

Wild canids and ecological traps, facing deforestation and climate change in the Amazon Rainforest

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Abstract

Ecological traps occur when species choose to settle in lower quality habitats, even if this reduces their survival or productivity. This normally occurs in situations of drastic environmental changes, resulting, for example, from anthropogenic pressures. In the medium and long term, this could mean the extinction of the species. We investigated the dynamics of occurrence and distribution of three canid species (*Atelocynus microtis*, *Cerdocyon thous*, and *Speotus venaticus*) related to human threats imposed on their habitats in the Amazon Rainforest. We analyzed the possible environmental thresholds for the occurrence of these species and confronted them with the future projections of climatic niches for each one. All three species will be negatively affected by climate change in the future, with losses of up to 91% of the suitable area of occurrence in the Brazilian Amazon. The occurrence of *C. thous* and *S. venaticus* has been positively influenced by anthropogenic open areas to the detriment of native environments, suggesting that these species are being attracted by ecological traps, which may put them at risk in the future in the Amazon Region. The *A. microtis* species is the most dependent on forest habitats, and thus the most significant threat would be forest loss. Using the canid species as a model, we could deeply investigate these ecological effects that can affect a large part of the Amazonian fauna in the current scenario. Considering the high degree of environmental degradation and deforestation in the Amazon Rainforest, the theory of ecological traps must be discussed at the same level that habitat loss is considered a decisive criterion of threat to biodiversity.

INTRODUCTION

The Amazon is home to thousands of species of terrestrial vertebrates, which interact among them and with the environment in a unique way. These interactions define the ecological niches of these species and how they are distributed in time and space (Hirzel and Le Lay, 2008). Deforestation, climate change, and other anthropogenic pressures have caused drastic changes in the structure of native habitats in the Amazon in the last 40 years (PRODES, 2021), which have consequences on the interactions of species with their environment (Coelho et al., 2014; Mendes-Oliveira et al., 2017; Sales et al., 2019). Deforestation and climate change already act as associated factors for the transformation of natural habitats into degraded areas of the Amazon, where the drought-deforestation feedback will leave the climate in these areas warmer and drier (Staal et al., 2020).

After nine years of reduction in deforestation, the Brazilian Amazon has experienced an increase in degradation. During the last two years (2019-2021), about 21,000 km² of the Brazilian Amazon Forest were

deforested (PRODES-Terrabrasilis/INPE, 2021). About 60% of this deforestation was concentrated in the States of Pará and Mato Grosso, which border the *Cerrado* Biome, also is called the Brazilian savannah. Significant forest losses and climatic variations are projected for this region in the coming years, increasing the transition zone area between forests and savannah (Lyra et al., 2016). These changes can negatively affect specialist forest species, and in turn favor the use of the degraded landscape by species able to use savannah habitats (Sales et al., 2020). Nevertheless, degraded landscapes can lead species into ecological traps, where modified environments may lead to false clues to favorable habitats, making it impossible to accurately assess the suitability value for species in these habitats (Hale and Swearer, 2016).

Ecological traps occur when species settle in lower quality habitats, even if this reduces their productivity or survival (Hale and Swearer, 2016). This situation has been happening mainly due to the rapid environmental changes caused by anthropogenic actions, which generate new conditions in the habitats, different from the original ones, but which may be somehow related to the evolutionary history of the species (Robertson et al., 2013). In this way, species capture signals, which are not indicative of habitat quality, and mistakenly establish themselves in unfavorable locations for their survival in the medium and long term (Robertson and Hutto, 2006). In this paper, we raise the possibility that this process occurs with some species in the Amazon region, driven by the intense dynamics of land use and rapid environmental changes caused by degradation, deforestation, and climate change. In this way, understanding the factors that determine the occupation of high-quality sites by species can help to mitigate the harmful effects of choosing poorly adapted habitats (Robertson and Hutto, 2006; Gilroy and William, 2007).

Most neotropical vertebrates live in natural environments already altered at some level, directly or indirectly, by human activities. The response of the fauna to significant changes in their native habitats can vary according to their ecological demands and niche differences (Sih et al., 2011; Hagen et al., 2012). Also, a species' fitness is closely related to its evolutionary history, shaped by environmental factors that influenced the ecological preferences and demands of the species over an evolutionary time (Harper et al., 1961). Although the main question is how recent significant changes in natural environments are altering patterns shaped during evolution and whether species' responses can mislead them into ecological traps and thereby reduce their fitness. In this sense, it is necessary to have a baseline knowledge about species' original distribution, habitat preferences, and what determines their occurrences.

Members of the Canidae family have undergone morphological and behavioral changes due to environmental changes and degradation of their native habitats (Yom-Tov et al., 2007; Figueirido et al., 2015; De Moura Bubadué et al., 2016). Canids appeared around 40.Ma in North America (Wang et al., 2007). They diversified throughout the Pleistocene and occupied different niches and geographical locations (Berta, 1987; Tchaicka et al., 2016). The emergence of a wide variety of morphologies and diets over a relatively short evolutionary period (Perini et al., 2010; Nyakatura and Bininda-Emonds, 2012; Figueirido et al., 2015), make canids a very interesting group for studies of ecological plasticity. For instance, small variations in masticatory or locomotor systems have caused large differences in their adaptive capacity (Figueirido et al., 2015; Penrose, 2019). Currently, 10 species of canids occur in South America, with high morphological and ecological diversity among them (Perini et al., 2010).

Three species of canids are represented in the Amazon: *Atelocynus microtis* (Sclater, 1883) (short-eared dog), *Speothos venaticus*(Lund, 1842), (bush dog), and *Cerdocyon thous*(Linnaeus,1766) (crab-eating fox) (Appendix, Figure 1). These are small to medium-sized (from 4 to 11 Kg) canids with a broad and partly sympatric distribution in the Amazon region. The occurrence and distribution of canids have been associated with environmental characteristics and interspecific competition (De Oliveira and Pereira, 2014; De Moura Bubadué et al., 2016; Rocha et al., 2020). Rocha et al. (2020) showed a strong connection of *A. microtis* to forest habitats, and how it has been negatively affected by deforestation in the Amazon.

Competition between canid species that occur in sympatry is commonly reported in the literature (Cypher, 1993; Johnson et al., 1996; Di Bitetti et al., 2009). Under environmentally favorable conditions, sympatry species can coexist by partitioning spatial or temporal niches (Bueno and Mota-Junior, 2004; Di Bitetti et al., 2009). Usually, the dominant species with greater body mass consume the larger prey species, while the

sub-dominant species consume foods with lower nutritional value (Penrose, 2019). There are several reports of sympatry between *A. microtis* and *S. venaticus* (Michalski, 2010; Santos and Mendes-Oliveira, 2012), and between *C. thous* and *S. venaticus* (Da Silva et al., 2013; Vieira and Oliveira, 2020); however, to our knowledge only one occurrence of sympatry has been reported between *A. microtis* and *C. thous* (Carvalho et al., 2014).

In this paper, we investigate the dynamics of occurrence and distribution of *A. microtis*, *C. thous*, and *S. venaticus* related to anthropogenic threats imposed on their habitats in the Amazon Forest. We investigate the possible environmental thresholds for the occurrence of the three species and how their distribution might be influenced by climate change and deforestation, and whether these factors can lead these species to fall into ecological traps in the Amazon Rainforest. We also model the future occurrence and distribution of those species, considering a pessimistic climate change scenario. Our hypothesis is that all species are influenced by different environmental variables, and changes in these variables can lead species to ecological traps. We also believe that these environmental variables explain different patterns of occurrences and niche distributions now and in the future.

METHODS

The target species

Atelocynus microtis (Appendix-Figure 1, A and B) is the only endemic species in the Amazon Biome, but with a wide distribution in the region, extending from Ecuador to Brazil (Leite-Pitman and Willians, 2011). It is considered rare, based on a low number of records by most studies during the last 30 years (Peres, 1991; Koester et al., 2008; Michalski, 2010; Blake et al., 2012; Ayure and González-Maya, 2014). However, this species seems to have been more frequently recorded previously (Grimwood, 1968). Possible reasons for its apparent reduced population size are infection by diseases acquired through contact with domestic dogs and the loss of habitat (Leite-Pitman and Willians, 2011). *Atelocynus microtis* is a mesocarnivorous canid with a generalist carnivore diet but also including fruit (Leite-Pitman and Williams, 2004; Blake et al., 2012; Penrose, 2019). It is solitary (Peres, 1991), usually with a diurnal activity (Leite-Pitman and Williams, 2004; Blake et al., 2012). Individuals of this species does not seem to tolerate disturbed habitats and prefer continuous primary lowland and upland forests (Michalski, 2010; Leite-Pitman and Willians, 2011; Rocha et al., 2020). This species is classified as "Near Threatened" in the IUCN Red List of Threatened Species (Leite-Pitman and Willians, 2011).

Cerdocyon thous (Appendix-Figure 1, C and D) has the smallest distribution area in the Amazon Biome of the three species. However, it has a wide distribution in the rest of South America. It is common in the *Pantanal*, Atlantic Forest, *Cerrado*, Amazon, and *Caatinga* biomes, and frequently recorded in forest edges (Brady, 1979; Courtenay and Maffei, 2004). Individuals of this species have a twilight and nocturnal habits, are solitary or lives in small groups (Macdonald and Courtenay, 1996). Their diet is considered omnivorous, generalist, and opportunistic, feeding on invertebrates, small vertebrates, and even carrion, but they also frequently feed on fruits (Bisbal and Ojasti, 1980; Macdonald and Courtenay, 1996). Of the three species, *C. thous* can be considered the one that least depends on the forest, and being quite adapted to open environments, including human-made areas (Faria-Corrêa et al., 2009; Ferraz et al., 2010). This species is classified as "Least Concern" in the IUCN Red List (Lucherini, 2015).

Speothos venaticus (Appendix-Figure 1, E and F) is the canid with the broadest distribution in the Amazon, although it is not common where it occurs (DeMatteo and Loiselle, 2008; Guimarães et al., 2015; De Oliveira et al., 2018). In Brazil, this animal occurs in the Amazon, *Pantanal*, Atlantic Forest, *Cerrado* and *Caatinga* biomes, especially in humid forests and preserved riparian forests. Individuals of this species have a strong relationship with forest environments (DeMatteo and Loiselle, 2008; Michalski, 2010). However, it has also been recorded in open areas of the *Cerrado* (Silveira et al., 1998; Lima et al., 2015), and altered and fragmented environments in the Amazon (DeMatteo and Loiselle, 2008). Recently, its suitability for native environments in the Cerrado was confirmed (Lima et al., 2015). *Speothos venaticus* can be considered a hypercarnivore, feeding on small vertebrates and larger mammals such as pacas, agoutis, and even capybaras

(Beisiegel and Ades, 2002; Zuercher et al., 2005). They are social animals, which may have a cooperative hunting system, but lone individuals are also frequently observed (Beisiegel and Ades, 2002; DeMatteo et al., 2011). This species is classified as “Near Threatened” in the IUCN Red List (DeMatteo et al., 2011). Its greatest threat appears to be habitat degradation.

Species occurrence data

The study area encompasses the whole Amazon Biome, also known as the Amazon Rainforest, which constitutes the largest tropical forest in the world, covering nine countries in South America: Bolivia, Brazil, Colombia, Ecuador, French Guyana, Guyana, Peru, Suriname and Venezuela (IBGE, 2004; Junk et al., 2011). Despite that our discussion is focused on the Amazon Biome, our species distribution database was built considering the whole South America, so that the potential distribution model covered the entire range of the species studied (Figure 1).

The database of geographic records of the three species was built from literature data and online databases, such as Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>; GBIF Occurrence Download <https://doi.org/10.15468/dl.dyy7qk>) and Species Link (<http://splink.cria.org.br/>) (Figure 1, Supplemental Material-Table S1). Especially for *A. microtis*, we used most of the records from Rocha et al. (2020) publication. In addition, we used data from unprecedented inventories of camera traps and Linear Transection census, carried out by the team of the Laboratory of Ecology and Zoology of Vertebrates of the Federal University of Pará (Brazil), between 2000 and 2019 (Appendix-Figure 1 and Supplemental Material-Table S1).

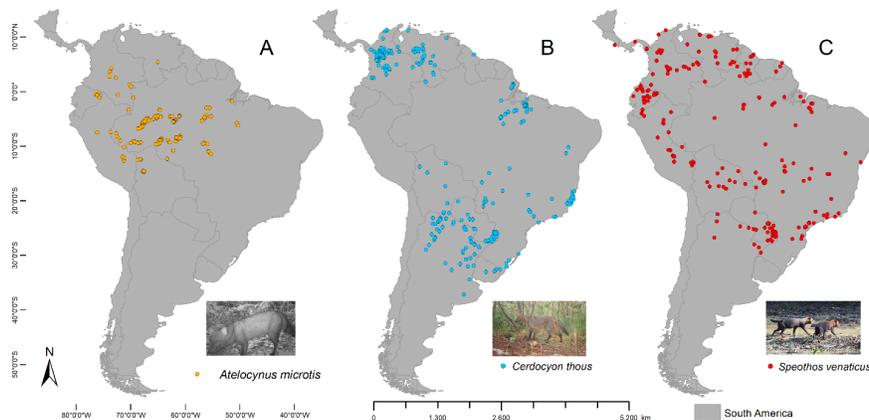


Figure 1. Distribution of occurrence records of the three species of Amazonian wild canids in South America. Data obtained through literature, databases, and field inventories. A - *Atelocynus microtis* (short-eared dog); B - *Cerdocyon thous* (crab-eating fox); and C - *Speothos venaticus* (bush dog).

We searched for geographic information on the rare localities and municipalities whose coordinates were unavailable using Google Earth v7.1.2 (<https://www.google.com/earth/>) and online gazetteers (e.g., directory of cities and towns in the world; www.fallingrain.com/world). Using these same resources, we checked all records with coordinates to ensure the best reliability of the occurrences used in this study. Specifically, we evaluated whether each point was minimally consistent with what is already known about each species’ distribution. Some doubts were solved by the researchers who collected the data. In addition, points that did not have precise information on geographic coordinates, or corresponded to questionable places, such as rivers or lakes, were discarded. Also, duplicated coordinates recorded in different databases were discharged. The remaining records (Supplemental Material-Table S1) were used for niche modeling, producing maps of the potential distribution for each species, considering the climatic variables, and analyzing generalized linear models (GLM) based on land use data.

Climatic Variables and Niche Modeling

To generate the distribution predictions for the three canid species, we gathered 19 climatic variables (Hijmans et al., 2005), available for the current, and future projections of the SSP585 climate scenario from global climate models (GCM's: BCC-CSM2-MR; CanESM5; IPSL-CM6A-LR; MIROC-ES2L; and MIROC6), selected by a cluster analysis (Varela et al., 2015) in the WorldClim v2.1 database. We cut all variables to the extent of the South American continent, with a grid resolution of 0.041° at the Equator (~ 4 Km or 2.5 arc-min).

We standardized all variables, so they had their means equal to 0 and their variance equal to 1. Later, we applied a spatialized principal component analysis (PCA) based on a correlation matrix of the variables to produce 19 orthogonal/independent principal components (PCs) to be used as our new environmental variables (De Marco and Nóbrega, 2018). We selected the first six PCs from those, responsible for $\sim 97\%$ of the original raw climatic variance of the predictor variables (Appendix, Table 1). These independent variables allow us to produce more reliable predictions for the species distributions and avoid model overfitting (Jiménez-Valverde et al., 2011).

We partitioned the three species occurrences using a checkerboard pattern (Muscarella et al., 2014; Roberts et al., 2017), with an aggregation factor of two. According to this partitioning pattern, the species occurrences are divided into two subsets geographically structured as a checkerboard table. One of these subsets is used to train the models on a first run, while the other is used to evaluate the models. In a second run, these subsets are inverted, and the subset used to evaluate the models will be used to train the models, and that used to train the models will be used to evaluate the models. We consider the proportion of subsets always 30% of data for testing and 70% for training.

We considered three different modeling methods to produce our models, ranging from statistical methods [i.e., Random Forest (RDF)], machine learning methods [i.e. MaxEnt (MAX) and Support Vector Machines (SVM)]. We trained the models for the three species considering the ecoregions shapefile provided by the World Wildlife Fund website (<https://www.worldwildlife.org/biomes>), restricting the climatic variables to ecoregions with known occurrences for the species. This procedure is very important to delimit the M section of the Biotic-Abiotic-Migration diagram (Soberón and Peterson 2005; Soberón 2007; Barve et al. 2011; Saupe et al. 2012) and improve the model predictions for the focus species.

We made use of pseudo-absences to train the models. Therefore, we restricted their allocation in the geographic space after they were environmentally restricted, considering an environmental space based on a climatic environment (VanDerWal et al. 2009; Lobo and Tognelli 2011).

To evaluate our models, we considered the Jaccard's similarity index proposed by Leroy et al. (2018), which varies from 0 to 1, where around zero values indicate no-better-than-random predictions, while values higher than 0.5 are considered as acceptable predictions. Differently from other metrics commonly used in distribution modelling studies [e.g., area under the curve (Fielding and Bell, 1997) or true skill statistic (Allouche et al., 2006)], the Jaccard index is both prevalence and pseudo-absence independent, yielding less uncertain metrics for the models.

To cut the suitability matrices into presence/absence matrices, we considered the threshold that maximized the Jaccard index. Finally, we used a mean ensemble weighted by the best Jaccard values in each modeling method in order to produce the species final distribution range (Figure 2). We perform the modeling by the package ENMTML (De Andrade et al., 2020) in *software* R (v4.0).

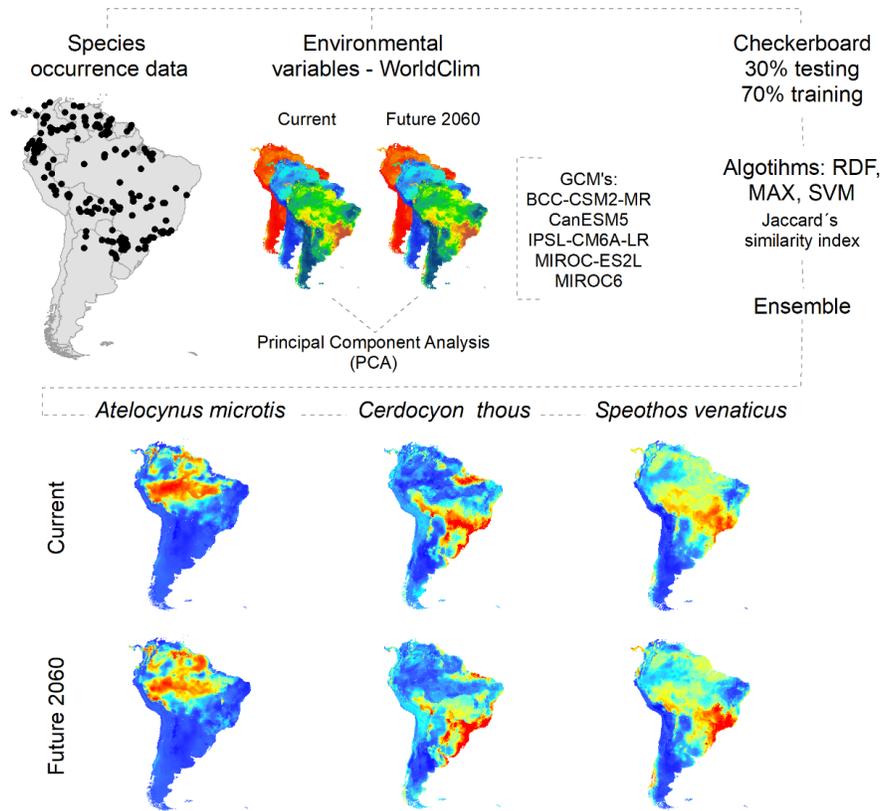


Figure 2. Methodological procedure for obtaining Niche Modeling, using climate variables for the current and future period (2060), configuration and evaluation of ENM available in the ENMTML package.

Environmental factors determining the occurrence of the canids

We only used the records of the three canid species occurring within Brazil to analyze which environmental variables and landscape structures influence each species' occurrence. We limited it to Brazilian points using the Landsat classified image database from MapBiomas. v5.0 collection available just for this country (<https://mapbiomas.org>). In the GeoTiff scenario, this collection informs the annual mapping of land cover and land use in Brazil between the historical period of 1985 to 2019 (MapBiomas, 2021). We listed the coordinates of each occurrence of *A. microtis*, with information on scenarios in the Amazon Biome, from 2002 to 2019, a period that includes all records of occurrences of this species. We did the same thing for *C. thous*, but using data from 1988 to 2016, including the Amazon, *Caatinga*, *Cerrado*, Atlantic Forest, *Pantanal*, and *Pampas* biomes. For *S. venaticus*, we used data from 1900 to 2017, including biomes from the Amazon, *Cerrado*, *Caatinga*, Atlantic Forest, and *Pantanal* (Figure 3).

For each coordinate of occurrence of each species, we delimited a buffer with a radius of 1 km, from which we extracted information on land use. We obtained the pixel values and land-use class codes in each buffer (available at: <https://mapbiomas.org/downloads.codigos>) and transformed these values into categories of percentages. If the buffer areas overlap by more than 20%, the rightmost occurrence point was excluded for this analysis. After eliminating buffers with overlapping criteria, we selected 277 independent records with a minimum distance of 2 km between them. We set 64 records of *A. microtis*, 63 of *C. thous* and 100 of *S. venaticus* (Supplemental Material-Table S2).

About 16 land-use classes were recorded in the occurrence scenarios of the buffers. Some classes with similar landscape effects were grouped into new more significant categories, and others with lower registration frequency than three occurrence points were discarded (Supplemental Material-Table S2). In the end, we

considered five significant land use categories to assess the environmental factors that determine the occurrence of species. They are: (Forest) Percentage of forest cover, which includes all native forest formations of the Amazon; (Water) Percentage of water bodies, including streams, rivers, lakes and non-forest natural wetlands; (Nat_open_areas) Percentage of natural open areas, including savannas, grasslands and rocky outcrops; (Urban_areas) Percentage of urban infrastructure; and (Anthr_open_areas) Percentage of anthropogenic open areas, including pasture, perennial annual crop, agriculture and pasture mosaic (Appendix-Figure 2, Supplemental Material-Table S2).

In addition to the land-use variables, we also extracted the altitude (Alt) and the Enhanced Vegetation Index (EVI). The altitude was extracted from each point of occurrence of the species from the satellite images of Google Earth Pro (version 7.3.1). The Enhanced Vegetation Index (EVI) is an index related to plant complexity and heterogeneity, since it is based on plant cover and the fraction of absorbed photosynthetically active radiation (Gurung et al., 2009). The EVI was extracted from the Earth Explorer platform (available at: <https://earthexplorer.usgs.gov/>). For each year of occurrence of the species, we extract images in the rasters format and calculate the statistical average of the index using the Quantum Gis *software*(v2.8.4).

To avoid data multicollinearity, we used Principal Component Analysis (PCA) to select correlated variables from the first two axes for further explanation of the results (Kassambara, 2017) (Appendix-Figure 2). We used the Kaiser criterion to select the variables by eigenvalues, not including those that were correlated on the same axis (Jackson, 1993). We selected the following predictor variables to be used in Generalized Linear Models (GLM's) analyses: Forest, Water, Nat_open_areas, Urban_areas, and Anthr_open_areas (Figure 3, Supplemental Material-Table S2). We constructed GLM's with binomial distribution and logit linkage function to verify the influence of environmental predictors on the occurrence of the three canids. We initially ran all models with binomial distribution and evaluated the dispersion assumption. In the case of *A. microtis*, which had a dispersion greater than 1, we used quasibinomial correction. To analyze the possible effects of predictor variables on the occurrence of the three species, we built six models considering different combinations of the predictor variables (Appendix-Table 2). We use the *glm* function (Hardin et al. 2007) from the *stats* package (Marschner and Donoghoe, 2018). We evaluated the dispersion of residues to confirm the absence of overdispersion. We then ran the analysis and selected the best model using the table ANOVA criterion, including the null model, and we used the data generated in the GLM's analysis to interpret the size measure of the effects of the predictor variables on the occurrence of species (Figure 3). We considered values for $p < 0.05$ as level of significance.

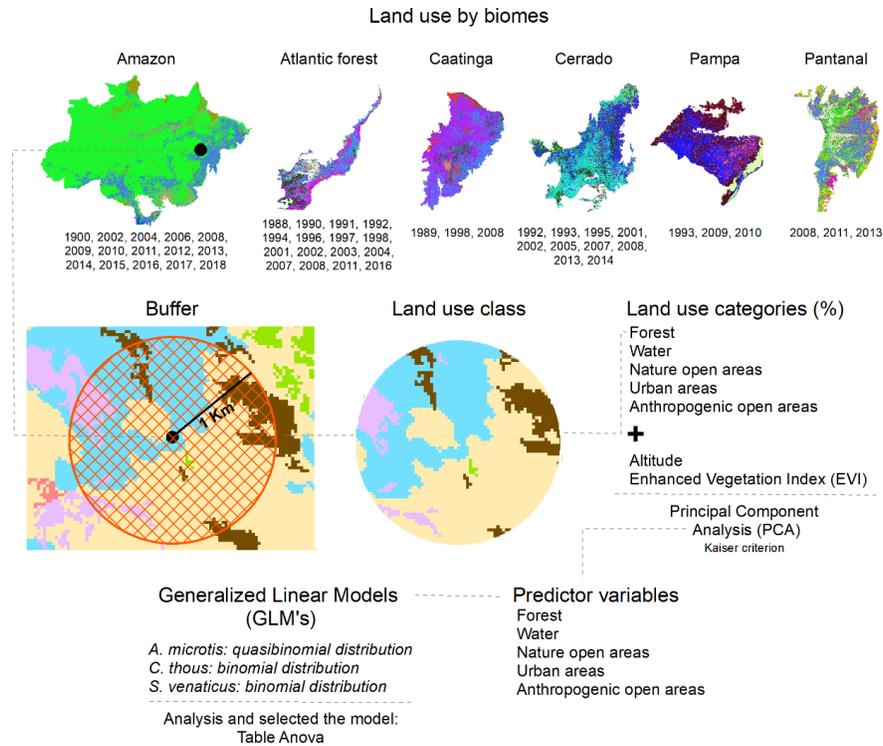


Figure 3. Methodological procedure to obtain the environmental factors that determine the occurrence of *Atelocynus microtis*, *Cercodyon thous* and *Speothos venaticus*, through the analysis of Generalized Linear Models (GLM's).

RESULTS

Niche Modeling

Overall, we recorded 319 presences of *A. microtis*, 691 of *C. thousand* and 271 of *S. venaticus*, throughout South America (Appendix-Figure 1 and Supplemental Material- Table S1). In general, our species niche distribution models reached adequate values for the Jaccard index (0.612 ± 0.371 ; average \pm standard deviation), reaching higher predictive values than those that would be expected by chance. All models generated from the three species and the ranges of suitability of their respective algorithms are found in the Appendix (Figure 3).

Considering the final weighted ensemble for the three species (Figure 4), *A. microtis* in both current and future scenarios was more restricted to the western part of the Amazon Forest, including Colombia, Peru, Bolivia, but also in the northern part, including Venezuela, Suriname, Guyana, and French Guyana. However, we found that in the extreme northeast of the Brazilian Amazon, which includes the east of the state of Amapá and further north, in the south of Guyana near the northeast of the state of Roraima (Brazil), there are two spots of non-suitability for this species, which coincides with large patches of Brazilian savannah. When comparing the current and future distribution models, we observed a loss of 18.43% of the total *A. microtis* climate suitability area in South America in the future. Of this total loss, about 15% is supposed to occur in the Brazilian Amazon. In this region, these losses are distributed in areas with high anthropic pressure, close to the southern limit of the Forest, in a transition zone with the *Cerrado*, in the states of Acre and Rondônia. However, we also observed areas of loss concentrated in the eastern borders of the species distribution, which are areas of high anthropic pressure in the Forest (Figure 4).

Cercodyon thous has a high climatic suitability in open areas and anthropogenic landscapes, inside or outside

the Amazon Biome, in both current and future scenarios. Its potential distribution within the Amazon natural savannahs in eastern Amapá state and part of Roraima state in northern Brazil. The species also shows suitability in anthropized areas in the southern limits of the Amazon region, and in the transition zone with the *Cerrado* Biome, especially in the states of Mato Grosso and Rondônia (Figure 4). In the current scenario, the area of climatic suitability includes a strip in the northeast of the Brazilian Amazon, where high anthropogenic pressure is concentrated in the region. Outside the Amazon, this species also had climatic suitability for natural areas of *Cerrado* and anthropized open areas in the central-western, southeastern, and southern areas of Brazil east-central Bolivia, southeastern Paraguay, Uruguay, and northeast of Argentina. The future projected ensemble model predicts the loss of 56.54% of the *C. thous* climate suitability area across South America (Figure 4). About 88% of this total loss could occur in the Brazilian Amazon.

The projected area of climatic suitability for *S. venaticus* is almost as wide as for *C. thous* (Figure 4). However, the current distribution of *S. venaticus* includes both areas of *Cerrado* and dense forests, but also other Brazilian biomes and anthropogenic open areas (Figure 4). When we analyze the projection for the future, *S. venaticus* is the species that loses the most area with climatic suitability, among the three canids, with a reduction of 57.18% for all of South America. However, about 91% of this total loss will occur in the Brazilian Amazon (Figure 4).

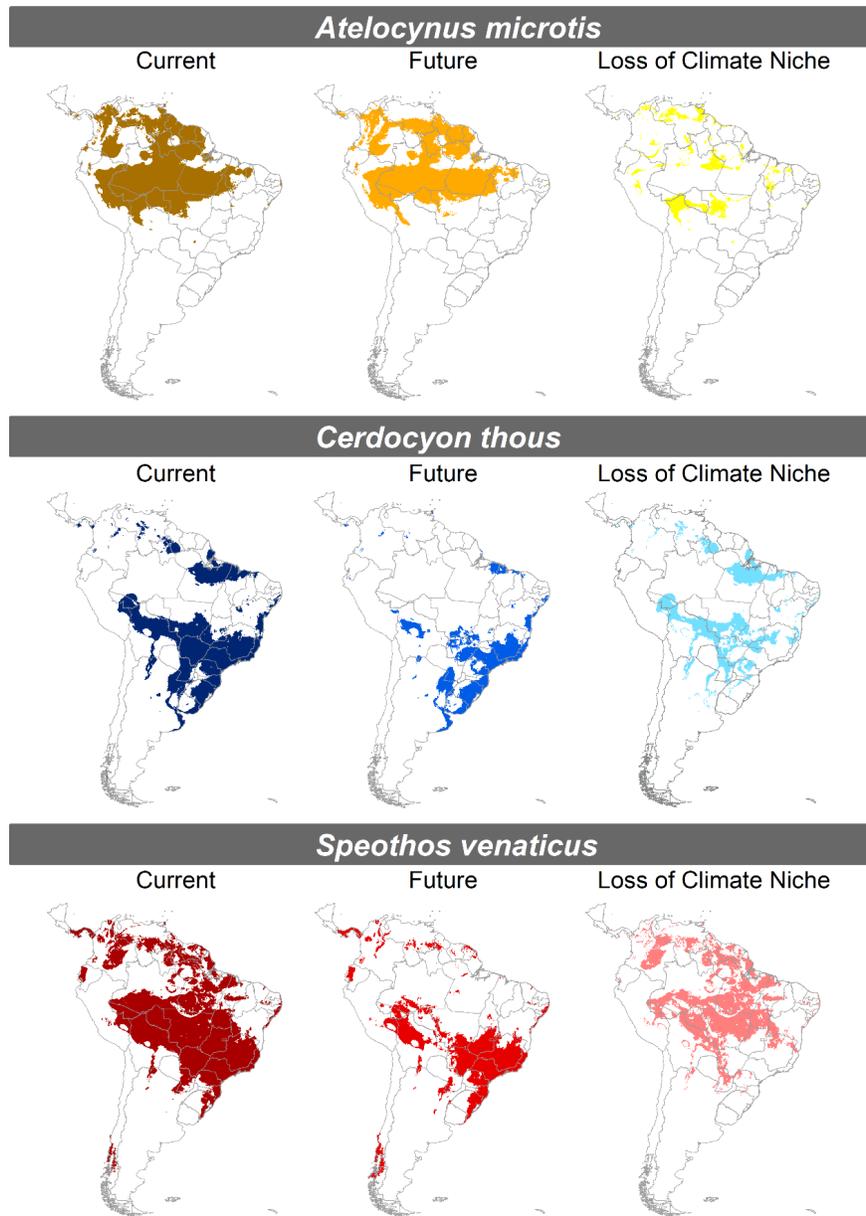


Figure 4. Predictions of climatic niche distributions for the three species of wild Amazon canids (*Atelocynus microtis*, *Cerdocyon thous*, and *Speothos venaticus*) in South America, based on a mean ensemble weighted by the best Jaccard values in each modeling method. Current – Areas of occurrence considering the current climate suitability for the species; Future – Climate niche projections for 2060 for each species; Loss of Climate Niche – Areas that will lose climate suitability for the species in the future.

Generalized Linear Models (GLM's)

For *A. microtis*, the global model including all predictor variables was the most adequate model to explain the variation in the occurrence of this species (Appendix-Table 3). When evaluating the isolated effect of each variable, we observed that only Nat_open_areas did not affect the distribution of *A. microtis* (Table 1). The variables, Forest, Water, and Anthr_open_areas had a positive effect on the occurrence of the species (Table 1) (Figure 5A). We observed an increase in the probability of *A. microtis* by 74.4% for areas with

higher percentages of these variables, especially Forest and Water. The Urban_areas variable negatively affected the occurrence of *A. microtis* (Figure 5A). We estimated that this variable reduces the occurrence of the species by about 50%.

Table 1. Predictive variables selected for *Atelocynus microtis* by the ANOVA, using the most adjusted model: $A. microtis \sim Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water$.

Variable under test	η^2	df	F	p
Null				
Forest	50,896	1	79,42	$p < 0.001$
Anthr_open_areas	3,032	1	4,732	0,03
Water	24,873	1	38,813	$p < 0.001$
Urban_areas	2,396	1	3,738	0,05
Nat_open_areas	0,682	1	1,064	0,3

For *C. thous*, the global model was also the most adequate to explain the variation in occurrence of this canid in the landscape (Supplementary Material, Table S4). Analyzing the variables separately, only the percentage of Water did not affect the occurrence of this species (Table 2). The variables Anthr_open_areas and Urban_areas positively affected the occurrence of *C. thous* (Figure 5B), providing a 73% increase in the probability of occurrence of this species. On the other hand, the percentage of Forest and Nat_open_areas negatively affected the occurrence (Figure 5B), reducing the probability of occurrence by 72%.

Table 2. Predictive variables selected for *Cerdocyon thous* by the ANOVA, using the most adjusted model: $C. thous \sim Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water$.

Variable under test	η^2	df	p
Null			
Forest	20,597	1	$p < 0.001$
Anthr_open_areas	24,365	1	$p < 0.001$
Water	0,02	1	0,88
Urban_areas	4,451	1	0,03
Nat_open_areas	7,472	1	$p < 0.01$

Also, for *S. venaticus*, the global model was the best to explain the species occurrence in the landscape (Table S5, Supplemental Material). The single variables that had an effect on the occurrence of *S. venaticus* was the percentage of Forest, Anthr_open_areas, and Urban_areas, all of which positively influenced the occurrence of the species (Table 3, Figure 5C). On average, areas with higher percentages of forest and urban areas have a 74% increase in the species' probability of occurrence, while in open anthropic areas, the probability increased by 73%.

Table 3. Predictive variables selected for *Speothos venaticus* by the ANOVA, using the most adjusted model: $S. venaticus \sim Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water$.

Variable under test	η^2	df	p
Null			
Forest	3,585	1	0,05
Anthr_open_areas	12,952	1	$p < 0.001$
Water	0,697	1	0,4
Urban_areas	9,106	1	$p < 0.01$

Variable under test	η^2	df	p
Nat_open_areas	3,175	1	0,07

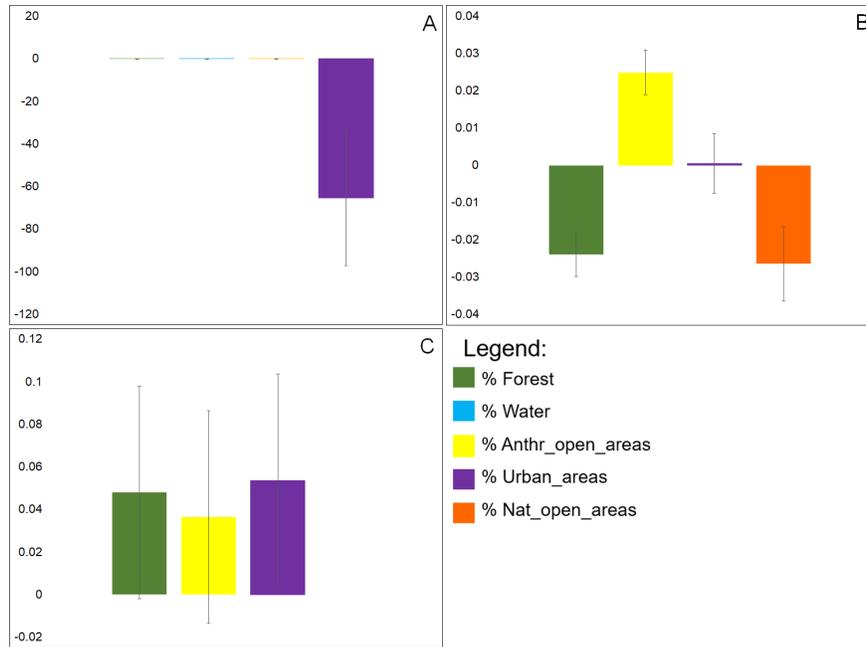


Figure 5. Effect direction (positive or negative) of the variables selected by the GLM's as main predictors of the occurrence of canid species in the Amazon. (A) *Atelocynus microtis* ; (B) *Cerdocyon. thous* , and (C) *Speothos venaticus* .

DISCUSSION

Our results show that the occurrence of the three Amazonian canid species *C. thous*, *S. venaticus* and *A. microtis* may be negatively affected by climate change in the future, with losses of their entire suitability area in South America from 15% to 91% and in the Brazilian Amazon losses ranging from 18% to 56%. However, the effects can be differentiated between the species according to their ecological demands and the environmental variables that can modulate their climatic niches. For *C. thous* and *S. venaticus* , the climate variables and those associated with anthropogenic disturbances that modulate their niches today, may not act in the same way in the future. Thus, the rapid environmental changes might function as ecological traps for these species (Robertson and Hutto, 2006), and in the future they may no longer survive in most of the areas considered suitable for them today.

Among the three species *A. microtis* has the most restricted distribution confined to the Amazon Forest and the one with the least projected loss of suitable climatic areas in the future. Apparently, this species is a specialist in forest habitats, in particular in continuous and preserved forest (Michalski, 2010; Leite-Pitman and Willians, 2011). Probably, the loss of suitability for this species is directly related to the loss of deforestation and forest degradation (Rocha et al., 2020). In addition to the distribution of the climatic niche of this species mainly coinciding with the most conserved regions of the Amazon Forest, our results showed a strong influence of Forests and Water on the occurrence of *A. microtis* . The association of this species with watercourses is also known from the literature and is suggested by interdigital membranes which may be an adaption for moving on soft soil (Leite-Pitman and Willians 2004; Castelló, 2018). Although the proximity to urban areas was not one of the main variables determining the occurrence of *A. microtis* , we

found that this variable was negatively related to its occurrence, corroborating its low tolerance to disturbed habitats (Michalski, 2010; Leite-Pitman and Williams, 2011; Rocha et al., 2020). Thus, the loss of suitability areas in the future for *A. microtis* cannot be related to the ecological trap theory. This species will probably no longer occur in unfavorable habitats due to its fitness for higher-quality forest habitats.

For *A. microtis*, one of the consequences of deforestation and human pressure is increased hunting (Constantino, 2016), including hunting with domestic dogs. Thus, disease transmission by domestic dogs will pose a threat to *A. microtis* (Schenck and Stail, 2004; Leite-Pitman and Williams, 2011). Our results corroborate those of Rocha et al. (2020), who expected a loss of 30% of the *A. microtis* distribution area by 2027, due to forest loss. Based on the last three years of high deforestation rates in the Amazon (PRODES, 2021), and using a pessimistic projection for the future, the loss of area of occurrence of this species could be much more severe.

Considering habitat selection, an animal cannot always make the best choice about where to live (Kristan, 2003; Stamps and Swaisgood, 2007), but its initial choice may later affect the individual's survival and its reproductive success. However, the ultimate reason that determined the choice may have not been evident when the choice was made (Hutto 1985; Kristan, 2003). In the case of altered environments in the Amazon, it is possible that the attractiveness of these habitats by species such as *C. thous* or *S. venaticus*, are detaching themselves from the species' aptitude for survival and reproduction. The preference of these species for anthropogenic environments was evident from our GLM analyses, where natural open areas negatively influenced the occurrence of *C. thous*, while anthropogenic open areas had a positive impact. The same was apparent for *S. venaticus* where anthropogenic open areas had a positive effect on its occurrence. These lower-quality habitats may at some point be just as attractive as preserved native habitats. This can happen when animals whose behaviors have been shaped by exposure to different environmental conditions in their evolutionary history, are suddenly confronted by altered or novel environments (Iwasa and Levin, 1995). In these situations where impoverished environments become more attractive and "bait" individuals, these environments are called ecological traps (Gates and Gysel, 1978; Robertson and Hutto, 2006).

Of the three species surveyed, *C. thous* appears to be the least demanding in terms of habitat, with aptitude for open environments and a high tolerance for anthropogenic habitats (Ferraz et al., 2010). In the Amazon, this species is common in natural non-forest environments, such as in areas of Canga Metalófila in Carajás, State of Pará (Carvalho et al., 2014), or in areas of the Amazon Cerrado in the State of Amapá (Coelho et al., 2014). In our occurrence database from the Amazon, we had no record of *C. thous* in areas of continuous forest and outside naturally open environments. On the other hand, *C. thous* has been commonly recorded in areas with eucalyptus (Coelho et al., 2014) and oil palm plantations (Mendes-Oliveira et al., 2017), and may occur at the edge of adjacent forests, but not inside them. It also occurs in mining areas, with a high level of degradation and locations in the initial phase of forest recovery in the region of Paragominas State of Pará. Interestingly, two individuals of *C. thous* were recorded in 2020 within the city of Belém, State of Pará, in the Amazon (Mendes-Oliveira, personal comm.). *Cerdocyon thous* does not seem to be distributed within forests, and deforestation has favored its expansion in the Amazon biome. The same occurred with *Chrysocyon brachyurus*, (maned wolf), which expanded its extent of occurrence in southwestern Amazonia (see Silva-Diogo et al., 2020), precisely due to the conversion of forests into open areas in southeastern Amazonia (Silva-Diogo et al., 2020).

Our current model showed more outstanding suitability of *C. thous* to more open environments, such as *Cerrado* and more anthropized open areas in the Amazon, with restrictions to more forested areas, such as in the central and northwestern portions of the Amazon. The GLM results also corroborate the conclusion that *C. thous* has been positively influenced by urban areas and anthropogenic open areas and has been negatively by forest. However, this species was also negatively influenced by natural open areas, suggesting a greater fitness for anthropogenic habitats over natural areas. Although canids generally do not show cursorial adaptations like those of ungulates (Smith and Savage, 1965), *C. thous* has a more cursorial form than the other two canid species studied in this research (Penrose, 2019). Longer limbs favor more extended travel, especially in open areas. Faced with a scenario of degradation and deforestation, this may be a morphological

adaptation that favors the entry of this species into degraded, previously forested environments. Another characteristic that confers an advantage to the ecological plasticity of *C. thous*, about *A. microtis* and *S. venaticus* in the Amazon, is its greater tendency to omnivory. The ability of this species to have a poor or meatless diet for long periods, feeding opportunistically on what the environment offers (Macdonald and Courtenay, 1996; De Oliveira, 2009), allows it a more remarkable ability to thrive in a broader range of backgrounds and conditions. Considering all these characteristics, we would imagine that the deforestation of the Amazon Forest has been favoring *C. thous*. However, in the long term, this species may be be “baited” by lower-quality environments, reducing its success and leading it to extinction in certain areas in the future.

Considering our future projections of climate suitability for *C. thous*, we observed a significant loss of suitable areas, especially in regions already open or currently degraded by anthropogenic action, mainly in the southern limits of the Amazon Forest and the northeast of this biome. These climate niche loss projections suggest that impoverished environments currently suitable for *C. thous* may not perpetuate in the future. Thus, these new anthropogenic environments may be working as an ecological trap for *C. thous* in the Amazon.

The same may happen with *S. venaticus*. This species is considered rare (De Moura Bubadue et al., 2016), and occurs in forest habitats and forest edges (Zuercher et al., 2005), open areas such as savannah (Zuercher, 2001), and altered habitats (DeMatteo and Loiselle (2008). Despite not being a habitat specialist, *S. venaticus* is the most carnivorous canid in South America. And this is due to the presence, in individuals of this species, of a large zygomatic arch, a short snout with a reduced number of molars and a pointed lower first molar (LM1), important adaptations for hypercarnivory, which increases the efficiency of meat consumption (Ewer, 1973; Van Valkenburgh and Koepfli, 1993; Beisiegel and Zuercher, 2005; De Moura Bubadue et al., 2016)

Thresholds for the occurrence of *S. venaticus* appear to be less restrictive than for *A. microtis* but more stringent than for *C. thous*. DeMatteo and Loiselle (2008) mention that 20% of the potential distribution areas of *S. venaticus* were associated with degraded areas, using land-use data from 1992 to 1993. However, Michalski (2010) recorded *S. venaticus* only in continuous regions of Forest, even applying an effort using camera traps in fragments adjacent to continuous areas. In our study, the current model showed broad distribution suitability in South America for this species, but with a significant loss in the future (the most extensive loss among the three species), especially in the Amazon region. The future loss of climatic niches in the Brazilian Amazon is concentrated both in forest areas and areas already anthropized, indicating that this species may suffer from the loss of high and low-quality habitats. However, the GLM indicated that *S. venaticus* is positively influenced by forest, urban areas, and anthropogenic open areas. This suggests that *S. venaticus* may also be involved in an ecological trap when it chooses lower quality habitats that may not be enough to maintain its survival in the future. However, unlike *C. thou*, *S. venaticus* also uses forest habitats, which allows it to survive in areas that can be protected in the future in the Amazon.

Evolutionarily seen, the climate has been a more decisive factor than competition in explaining morphological variation and habitat options in canids (De Moura Bubadue et al., 2016). They showed that the skull morphology of *A. microtis* and *S. venaticus* is more related to warm, humid, and less seasonal environments than *C. thous*. The use of different habitats and different diets reduces competition between them. In this way, the coexistence of these species can be compromised not by competition between them but, on the contrary, by differences in climatic adaptations and habitat options, as our results show.

Ecological traps occur when species erroneously choose niches where their suitability is lower than in others after changes in the environment (Robertson et al., 2013). Considering the evolutionary history of species, environments altered by human actions could provide false clues to their adaptation (Sclaepfer et al., 2002). In the medium and long term, these ecological traps can lead to significant decrease or even extinction of populations in these habitats before adaptation to the new modified environment has occurred (Hale and Swearer, 2016). For *C. thous* and *S. venaticus*, we believe that rapid changes in landscapes (habitat degradation) will lead to “wrong choices” for environments that will soon have large climatic variations,

leading these species to be trapped in these ecosystems, without time to adapt to them.

Further, both *S. venaticus* and *A. microtis* appear to be forest-dependent and must rely on the goodwill of decision-makers to be maintained in the future. However, even though *C. thous* is least dependent on the Amazon Forest, this species is probably the one that will be most affected in the future due to the ecological traps that the region has offered. *Speothos venaticus*, can also suffer from the same process, but if the forest is maintained, the impact on this species can be less intense. Using the canid species as a model, we could deeply investigate these ecological effects that can affect a large part of the Amazonian fauna in the current scenario. The future perspectives for preserving terrestrial vertebrate fauna in this region are pretty pessimistic. When it comes to the conservation of impoverished regions in the Amazon, the theory of ecological traps must be studied and discussed at the same level that habitat loss is considered a decisive criterion for biodiversity threat.

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Appendix



Figure 1 Appendix . Photos of camera traps of wild dog recorded in the Amazon. (A) *Atelocynus microtis* , photo captured at FLONA Caxiuanã, Pará-Brazil (TEAM-Caxiuanã/Fernanda Santos); (B) *Atelocynus microtis* , photo captured at ESEC Terra do Meio, Pará-Brazil (Monitora ICMBIO/Cintia Lopes); (C and D) *Cerdocyon thous* , photo captured at FLONA Carajás, Pará-Brazil (Ana Cristina Mendes-Oliveira); (E) *Spheotos venaticus* , photo captured at CKBV’s Company area, Paragominas, Pará-Brazil (Ana Cristina Mendes-Oliveira); (F) *Spheotos venaticus* , photo captured at HYDRO Company area, Paragominas, Pará-Brazil (Ana Cristina Mendes-Oliveira and Oystein Wiig).

Table 1 Appendix . Principal Component Analysis (PCA) results, considering the variables to generate distribution models for Amazonian canid species.

Variable	Name	PC1	PC2	PC3	PC4
Bio1	Annual Mean Temperature	-2,7E+14	-2,3E+14	1,29E+14	-4,2E+14
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	1,84E+14	-2,3E+13	1,06E+14	4,81E+14
Bio3	Isothermality (Bio2/Bio7) (* 100)	-2,4E+13	3,51E+14	-3,3E+14	9,88E+14
Bio4	Temperature Seasonality (standard deviation *100)	2,47E+14	1,02E+14	3,86E+14	-6,7E+14
Bio5	Max Temperature of Warmest Month	-1,9E+14	-3,2E+14	3,45E+14	-4,2E+14
Bio6	Min Temperature of Coldest Month	-2,9E+14	-1,2E+13	-3,5E+14	-1,5E+14
Bio7	Temperature Annual Range (Bio5-Bio6)	2,5E+14	-1,2E+14	3,2E+14	1,83E+14

Variable	Name	PC1	PC2	PC3	PC4
Bio8	Mean Temperature of Wettest Quarter	-2,3E+14	-2,6E+14	2,32E+14	7,28E+14
Bio9	Mean Temperature of Driest Quarter	-2,8E+14	-1,5E+14	-1,8E+14	-1,7E+14
Bio10	Mean Temperature of Warmest Quarter	-2,3E+14	-2,6E+13	3,08E+14	-9,8E+14
Bio11	Mean Temperature of Coldest Quarter	-2,8E+13	-1,8E+14	9,08E+14	-2,6E+14
Bio12	Annual Precipitation	-2,6E+14	2,14E+14	3,34E+14	1,79E+14
Bio13	Precipitation of Wettest Month	-2,7E+14	7,04E+14	-1,2E+14	2,23E+14
Bio14	Precipitation of Driest Month	-1,5E+14	4E+14	2,39E+14	4,06E+14
Bio15	Precipitation Seasonality (Coefficient of Variation)	3,78E+14	-3,5E+14	-4,1E+14	3,13E+14
Bio16	Precipitation of Wettest Quarter	-2,7E+14	7,82E+14	-1,1E+14	2,29E+14
Bio17	Precipitation of Driest Quarter	-1,6E+14	3,99E+14	2,3E+14	3,94E+14
Bio18	Precipitation of Warmest Quarter	-1,6E+14	1,79E+14	1,92E+14	5,98E+14
Bio19	Precipitation of Coldest Quarter	-2E+14	2,07E+14	-7,5E+13	-2,4E+14

Table 2 Appendix . Predictor variables used in the construction of Generalized Linear Models (GLM's)

Models	Variable under test
Model 1	Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water
Model 2	Forest + Anthr_open_areas + Urban_areas
Model 3	Anthr_open_areas + Urban_areas + Nat_open_areas
Model 4	Forest + Anthr_open_areas
Model 5	Anthr_open_areas
Model 6	Null

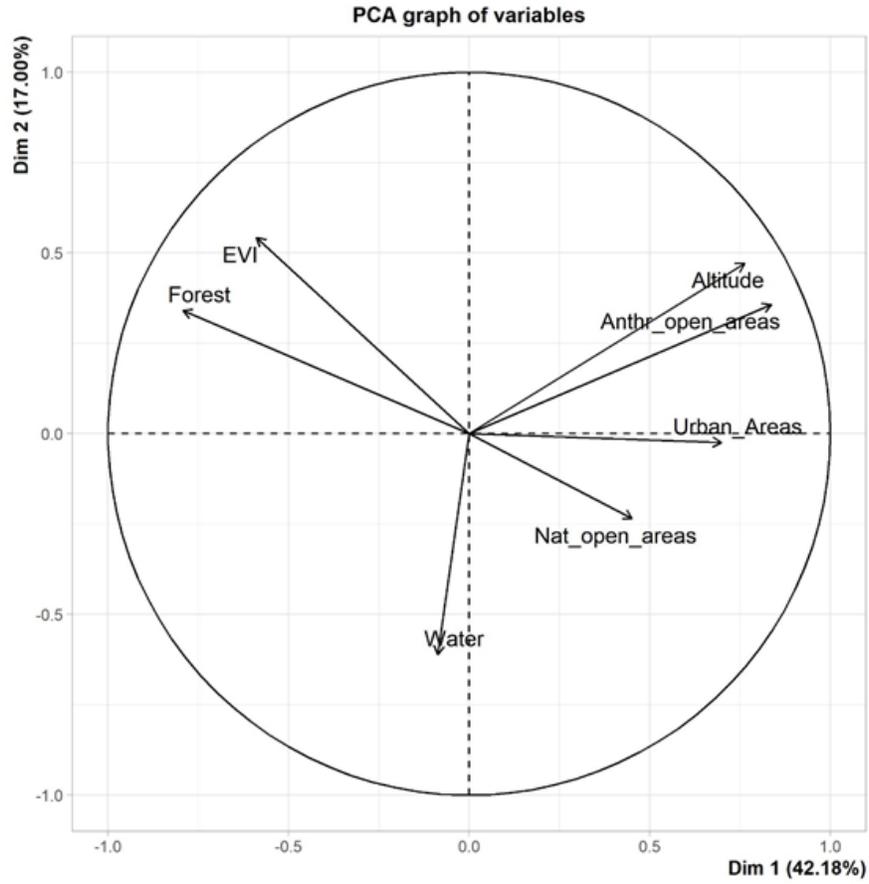


Figure 2 Appendix. Principal Component Analysis (PCA) to select correlated variables for explanation of the results

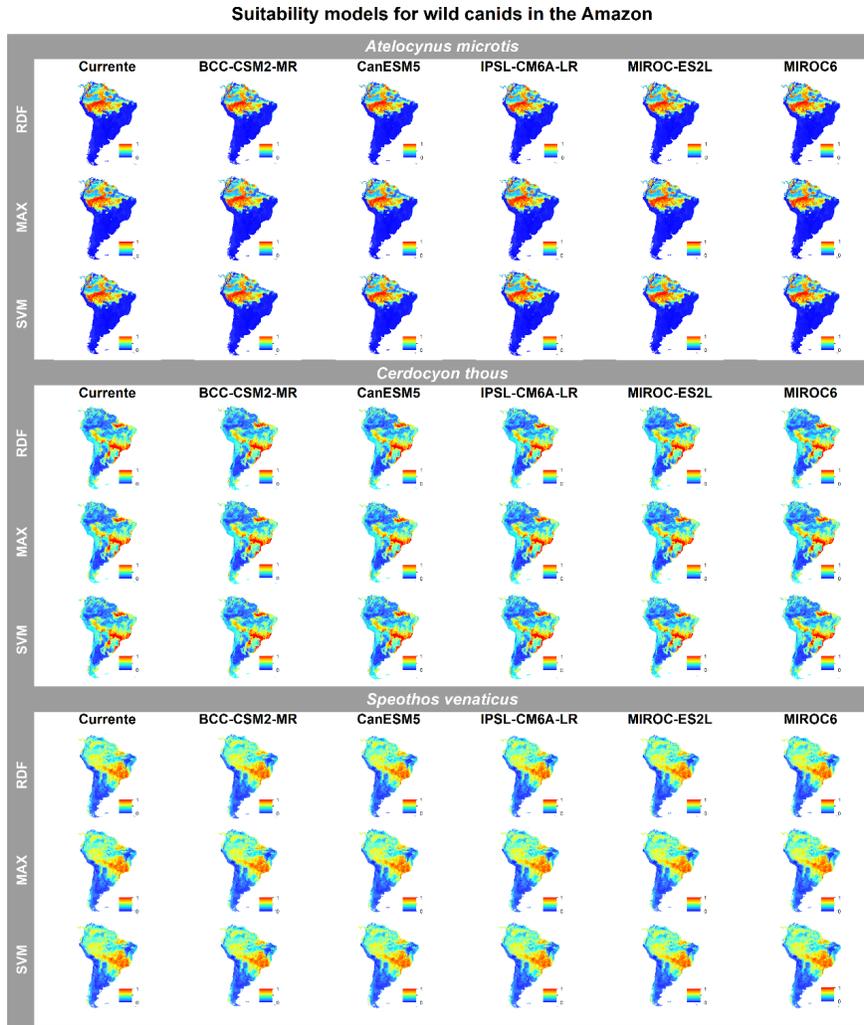


Figure 3 Appendix. Models generated from the three species of canids and the ranges of suitability of their respective algorithms

Table 3 Appendix . Results for the models selected by the GLM's for species through the Anova table.

Model - *Atelocynus microtis*

- A. microtis* ~ Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water
- A. microtis* ~ Forest + Anthr_open_areas + Urban_areas
- A. microtis* ~ Anthr_open_areas + Urban_areas + Nat_open_areas
- A. microtis* ~ Forest + Anthr_open_areas
- A. microtis* ~ Anthr_open_areas
- A. microtis* ~ 1

Model - *Cerdocyon thous*

- C. thous* ~ Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water
- C. thous* ~ Forest + Anthr_open_areas + Urban_areas
- C. thous* ~ Anthr_open_areas + Urban_areas + Nat_open_areas
- C. thous* ~ Forest + Anthr_open_areas
- C. thous* ~ Anthr_open_areas

Model - *Atelocynus mic*

- A. microtis* ~ Forest + An
- A. microtis* ~ Forest + Anth
- A. microtis* ~ Anthr_open_ar
- A. microtis* ~ Forest + Anth
- A. microtis* ~ Anthr_open_ar
- A. microtis* ~ 1

?²

- 76,161
- 60,132
- 16,852
- 19,938

Model - *Atelocynus microtis*

C. thous ~1

Model - *Speothos venaticus*

S. venaticus ~Forest + Anthr_open_areas + Urban_areas + Nat_open_areas + Water

S. venaticus ~Forest + Anthr_open_areas + Urban_areas

S. venaticus ~Anthr_open_areas + Urban_areas + Nat_open_areas

S. venaticus ~Forest + Anthr_open_areas

S. venaticus ~Anthr_open_areas

S. venaticus ~1

Model - *Atelocynus microtis*

-25,026

?²

-57,324

45,197

-11,766

-11,776

-47,626

