selected for the models included variables related to temperature, evapotranspiration process, and terrain (e.g., rugosity) obtained from the ENVIREM database (http://envirem.github.io/, Title and Bemmels 2018; Supplementary Data SD2). All variables had a resolution of 5 km^2.

Ecological niche modeling and barrier identification.

We constructed models for different combinations of geographic units that may comprise the complex, reflecting previous genetic- and/or morphology-based classification schemes. We initially modeled the distribution of the complex as a whole, assuming 2 versions: (i) a “classical” version (e.g., assumed by Johnson et al. 1999) comprising all tigrina units including *L. guttulus*; and (ii) a more modern version (e.g., assumed by Kitchener et al. 2017), recognizing *L. guttulus* as a distinct species and excluding it from the complex. This initial modeling step aimed to broadly characterize the ecological niche of the *L. tigrinus* complex as a whole, and to identify areas of overall low habitat suitability that may have acted as historical barriers among regional units (see below).

A second modeling strategy addressed geographic units separately to characterize their ecological divergence and to investigate whether their predicted distributions could overlap in the present and/or in the past. For that purpose, we considered 2 sets of geographic units. The first was derived from the morphology-based proposal by Nascimento and Feijó (2017), with each species recognized in that study (*L. tigrinus*, *L. guttulus*, and *L. emiliae*) being modeled separately (Fig. 1c). The second set comprised geographic units whose evolutionary distinctiveness has been detected with genetic analyses (Johnson et al. 1999; Trigo et al. 2013; Trindade et al. 2021; Diana Buitrago-Torres, Pontificia Universidade Catolica de Rio Grande do Sul, Porto Alegre, RS, Brazil, personal communication, June 2019; see Fig. 1d). The *L. guttulus* model was the same for both the morphologically- and genetically defined sets, and the *L. emiliae* model of the morphologically defined set was the same as the NE tigrina model in the genetically defined set.

Finally, we performed several exploratory modeling analyses of the Guiana Shield unit. Due to the lack of genetic samples from the Guiana Shield and Amazon regions, and the evidence found by de Oliveira et al. (2022), we modeled the ecological niche of *L. tigrinus* in this region considering 4 different data sets to assess whether environmental conditions associated with the Guiana Shield records are similar to those from the Amazon or the Cerrado and Caatinga biomes (Supplementary Data SD1): (i) Guiana Shield alone including only records from Guiana, French Guiana, Suriname, southern Venezuela, and northern Brazilian Amazon (Guiana Shield Strict—GSstrict); (ii) Guiana Shield plus records from the entire Amazon biome in Brazil (GSAmaz); (iii) only records from the Amazon biome in Brazil (Amaz); and (iv) NE tigrina plus records from the Brazilian Amazon (NE tigrina + Amaz). No model from the Guiana Shield exploratory analysis was compared with *L. guttulus* because this species is clearly differentiated from *L. tigrinus* (sensu Kitchener et al. 2017), and its affinity with the Guiana Shield population is not relevant for the purpose of this analysis.

We constructed models using the Maximum Entropy (MaxEnt) algorithm (Phillips and Dudík 2008). To calibrate the models, we selected different areas according to each assessed scenario, and delimitation of these areas was conducted following the criterion proposed by Anderson and Raza (2010). The occurrence data were divided into training and test sets by randomly selecting 25% of the total records for the test set. This process was performed for each record set, filtered in each of the assessed scenarios (Sobek-Swant et al. 2012; Fitzpatrick et al. 2013; Fand et al. 2014; Silva et al. 2019). To evaluate candidate models, we used the area under the receiver operating characteristic partial curve (AUC of partial ROC) based on training data with the omission rate criterion at 5%, and the AIC (Akaike Information Criterion) delta selecting models with AIC delta < 2 to avoid overparameterization (Burnham and Anderson 2002). For geographic units with small sample size (less than 25 records), the jackknife approach proposed by Pearson et al. (2007) was used, with the R package "ENMeval" (Muscarella et al. 2014). The best model of each variable set (see below) was selected based on an AIC delta value. The best model for each record set was selected based on the highest value of AUC_{test} (Warren and Seifert 2011). For each taxonomic group, 10 models were generated selecting different training and test records using a bootstrap approach and then a consensus model was constructed.

We evaluated sets of independent variables for each of the assessed groups or group sets to avoid model overfitting. To construct these variables sets, first we evaluated a set that included all variables and in the best model chosen for this set, selected variables with "permutation importance" greater than 1 (Cao et al. 2013). We then checked the independence of variables based on the Spearman correlation index, excluding variables highly correlated ($-0.8 \leq r \geq 0.8$). Finally, we constructed environmental niche models for each taxonomic approach from these variable sets. The selected models were projected in the present and 2 periods in the past, mid-Holocene and Last Glacial Maximum (LGM), to evaluate whether the connectivity of species distribution changed across potential barriers in different time periods. Finally, we constructed a "consensus model" for each time scenario between the final projections made for each record set by calculating the average of all models (Supplementary Data SD3).

Ecological niche divergence.

The regional groups identified as putative taxonomic entities (Fig. 1) based on morphological and/or genetic data were compared in geographic and environmental space. For the geographic space, we used 3 analyses. First, we performed a Pearson correlation analysis using the R package "raster" (Hijmans et al. 2019) to determine whether there is an association between the best-supported models. Second, we performed an overlap analysis using the R package "ENMeval" (Muscarella et al. 2014) based on Schoener's *D* index to compare the suitable areas predicted with each model. We used 5 categories to determine the level of overlap following Rödder and Engler (2011): no or very limited overlap (0 to 0.2); low (0.21 to 0.4); moderate (0.41 to 0.6); high (0.61 to 0.8); and very high overlap (0.81 to 1). We also assumed this categorization for the correlation values. Finally, we graphically compared predictions obtained between each pair of suitability maps by subtracting one map prediction from the other.

To assess the environmental space occupied by each putative taxonomic entity and their climatic niche segregation, we performed a principal component analysis (PCA) of the environmental variables associated with each record (Nascimento et al. 2020). All environmental variables were standardized prior to analyses. In addition, we built density profile plots to compare the density distribution of each group related to each variable with the R package "sm" (Bowman and Azzalini 2018). These analyses could help to assess whether differences observed in the niche models reflect differences in the underlying distributions, or alternatively are random (Bowman and Azzalini 1997). In all analyses, we only compared groups that do not share records (e.g., *L. tigrinus* morphological and N. Andean tigrina were not compared).

Results

Ecological divergence among tigrina geographic units.

The models generated for each geographic unit (Supplementary Data SD1–SD3). Comparisons between highland groups showed a high–moderate correlation and moderate overlap (Table 1). The C. Am. tigrina and N. Andean tigrina presented higher suitability across almost the entire Andean region and Central America, except in the eastern region of the southern Andes where S. Andean tigrina presented higher suitability (Supplementary Data SD1). Comparisons of NE tigrina and NE tigrina + Amaz showed limited correlation and moderate–low overlap with the Andean groups, *L. tigrinus* (m), and C. Am. tigrina (Table 1). The GSstrict and GSAmaz models presented low accuracy (were overfitted and did not predict areas with location points). Therefore, only their density curves results were compared with the other taxonomic groups. In the paired model (i.e., model subtraction) analyses, we observed that NE tigrina models presented higher habitat suitability in lowlands such as Caatinga, Llanos, and Panama center than any other group (Supplementary Data SD1). When comparing the highland groups and *L. tigrinus* (m) with *L. guttulus*, they showed high–moderate correlation and overlap (Table 1). The main differences between the predictions of these groups are stronger predictions of *L. guttulus* models in the Atlantic Forest, and of the C. Am. and Andean tigrina models in the Andean region (Supplementary Data SD1). When exploring the environmental space occupied by the geographic units, we found that N. Andean and C. Am. tigrinas exhibit a high overlap to each other but are mostly differentiated from other groups, inhabiting areas with a high climatic-moisture index (Fig. 2). On the other hand, S. Andean tigrina show broad overlap with both *L. guttulus* and moderate overlap with the N. Andean group. *L. guttulus* occurs in areas with marked precipitation seasonality and continentality, while NE tigrina inhabits areas affected by multiple climatic parameters (Fig. 2). Interestingly, the environmental space occupied by the "Amaz" and "Gstrict" groups largely overlap with NE tigrina, with "Gstrict" also showing some overlap with the N. Andean unit (Fig. 2).

Table 1. Geographical correlation and overlap analysis between groups proposed within the *Leopardus tigrinus* complex. The upper diagonal shows the Pearson correlation value between each pair of groups. The lower diagonal shows Schoener's *D* overlap. "NA" indicates comparisons that were not performed due to shared records between the groups in order to avoid bias (see Materials and methods).

Group	*L. tigrinus* (m)	C. Am. Tigrina	N. Andean tigrina	S. Andean tigrina	NE tigrina	GS Amaz	Amaz	NE tigrina + Amaz	*L. guttulus*
L. tigrinus (m)		NA	NA	NA	0.14	NA	-0.40	0.04	0.60
C. Am. tigrina	NA		0.72	0.48	0.33	−0.27	−0.30	0.27	0.81
N. Andean tigrina	NA	0.52		0.46	0.16	−0.36	−0.53	0.03	0.82
S. Andean tigrina	NA	0.47	0.55		0.09	−0.32	−0.32	0.07	0.51
NE tigrina	0.55	0.36	0.60	0.47		0.31	−0.09	NA	0.21
GS strict	NA	NA	NA	NA	NA	NA	NA	NA	NA
GS Amaz	NA	0.25	0.56	0.44	0.74		NA	NA	NA
Amaz	0.45	0.21	0.46	0.40	0.66	NA		NA	NA
NE tigrina + Amaz	0.53	0.34	0.57	0.46	NA	NA	NA		NA
L. guttulus	0.70	0.60	0.77	0.62	0.55	NA	NA	NA	

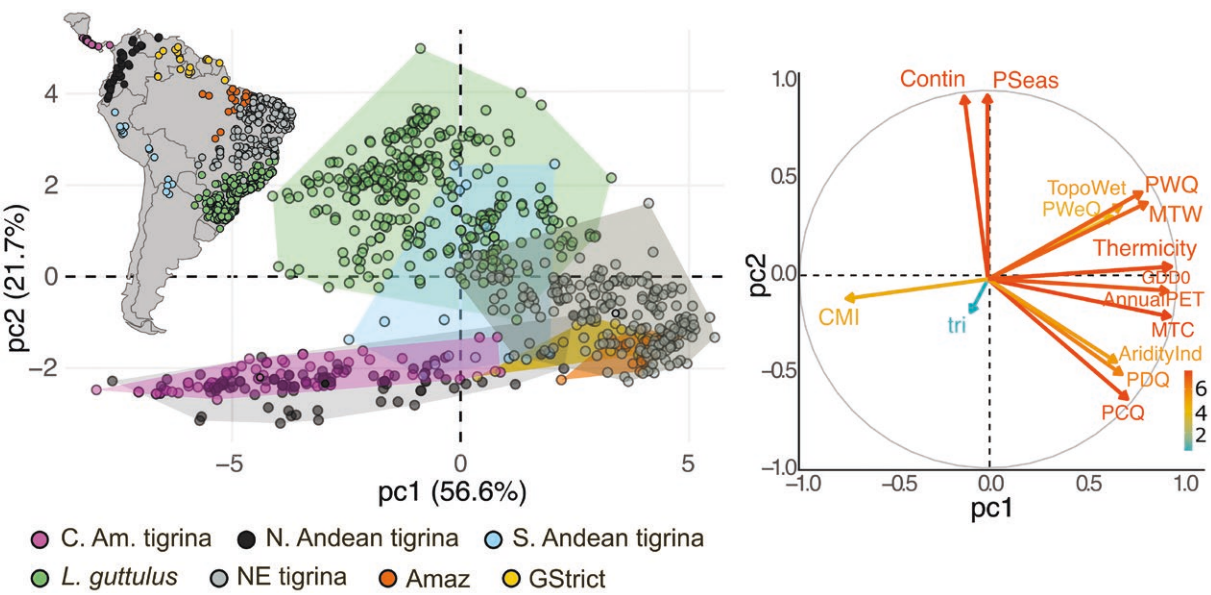

Fig. 2. Environmental variables associated with *Leopardus tigrinus* complex groups. Left: scatterplot of first and second principal components of the 16 environmental parameters clustered by geographic units comprising the *L. tigrinus* complex. The inset map shows the distribution of records for each group. Right: loading plot of the 16 environmental parameters. The colored scale bar represents the correlation of each parameter to the first principal component (see Supplementary Data SD2 for identification of the assessed variables).

Similarly, comparisons using density curves between the species proposed by Nascimento and Feijó (2017) demonstrated that populations from Andes (*L. tigrinus* (m)) and NE tigrina are ecologically divergent, with opposite optimal ranges for all variables, except for potential evapotranspiration seasonality (Supplementary Data SD1). On the other hand, curves showed similar optimal ranges for potential evapotranspiration in the wettest quarter and topographic wetness index for NE tigrina and *L. guttulus*. Overall, these 3 groups presented a gradient pattern for the other variables, with each group finding its optimal range at different values (all comparisons among them were statistically significant, $P < 0.05$; Fig. 3; Supplementary Data SD1). In agreement with the PCA, density curves revealed that C. Am. and N. Andean tigrinas are more similar to each other than to the S. Andean unit. Density curves of NE tigrina were usually closer to the range of S. Andean tigrina and quite different from those of C. Am. and N. Andean tigrina. When comparing these groups with *L. guttulus*, the optimal range of *L. guttulus* for several variables was between the optimal range of C. Am./N. Andean and S. Andean units. Finally, density kernel analysis for the exploratory scenarios of the Guiana Shield showed high overlap between them, yielding density curves that were remarkably close to those from the NE tigrina (Fig. 3; Supplementary Data SD1).

Potential barriers across the overall distribution of the *L. tigrinus* complex.

For all data sets, results regarding potential barriers to connectivity were very consistent across the 3 assessed time periods, i.e., despite inferred changes in the predicted distribution, our inferences of intervening unsuitable habitats were maintained. The most inclusive models for the *L. tigrinus* complex as a whole (sensu Johnson et al. 1999) indicated continuity across the highlands from Costa Rica to the Andean region of Colombia, without a barrier in the Panama center (Supplementary Data SD1). The predicted distribution in the Andes was also continuous, without a barrier between Ecuador and Peru (in the Huancabamba depression or at any other site). The Guiana Shield presented small patches of potential distribution for the complex without fully connecting with either the Andean region or the Caatinga and Cerrado biomes in Brazil. On the other

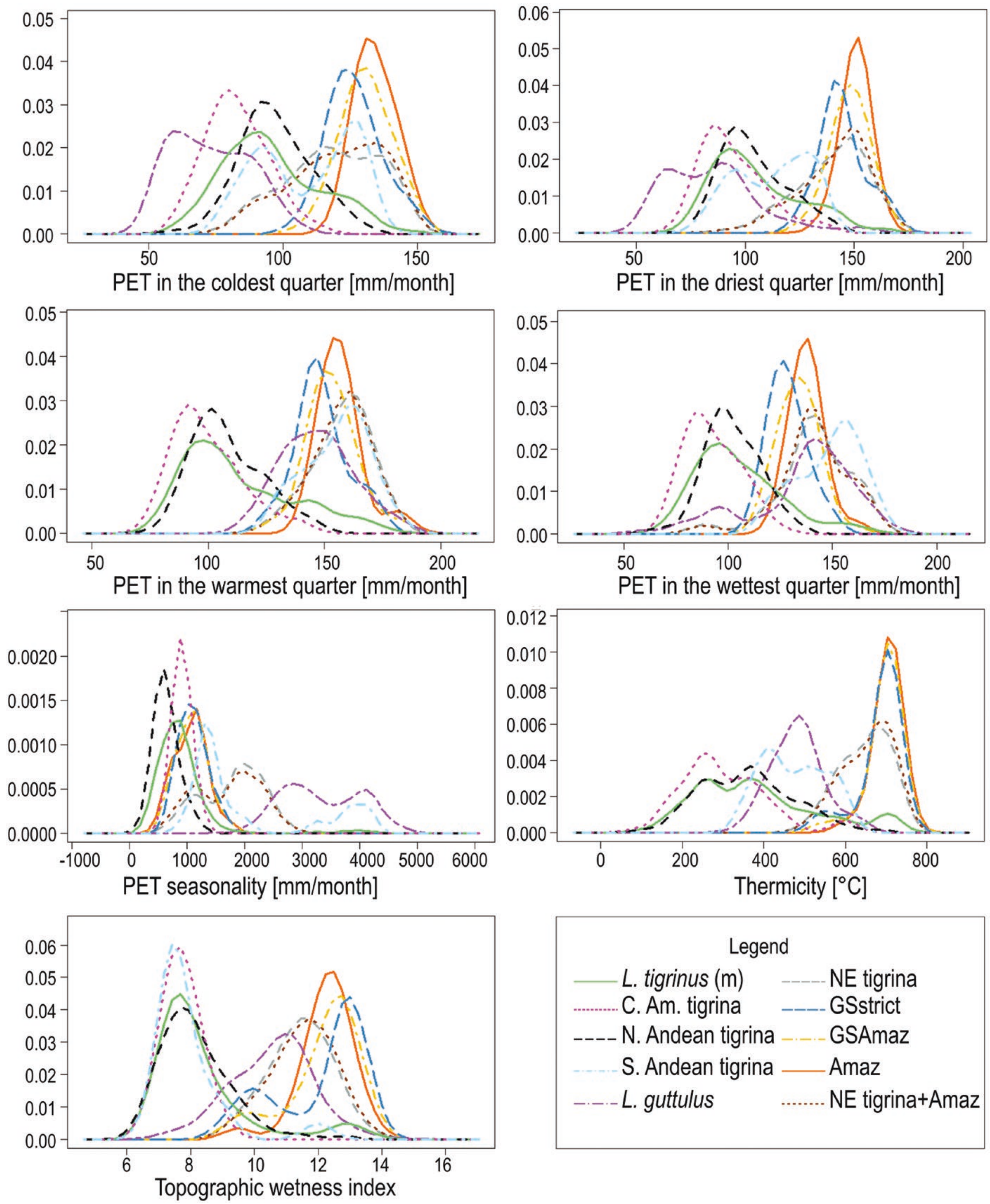

Fig. 3. Density kernel analysis for geographic units comprising the *Leopardus tigrinus* complex for the most important environmental variables according to habitat suitability models. The y axis corresponds to record density and x axis to the range of each variable (see Supplementary Data SD1 for all environmental variables).

hand, most of the Amazon region and the Llanos were inferred to be unsuitable habitats for the complex in the 3 time periods, and thus identified as potential historical barriers to connectivity among its units (Supplementary Data SD1). An identical result was observed with the *L. tigrinus* (m) models (Supplementary Data SD1). The models constructed for the *L. tigrinus* complex sensu Kitchener et al. (2017) also yielded similar results, but identified the northwestern region of the Llanos as suitable habitat, suggesting a possible historical connectivity route between the north–northwestern portion of the continent and the Andean region throughout the Cordillera de la Costa, in Venezuela (Fig. 4b; Supplementary Data SD1).

When we assessed models reconstructed for regional tigrina units separately, we also observed consistent results, and could dissect inferences on each barrier more precisely since only adjacent populations were considered. For example, predictions based on the C. Am. and N. Andean tigrina units were very similar to each other and suggested the existence of suitable habitat exclusively in highland areas, with a gap (i.e., historical barrier) in the Panama center (Fig. 3a; Supplementary Data SD1). In the case of the Huancabamba depression, the predictions of both N. and S. Andean units reconstructed a distribution restricted to highland areas but did not indicate a discontinuity in the area, as they identified small patches connecting the 2 regions (Fig. 3b; Supplementary Data SD1).

The most consistent barriers, which were identified with inclusive (complex-wide) as well as regional models, were the Amazon and the Llanos. Both barriers were clearly supported by the models reconstructed from the 2 Andean groups. The Guiana Shield models presented low accuracy (i.e., were overfitted and did not predict present areas with actual location points; Supplementary Data SD3) and we thus considered them insufficient to reliably infer historical barriers. Finally, the NE tigrina models predicted small patches of suitable habitat in the eastern border of the Amazon region, but not in its central and western portions, supporting the inference that they act as a strong barrier between the northwestern and northeastern tigrina units (Fig. 3c; Supplementary Data SD1).

Discussion

Our analyses supported some of our initial predictions and provided evidence that some geographic units within the *L. tigrinus* complex seem to be ecologically divergent, while others are ecologically similar. Our ecological models allowed us to assess the effects of hypothesized geographic barriers across time, from the LGM to the present, identifying areas of consistently low suitability that may have induced isolation among regional units. These results shed light on the eco-evolutionary history of the *L. tigrinus* complex and contribute to our ability to clarify its recalcitrant taxonomy.

The recognition of *L. guttulus* as a distinct species and its exclusion from the *L. tigrinus* model caused a notable change in the ecological niche and predicted geographic distribution of the pruned complex. This was especially reflected in the Atlantic Forest, where *L. guttulus* occurs, predicted only in models for the *L. tigrinus* complex sensu Johnson et al. (1999; Fig. 3; Supplementary Data SD1). Environmental conditions of the Atlantic Forest and their differences from other forested areas may explain the significant changes caused by the inclusion/exclusion of *L. guttulus* records in the habitat suitability maps generated for the entire complex. Another possible explanation for the change between the Johnson-based and Kitchener-based model predictions may be related to the large number of records for NE tigrina and its very distinct environmental

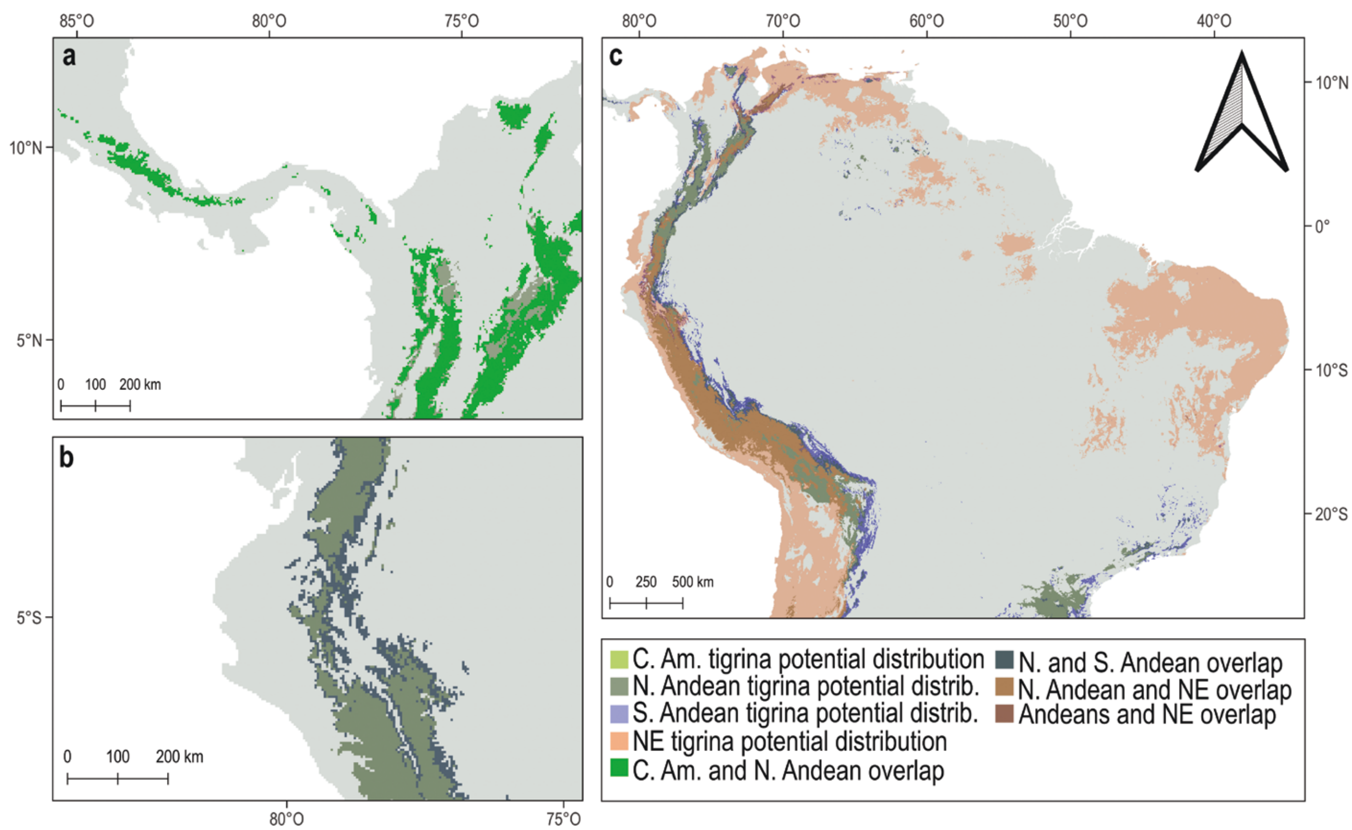

Fig. 4. Overlap of *Leopardus tigrinus* complex distributions to evaluate geographic barriers: (a) Panama center, evaluated with C. Am. tigrina and N. Andean tigrina distributions; (b) Huancabamba depression, evaluated with N. and S. Andean tigrina distributions; and (c) Llanos and Amazon, evaluated with Andean tigrinas and NE tigrina distributions.

requirements (Fig. 2). The sample size disparity between NE tigrina and the Andean groups may have influenced the model to predict suitable areas that are more similar to NE tigrina requirements than to *L. tigrinus* (m) in the *L. tigrinus* complex sensu Kitchener et al. (2017) models. Interestingly, there were some differences between the *L. tigrinus* (m) and *L. guttulus* models that could be related to the greater seasonality of southern areas in the Atlantic Forest. Seasonality has been identified as an important factor related to reproductive characteristics in carnivores such as gestation length, weaning age, and age at sexual maturity (Tökölyi et al. 2014). This adaptation to seasonal environments is a marked characteristic of *L. guttulus* if compared with the other groups, which is apparent in our analyses (Fig. 2; Supplementary Data SD1). At the same time, *L. guttulus* showed some similarities with NE tigrina—an unexpected result because these groups occupy very distinct habitats. However, because these groups have adjacent distributions, and only bioclimatic variables were assessed in this study, it is possible that there exist intermediate areas with environmental conditions that are favorable for both species. This possibility is visible in our environmental space analyses; for example, for several variables the optimal range for *L. guttulus* is followed by the optimal range for NE tigrina (Supplementary Data SD1). Another possible explanation is that NE tigrina may be expanding its distribution into fragmented areas of the Atlantic Forest that were once unsuitable for the species and/or occupied by *L. guttulus*. Future studies with land cover change should enable further analysis of this hypothesis.

The models of the Andean and C. Am. tigrinas showed the role of lowland forests (Amazon and Panama center) as historical barriers for populations specialized for montane environmental conditions. According to models, the distribution of the Andean groups are limited within the high temperatures experienced in lowland forests in the coldest and warmest months. Furthermore, a niche conservatism process between the C. Am. and N. Andean units was identified (i.e., high overlap in environmental and geographic space), which is commonly seen in sister taxa generated by allopatric processes (Peterson et al. 1999; Alvarado-Serrano and Knowles 2014). This pattern is consistent with recent genetic results indicating a close relationship between these groups (Lescroart et al. 2023). Their current allopatry is supported by the inference that the Panama center has acted as a barrier between them, even in the LGM. Although the more precise regional models indicated such historical discontinuity, it may be noted that the more inclusive *L. tigrinus* (m) model indicated potential connectivity between the Talamanca Mountain range and the Colombian Andean region in the LGM (Supplementary Data SD1). Distributional changes experienced by highland forests in the LGM also suggest a possible connectivity between both groups during these periods (Barrantes 2009; Weir 2009). For montane forests in the Andean region, it is proposed that during the LGM the forests prevailed but were displaced downslope 1,000 to 1,500 m below their present range (Ramírez-Barahona and Eguiarte 2013). This downslope migration was also reported for the montane forest in Costa Rica (Islebe et al. 1995; Islebe and Hooghiemstra 1997), supporting the possibility of gene flow between C. Am. and N. Andean tigrina during the LGM, and/or during a previous glacial maximum. It is also possible that these 2 groups still comprise a single species that, despite the current lack of connectivity between them, have not differentiated enough due to the similarities of their habitats and/or the short time since interruption of gene flow between them.

Despite differences in the environmental requirements between the North and South Andean groups, the Huancabamba depression was never recovered as unsuitable for these groups. These results are consistent with other studies that indicated that, despite changes in elevation in this area, there was no conclusive evidence for its role in limiting dispersal of high-elevation species of small mammals (volant and nonvolant) and birds (Pacheco and Patterson 1992; Vivar et al. 1997; Lunde and Pacheco 2003). Therefore, it is possible that there exists some level of gene flow between these populations that was not recovered by the mitochondrial markers used by Diana Buitrago-Torres (Pontificia Universidade Catolica de Rio Grande do Sul, Porto Alegre, RS, Brazil, personal communication, June 2023). It is also possible that the 2 Andean groups may be reproductively isolated due to their distinct environmental preferences even in the absence of a barrier of unsuitable habitat. This possibility may result from the latitudinal changes in environmental variables across the Andean region. In that sense, the groups identified within *L. tigrinus* (m) may have a specialization for distinct local environmental conditions (Fig. 2; Supplementary Data SD1).

Despite their limitations, the Guiana Shield models suggested that environmental conditions of this region may overlap with parts of the Andes as well as NE Brazil (Supplementary Data SD1). The Guiana Shield includes vegetation cover that varies from high forest with regular canopy to savanna patches (Gond et al. 2011). Indeed, the tigrina records in this region are associated with habitats such as savanna, grasslands, and forests with disrupted canopy. Therefore, although the *L. tigrinus* (m) models predicted the highlands and high forest with regular canopy in the Guiana Shield as potential distribution for the species, the available records of Guiana Shield tigrinas are located in different habitats, highlighting the complexity of this modeling problem. Interestingly, when past periods were assessed, the inclusive *L. tigrinus* (m) models predicted an expansion of potential distribution along the Amazon region, although some portions remained unsuitable (Supplementary Data SD1). During the LGM, when the typical lowland forests of Amazonia retracted into refugia, it has been inferred that other forest species with preferences for a cold and wet climate expanded in these areas (Arruda et al. 2018), which were likely not suitable for tigrinas. Thus, considering the identified historical unsuitability of the Amazon and Llanos regions, we infer that if there was connectivity between the Andean and Guiana Shield populations, it occurred more deeply in the past.

Interestingly, the areas where Guiana Shield tigrinas do occur have similar environmental conditions to those found in the Cerrado and Caatinga biomes (de Oliveira et al. 2022) and were predicted by the NE tigrina models. These patches of open vegetation in the Guiana Shield could be intermittently connected (through Amazon savanna patches) with the Caatinga and Cerrado biomes where NE tigrina occurs (Sarmiento 1984), suggesting that there could exist some level of historical gene flow between Guiana Shield and NE tigrinas. These savanna patches were recovered by NE tigrina models for the mid-Holocene and present time periods, identifying suitable areas between the northeastern region of Brazil and the Guiana Shield (Supplementary Data SD1), similar to what was found by de Oliveira et al. (2022). On the other hand, it is noteworthy that no model identified a complete connection between these areas and that there were models in which a similarly patchy corridor was found between the Guiana Shield and the Andes (Supplementary Data SD1). Moreover, the Amazon River may have acted as a major barrier impeding contact between the Guianan and NE tigrina populations, as has been shown in several groups of mammals (e.g., Feijó and Cordeiro-Estrela 2016). These open questions, affected by the lack of precision in our Guiana Shield models, highlight the importance of obtaining more records from this region to better analyze its historical connectivity to adjacent areas.

An intriguing result was that the NE tigrina models also predicted high suitability in the eastern region of the Llanos, which could suggest connectivity between the Llanos and the Andean region in Venezuela. However, this result was not recovered in the regional models for adjacent units, and the Llanos have been documented to be unsuitable and/or unoccupied by the *L. tigrinus* complex (sensu Kitchener et al. 2017) by other authors (de Oliveira 2004; Payán-Garrido and González-Maya 2011; Payan and de Oliveira 2016; de Oliveira et al. 2022). Moreover, models for the global complex or particular groups always indicated the Llanos as a barrier in all 3 assessed time periods. This region has a marked seasonality with dry versus rainy periods, with the latter implying the flooding of a large area between July and September (Hamilton et al. 2004), likely making this area unsuitable for survival of the species. Finally, the core Amazon Forest was also identified as a barrier for the NE tigrina, as it is a very moist forest and this tigrina unit prefers drier climates, such as those found in the Caatinga and Cerrado. In addition, contrary to other groups that experienced an expansion in their distribution in the LGM, NE tigrina models showed a small retraction in their distribution in this period (Supplementary Data SD1), possibly due to the inferred restriction of dry vegetation to small areas of ecotone (Werneck et al. 2011).

This work supports ecological differentiation among most of the geographic units that comprise the *L. tigrinus* complex. Our results indicate that almost all groups demonstrate marked local adaptation to their respective environmental conditions. The only exception seems to be the C. Am. and N. Andean tigrina, which had high niche similarity but seem to be currently disconnected due to the unsuitable lowland areas in the center of Panama. The Amazon region and the Llanos are clear barriers for dispersal of the Andean groups, likely preventing their connectivity with eastern South America. On the other hand, we did not identify any physical barrier that impedes the contact between northern and southern Andean populations, with more records being required to further address this hypothesis. In addition, more records are necessary from the Guiana Shield to construct more robust niche models and to better determine their similarities with Andean groups and/or NE tigrina. We also identified ecological niche differences between *L. guttulus* and the rest of the *L. tigrinus* complex, supporting its recognition as a distinct species from an ecological perspective (in addition to the genetic and morphological data that have been reported previously). Overall, our results support the view that evolutionary differences and similarities among regional groups within the *L. tigrinus* complex are probably a product of vegetation distributional dynamics during glacial and interglacial periods, which has intermittently promoted or inhibited gene flow among populations. From a practical perspective, these findings demonstrate that several *L. tigrinus* geographic units are adapted to distinct ecological conditions and have been demographically disconnected due to historical barriers, which contributes to the ongoing effort to clarify taxonomy of this species complex. Furthermore, demonstrating the distinctness of these units is relevant in the context of conservation assessment, since each should have its population status evaluated separately. In addition, each unit has distinct ecological features and is likely to face its own combination of threats, highlighting the need to perform specific conservation plans on behalf of each.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Figures of barriers, methodology, and model results.

Supplementary Data SD2.—Tables of records, variables used, and model results.

Supplementary Data SD3.—Complementary text about the modeling process.

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Author contributions

AB-S, CCS, and EE designed the research. AB-S, CCS, LAF-R, AF, JDR-F, EB-M, MSM, SRB, CS-L, RZ, MJO, FON, PHDM, GBF, SS, and TGO provided the records. AB-S, AF, and CCS analyzed the data. EE supervised the project, with critical input from TGO. AB-S and CCS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

None declared.

Data availability

Sample locations are provided in the Supplementary Data SD2.

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