



Research Article

Updated distribution and conservation perspectives of marmosine opossums from Colombia

Baltazar GONZÁLEZ^{1,*}, Federico BROOK^{1,2}, Gabriel M. MARTÍN^{1,2}

¹Centro de Investigación Esquel de Montaña y Estepa Patagónica (CIEMEP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) y Universidad Nacional de la Patagonia "San Juan Bosco" (UNPSJB), Roca 780, Esquel (P.C. 9200), Chubut, Argentina

²Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Facultad de Ciencias Naturales y Ciencias de la Salud, UNPSJB, Esquel (P.C. 9200), Chubut, Argentina

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Abstract

Marmosini is the most speciose marsupial tribe of Colombia with 19 species, but basic aspects of their biology remain poorly unknown, including information on their distribution and conservation. The main objectives of this work were to study Marmosini species richness, potential distribution, and conservation throughout Colombia. To achieve this, we generated ecological niche models in a reproducible framework, in which we tested the use of different combinations of environmental data (WorldClim, ENVIREM, modified soil adjusted vegetation index (MSAVI)), modeling areas, cross-validation methods, and evaluation metrics using our data from Colombian Marmosini. Models for each species were explored for shared environmental and conservation patterns across all species, and using ecological and human-related (e.g., protected areas) data specific to Colombia. We found that models that included WorldClim, ENVIREM and MSAVI variables, and modeling areas based on ecoregions performed better with our sample. Precipitation variables were more important for 8 species, while temperature variables were more important for 5 species, and topographic variables were important in the remaining species. Marmosini species' potential distribution covers 87.2% of the country's continental area, and the protected area for any species of this group ranges between 5.4% and 29% of their modeled distribution. Most protected areas classified as strict-conservation presented small areas of high human pressure, while other categories (e.g., managed resources) presented large areas of high human pressure. We found that high potential species richness of Marmosini occurs at mid-elevations on the Andes with an upper elevation limit of maximum richness at ~2000 m. These species distributions are poorly covered by the natural protected areas of Colombia. We identified the transition zone between the Eastern Andes and Amazonian regions as a key area for conservation efforts in these little known marsupials.

Introduction

Forty marsupial species occur in Colombia, of which 19 belong to the tribe Marmosini (Voss and Giarla, 2021; Ramírez-Chaves et al., 2016; Solari et al., 2013). However, little information regarding the current distribution for most of those species is available (but see Gutiérrez et al., 2014), that represents fundamental information for species conservation planning and basic ecological research. Marmosini includes the genera *Marmosa*, *Monodelphis* and *Tlacuatzin* (Voss and Giarla, 2021; Voss et al., 2020; Rossi et al., 2010; Voss and Jansa, 2009), the latter exclusive to Central America, while *Monodelphis* is restricted to South America. Recently, both *Marmosa* and *Monodelphis* have been taxonomically revised, providing clarity about species identities and occurrence localities (Voss and Giarla, 2021; Voss et al., 2020, 2014; Pavan et al., 2014).

Colombia supports the highest species richness of Marmosini in South America with 19 species, followed by Perú with 18, Brazil with 16, Bolivia with 12, Venezuela with 10, and the rest of countries with less than 10 species (IUCN, 2021; Voss and Giarla, 2021; Tirira et al., 2020; Solari et al., 2013). Regarding their national threatened status, only one Marmosini species (*Marmosa xerophila* Handley and Gordon, 1979) is listed as Data Deficient in the last national assessment of threatened mammals of Colombia (Alberico and Rojas-Díaz, 2006). At a global scale, the International Union for the Conservation of Nature (IUCN) lists 12 species for Colombia, two of which are Vulnerable

(*M. xerophila* and *Marmosa phaea* Thomas, 1899), one is Data Deficient (*Marmosa rubra* Tate, 1931), and the remaining species are Least Concern (IUCN, 2021). In the last 12 years, new species have been described, mainly by splitting widely distributed taxa (Voss et al., 2020; Rossi et al., 2010), but no assessment exists for these species yet. Consequently, studying the biogeography of these species both globally and in Colombia is needful for any future efforts aimed at preserving them.

There are several ways to assess species' distributions. Recently, a variety of approaches including what is known as Ecological Niche Models (ENM) have gained strength in the scientific community (Urbina-Cardona et al., 2019; Peterson et al., 2011). These methods vary in their input requirements and output interpretation, but are based on a sound conceptual framework about species biogeography and their realized niche (Norberg et al., 2019; Peterson and Soberón, 2012; Peterson et al., 2011). Moreover, these methods allow generating species distribution models based on associated niche characteristics (Soberón et al., 2017; Peterson and Soberón, 2012). One of the most widely used and tested algorithms for ENM is Maxent (Phillips et al., 2017; Merow et al., 2013; Elith et al., 2011), but its implementation and results depend on several variables. For example, the area where the model is estimated on (Barve et al., 2011), the complexity of the model (Merow et al., 2014), and how accuracy is tested (Jiménez and Soberón, 2020; Qiao et al., 2015; Elith et al., 2011), among others.

The ecology and chorology of New World marsupials have been partially studied (poorly studied compared to other, most conspicuous mammals), and conservation efforts are hindered due to this lack of knowledge (Cayuela et al., 2009). Although the tribe Marmosini has

*Corresponding author

Email address: baltazargch@gmail.com (Baltazar GONZÁLEZ)

been recently revised regarding its taxonomy, there is little knowledge about its distribution and ecology, which could provide a baseline for any future conservation task. Altogether, the availability of powerful algorithms for ENM, the increased clarity of species identities and the updated list of marsupials that inhabit Colombia, provides an opportunity to assess the distribution and conservation of Marmosini species.

The main objective of this work was to model and analyse the potential distribution of Marmosini species using Colombia as a study case. We analyzed the spatial pattern of species richness and conservation throughout the country, using data on bioregions, protected areas, and human pressure, integrating what is known for ENM in an explicit, reproducible framework. Also, we discuss ENM and the use of different environmental data, modeling areas, model validation and evaluation using our data from Colombian Marmosini.

Materials and methods

There is no single best approach when modeling species' niches, and many algorithms are available varying in their strengths and weaknesses. In this study, most of the species have few records, and we were interested in their current potential distribution. Thus, we opted for a single-algorithm approach (Hao et al., 2020, 2019) rather than ensemble modeling (Araujo and New, 2007). To keep the text fluid, we give enough details herein for the reader to understand the methodology (Fig. 1). However, more details are offered as supplementary information describing other inputs and configurations that are known to affect final results (Norberg et al., 2019; Boria and Blois, 2018; Merow et al., 2014; Barve et al., 2011; Elith and Leathwick, 2009).

Occurrence and background data

For the list of species of Marmosini that inhabit Colombia, we followed Solari et al. (2013), Ramírez-Chaves et al. (2016), and Voss and Giarla (2021), although the genus-level classification follows Voss and Jansa (2009) (i.e., we considered *Micoureus* a subgenus of *Marmosa*). Occurrence records were gathered from both the literature, by using recent taxonomic revisions of the genera *Marmosa* and *Mondelphis* (see Tab. S1-Sheet 1 for full list of references), and the Global Biodiversity Information Facility (GBIF.org, 2021) by querying the database for records based on preserved specimens and material samples, and with less than or equal to 1000 m in coordinate uncertainty. We used standard best-practices to clean and prepare GBIF data using the R package *CoordinateCleaner* (Zizka et al., 2019) and corrected only obvious georeferencing errors such as positive-to-negative longitudinal or latitudinal coordinates. When available, we manually inspected locality coordinates for each species based on their taxonomic revision for possible inconsistencies. A complete account of the localities used for this study is presented in Tab. S1-Sheet 1.

To match the resolution of occurrences and predictors data ($\sim 1 \text{ km}^2$) and to reduce sampling bias, we kept single records per pixel. We use this resolution since many of the species we analyzed are found in forested areas in the Andean cordilleras, and more than one horizontal kilometer could include high altitude and climatic variability due to high slopes. For each species, we used 10000 random pseudo-absences, herein background points, that were specific for each modeling area tested (see 2.3 below and Supplement S2) and represented unique pixels in the predictors data set.

Environmental data

We modeled each species based on four sets of environmental data, that we call here predictors scenarios (Fig. 1b): three user-defined scenarios based on previous findings and our informed criteria about which variables could have higher explanation power, and one statistically-defined scenario in which predictors were selected in order to reduce collinearity among variables.

Current climatic conditions were represented by subsets of the following databases: WorldClim v. 2 (Fick and Hijmans, 2017), ENVIREM (Title and Bemmels, 2018), and the Modified Soil Adjusted Vegetation Index (MSAVI). MSAVI was derived from the red and near

infra-red bands of MODIS Terra imagery (Daac, 2017) and calculated as the mean for the year 2000 following Qi et al. (1994), which is the closest year available from MODIS Terra imagery to the bioclimatic variables mentioned above.

Using the criteria above, 11 layers were used in the four predictors scenarios as follows: 1) “onlywc”: only with WorldClim (8 variables), 2) “ud.noplants”: user defined with WorldClim + ENVIREM (10 variables), 3) “ud.all”: user defined with WorldClim + ENVIREM + MSAVI (11 variables), and 4) “uncorr”: collinearly reduced variables from the full set (species-specific number and type of variables). A complete account of the variables used in each scenario is given in Tab. S1-Sheet 2 and further details are given in Supplement S2. Each of the four scenarios were used for each species and each type of modeling area (see 2.3 below). All environmental data were downloaded as rasters of $\sim 1 \text{ km}^2$ spatial resolution at the equator (~ 30 arc-seconds).

Definition of modeling areas

The definition of a modeling area is a major step in ENM (Barve et al., 2011). We used two methods to estimate this area, herein referred to as M area, following the Biotic-Abiotic-Mobility diagram from Peterson and Soberón (2012). We used M1 and M2 to designate the two approaches to estimate M area for each species (see Supplement S2-Fig. SD2.1). First, we estimated a minimum convex polygon from all the occurrences; M1 was generated by adding a buffer of 300 km^2 (clipped to the coastline); M2 was generated by adding a buffer of 50 km^2 and selecting the ecoregions (Dinerstein et al., 2017) that overlapped with it. M1 was designed to include contiguous areas with similar climatic conditions based on visual exploration for all species. M2 followed a combination of two previously used modeling areas for ENMs in marsupials (i.e., Gutiérrez et al., 2014; Prieto-Torres and Pinilla-Buitrago, 2017). Minimum convex polygons were generated with the R package *adehabitatHR* (Calenge, 2006).

Modeling procedure and evaluation

We used Maxent v. 3.4.3 (Phillips et al., 2017) to generate the models through the function *ENMevaluate* of the R package *ENMeval* v. 0.3.0 (Muscarella et al., 2014) using the features: Linear (L), Quadratic (Q), Product (P), Hinge (H), and Threshold (T), depending on the number of occurrences (Fig. 1c) (Merow et al., 2013). These features were combined with different regularization multipliers (rm): from 0.5 to 5 in increasing steps of 0.5. We also tested different methods of cross-validation using a conditional approach (Fig. 1c). For all species, a block cross-validation method was used, if the species had less than 25 records we used a jackknife approach, and if the species had 25 or more records a random k-fold approach with 5 partitions was used.

In order to select the best combination of features, rm, M area, and predictors scenarios for each species, we evaluated the results through the next ordered-steps: i) Based on the average test value of the area under the receiver-operator curve (AUC), we kept models with AUC values in the third quartile of the values distribution, ii) choosing the models with minimum average difference AUC between test and training models, iii) models with minimum average test of omission rate at the minimum training presence (orMTP), iv) models with the minimum value for the corrected Akaike information criterion (AICc), and v) if more than one model remained after the previous steps, we chose the model that maximized (i.e., simpler models) the regularization multiplier (rm), maximized the train AUC, and minimized the number of parameters. In the rare cases where all previous filters ended in more than one model, a final model was chosen at random.

To transform continuous maps to binary predictions, several thresholds have been proposed (Liu et al., 2016, 2005). In this study, we used the value that maximized the sum of sensitivity and specificity (maxSSS). We then transformed the rasters to polygons, by smoothing their borders and removing holes and crumbs (Supplement S2). For each species, four final models were inspected manually, the two best for each M area. Finally, when deemed necessary based on each species information, final ranges were adjusted using known geographic barriers (Hazzi et al., 2018 and Supplement S3).

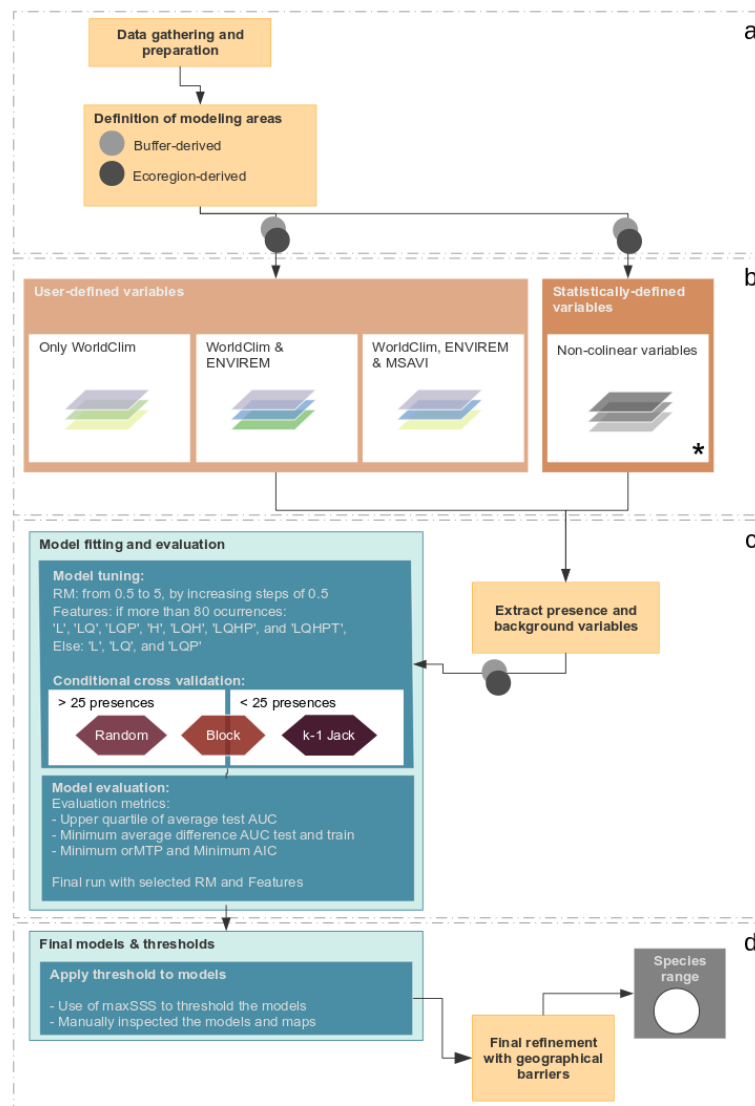


Figure 1 – Workflow scheme for modeling distribution maps of the *Marmosini* species of Colombia. First step (a) is standard for most modeling exercises but note that the “Definition of modeling areas” box presents two circles depicting two ways of estimating modeling areas (area M). For clarity, we depict the two same circles along the scheme to denote where models are being estimated for both areas. Second step (b) included estimation of four predictors scenarios. Although modeling is summarized by one arrow from b to c, models are run for each scenario and for each area M until “Model evaluation”. The third step (c) was model tuning, fitting, and evaluation. For each species, models were evaluated according to four metrics; models chosen passed to the next step. Last step (d) included the application of a threshold, visual evaluation and establishment of geographical barriers for final modifications. Note that the final arrow does not represent area M circles (M1 or M2), since each final species range is based on only one of them. Asterisk (*) in “Statistically defined variables” is to clarify that correlation was evaluated for each species and for each area M (i.e., 32 sets of uncorrelated variables).

Richness and conservation metrics

To explore the potential spatial richness of *Marmosini* within the country, we generated a richness map by dividing continental Colombia in a grid of 25 km² pixel size, and summed how many species occurred per pixel based on the final discretized model’s output per species (referred as final ranges herein).

For conservation analyzes and based on the final ranges, we calculated the area of each species’ potential distribution within continental Colombia, the area within the Natural Protected Areas (NPA) of the country, and the area under high and low human pressure, following the methodology of Martin et al. (2021). This methodology aims to explore conservation at different conservation categories (e.g., areas of strict conservation vs areas of managed resources) and governance types (e.g., national, subnational, private), and the impact of human activities (using human footprint data). For example, allowing to differentiate between protected areas with low and high human impact within a given species distribution. We used the same criteria for pooling governance and IUCN categories of NPAs. Further details of the methodology can be consulted in Martin et al. (2021). NPA data set

was downloaded from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2021, version February 2021), and was cleaned according to standard best-practices (Butchart et al., 2015; Runge et al., 2015) through the R package *wdpar* (Hanson, 2020).

To estimate areas of high and low human pressure, we generated a binary map from the Colombian Human Impact Index of 2015 (Correa Ayram et al., 2020), by selecting the lowest 40% of the values as low pressure, and the remaining as high pressure. These cutoffs were selected based on Correa Ayram et al. (2020) proposed deciles.

All areas were calculated in square kilometers using a geodesic approach and based on a WGS84 projection. All analyzes were run in R v. 4.0.2 (R Core Team, 2020) and RStudio 1.4 (RStudio Team, 2020). We used QGIS v. 3.18.1 to manually modify final range maps (QGIS.org, 2021). The entire code used for this study is available at the first author’s GitHub repository (https://github.com/baltazargch/sdm_marmosini_colombia).

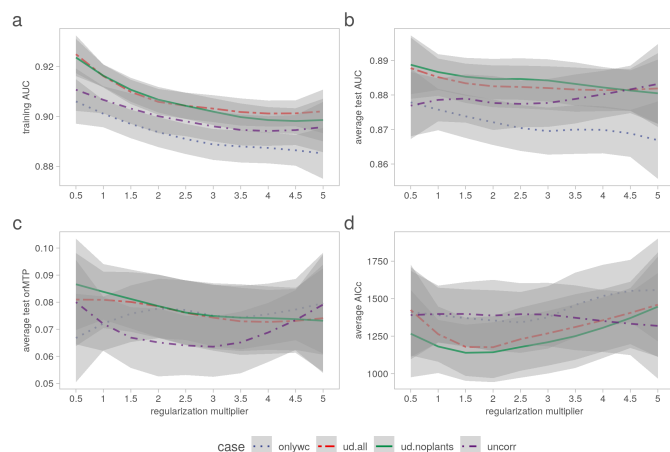


Figure 2 – Performance of different predictors scenarios for Maxent models of Marmosini species of Colombia, based on regularization multiplier and training AUC (a), average test AUC (b), average test orMTP (c), and corrected Akaike Information Criterion (d). Line represents a local polynomial regression among each predictors scenario (case), with standard error represented by the surrounding shaded area of each line. Case abbreviations: onlywc, only WorldClim data; ud.all, user-defined variables including MSAVI; ud.noplants, user-defined variables excluding MSAVI; and uncorr, uncorrelated variables.

Results

Occurrence data

From the original list of 19 species of Marmosini from Colombia, we gathered information on 16 species, 13 from the genus *Marmosa* and 3 from *Monodelphis*. A total of 648 records were compiled and visually verified. The number of species records varied from 9 (*M. phaea* and *Marmosa jansae* Voss and Giarla, 2021) to 199 (*Marmosa robinsoni* Bangs, 1898) after cleaning the data. From the 16 species included, 13 species had records within Colombia, while for the species *Marmosa regina* Thomas, 1898, *Monodelphis brevicaudata* (Erxleben, 1777) and *Monodelphis palliolata* Osgood, 1914 no records within the country were found, but the species were included because records fall within ecosystems that occur in the country.

The records of Marmosini species inhabiting Colombia were gathered from 19 different sources (Tab. S1–Sheet 1), with a geographic extent from 17°50' S and 86°1' W to 35°45' N and 51°763' W. Localities were compiled from fourteen countries: Bolivia (n=17), Brazil (n=28), Colombia (n=101), Costa Rica (n=30), Ecuador (n=49), French Guiana (n=1), Grenada (n=2), Guyana (n=8), Nicaragua (n=8), Panama (n=71), Peru (n=88), Suriname (n=6), Trinidad and Tobago (n=16) and Venezuela (n=208).

Analyses of the different models generated in this work are represented by the filtered results selecting the upper quantile of the average test AUC metric, except otherwise stated. A complete account of the unfiltered results is available in Tab. S1–Sheet 3.

Predictors scenarios

Predictors scenarios varied when model performance metrics were analyzed. The two best scenarios based on train AUC and average test AUC were user-defined with and without vegetation (“ud.all” and “ud.noplants”), which performed similarly, while “onlywc” and “uncorr” scenarios had the worst performance overall, irrespective of the rm analyzed (Fig. 2a,b). In contrast, for the orMTP and at low rm values, all models performed similarly, with “onlywc” being slightly better. As the rm value increased, “uncorr” scenario became better at intermediate values of rm, but all models performed similarly at the highest rm values. The “onlywc” scenario, was consistently worse from a rm value of 2, thus with a higher rate of omitting presences (Fig. 2c). For the AICc metric and at the lowest rm value (0.5), models performed distinctively, but at mid values of rm (1.5 to 4), models seemed to follow a similar performance pattern, with both user-defined scenarios being slightly better based on this metric. At the highest rm values all models performed similarly (Fig. 2d).

Modeling areas

When the different modeling areas were compared regarding their overall performance, M2 outperformed M1 in most of the cases with different predictor scenarios, cross-validation type and rm (Supplement S2–Fig. SD2.2). For train and test AUC, M2 was consistently better than M1, except for jackknife cross-validation with which models from M1 and M2 seemed to perform comparably (Supplement S2–Fig. SD2.2a–b). When evaluated with orMTP, both areas performed similarly with only small differences in the high values obtained for M2, jackknife and “onlywc” case from rm 2 to 3, and in the block type cross-validation, where M2 was slightly better than M1 (Supplement S2–Fig. SD2.2c). However, for AICc M1 was better than M2 in some of the comparisons (Supplement S2–Fig. SD2.2d).

Model results

A total of 8320 models were generated, 2080 for each predictors’ scenario, and between 280 and 120 models for each species, depending on the numbers of records (Fig. 1c). A total of 64 models were visually and critically inspected to decide, based on biological data, which best represented each species’ potential distribution. Most of the chosen models were from the predictors scenarios based on “ud.all” (n = 8), followed by “onlywc” (n=5), “uncorr” (n=3), and finally “ud.noplants” (n=1). Regarding cross-validation, 10 out of 16 final models were from those using random k-fold method, and 6 out of 16 used block method. Most of the models were from regularization multipliers smaller than two and had a train AUC>0.74. Other metrics and configurations of the final models are presented in Tab. S1–Sheet 3 and Supplement S2.

Variable contribution and permutation importance varied greatly between species (Fig. 3). Precipitation related variables were the most important (with values above 50%) in the models generated for 10 species, and temperature related variables were the most important in 6 (*Marmosa isthmica* Goldman, 1912, *Marmosa lepida* Thomas, 1888, *M. phaea*, *Marmosa rutteri* Thomas, 1924, *M. xerophila*, and *M. brevicaudata*) (Fig. 3 and Tab. S1—Sheet 4). In *M. regina*, temperature and precipitation related variables, and terrain roughness (tri) were the most important variables (Fig. 3 and Tab. S1—Sheet 4). In nine species, precipitation related variables represented the most important contribution and permutation values, while only four species had contribution and permutation values represented by temperature variables exclusively (Tab. S1—Sheet 4). Three species had a combination of precipitation and temperature (*M. regina* and *M. xerophila*) or temperature and precipitation (*M. brevicaudata*), as the highest contribution and permutation variables, respectively. *Marmosa regina* had “Minimum Temperature of the Coldest Month” (bio_6) as the variable with the highest information not present in the others (permutation importance), but different variables with the highest contribution to their models (i.e., topoWet). A similar pattern was found in *M. xerophila* and *M. brevicaudata* (Tab. S1—Sheet 4). The variable “topographic wetness” (topoWet) was markedly high for *Monodelphis* species, especially for *Monodelphis adusta* (Thomas, 1897) and *M. palliolata*. The best model configuration for *M. phaea* and *M. jansae* resulted in a single variable contributing to the model, “Mean Temperature of the Warmest Quarter” and “Precipitation Seasonality”, respectively. The model for *Marmosa germana* Thomas, 1904 only had three variables (“Mean Diurnal Range”, “Precipitation Seasonality” (Coefficient of Variation) and “Precipitation of the Driest Quarter”) (Tab. S1—Sheet 4).

Species’ potential distribution

After visual inspection of the final models, geographical barriers were taken into account to modify and generate final range maps. A complete account of the geographical barriers proposed for delimiting each species and final range maps are in Supplement S3 and available for download at the following link: <https://zenodo.org/record/4813016#.YXwfwvML0p>. Different spatial patterns were found regarding the potential distribution of Marmosini in the country. To describe them, we followed the national categorization of continental biogeographic regions for local relevance and clarity, published by the Insti-

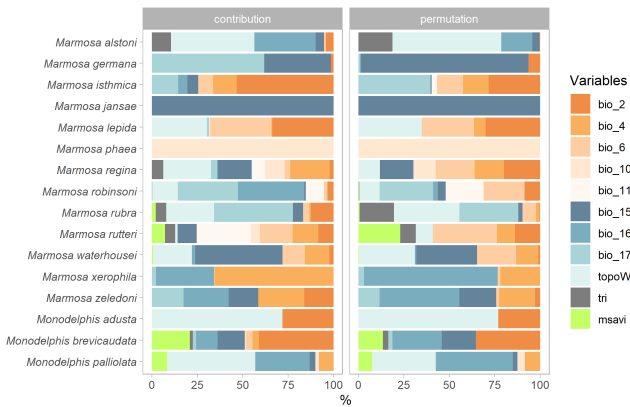


Figure 3 – Percentage of contribution and permutation importance for Maxent models of Marmosini species of Colombia. Orange colors are for temperature-related variables, blue colors for precipitation related variables, gray is for terrain and green for vegetation variables. Species in the y-axis are ordered alphabetically. Variable definitions: bio_2, mean diurnal range; bio_4, temperature seasonality; bio_6, min temperature of the coldest month; bio_10, mean temperature of the warmest quarter; bio_11, mean temperature of the coldest quarter; bio_15, precipitation seasonality; bio_16, precipitation of the wettest quarter; bio_17, precipitation of the driest quarter; topoWet, SAGA-GIS topographic wetness index; tri, terrain roughness index; and MSAVI, modified soil-adjusted vegetation index.

tuto de Investigación de Recursos Biológicos Alexander von Humboldt of Colombia (maps available at <https://www.redalyc.org/articulo.oa?id=49150103> and in inset map of Fig. 4a).

Marmosa germana, *M. jansae*, *M. regina*, *M. rubra*, *M. rutteri* and *M. brevicaudata* showed a potential distribution restricted to the Amazonian region, with several species showing small distribution areas in the Amazonian-Andean transition, east of Nudo de Los Pastos or in the Amazonian-Orinoquia transition (i.e., *M. brevicaudata*). *Marmosa lepida* and *M. phaea* were potentially distributed in the Andean, Orinoquia and Amazonian regions, with the former being mainly distributed in the Amazonian and Orinoquia regions, and a distribution area at mid-elevations of the Eastern Andean region, while *M. phaea* was mainly distributed in the Andean region and few areas in the Amazonian and Orinoquia region, especially east of Nudo de los Pastos and Sierra de La Macarena. *Marmosa waterhousei* Tomes, 1860 and *M. adusta* were potentially distributed mainly in the Andean, Pacific, and Amazonian regions, with the former being widely distributed in the Andean and Amazonian regions and partly in the Pacific and Orinoquia regions, with few areas in the Caribbean region, while the latter is mainly distributed in the Pacific and Andean region, including the Sierra Nevada de Santa Marta at the Caribbean region, and a few spots predicted in the Amazonian region. *Marmosa alstoni* Allen, 1900 and *Marmosa zeledoni* Goldman, 1917 showed an Andean-Pacific potential distribution, with the former being more widely distributed in the Andean region compared to the latter, and with some areas in the Serranía de San Lucas (Caribbean). *Marmosa robinsoni* and *M. isthmica* were potentially distributed mainly in the Caribbean region and the inter-Andean valleys, especially the Magdalena river valley, with the former having more predicted areas in the Andean region, and the latter with more predicted areas in the Pacific region. The potential distribution of *M. palliolata* was mainly concentrated in the Andean and Caribbean regions, limited to mid-low elevations at the northern end of the Eastern Andean region, Catatumbo, and low elevations of the Sierra Nevada de Santa Marta. Finally, *M. xerophila* had a restricted potential distribution concentrated in the Guajira, north of the Caribbean region.

The areas of the final ranges varied from 631759 km² in *M. waterhousei* to 5347 km² in *M. rubra*, with a median area of 92099 km². Taken together, the combined potential distribution of all Marmosini species' covers 990111 km² of continental Colombia, about 87.22% of the continental area of the country, being absent only in parts of the Orinoquia region, north to the Meta river and east of the Eastern Andes near the border with Venezuela, and two small portions west and east of the Serranía de San Lucas, at low elevations.

Richness and conservation metrics

Richness of Marmosini in Colombia, based on our potential distribution models, varied from a maximum of 9 species to a minimum of 1 species per 25 km² (Fig. 4). We found a clear pattern of maximum and sub-maximum richness concentrated at mid-elevation slopes of the Andes, with an approximate upper elevation limit of richness at 2000 m, especially for the Central and Eastern Andes, and northern end of West Andes (Fig. 4b). The highest richness (9–8 species) was found in the Amazon-Andes transition, east of Nudo de los Pastos, and southeast of the Colombian massif (Fig. 4c). A mid-high richness (7–5 species) was found mainly at the eastern slope of the Eastern Andes, Sierra de La Macarena, Catatumbo (northwest of the Táchira depression at the limit between Colombia and Venezuela in the Eastern Andes), Serranía de San Lucas northwest of the Central Andes, in the northern end of the Western Andes, the northwestern coast of the Pacific region and southern Amazonas in the region contained between the Putumayo and Caquetá rivers (Fig. 4a,b). A mid-low richness (4–2 species) was found mainly at the Amazon (north of Caquetá river), the transition zone between Amazonas and Orinoquia regions, inter-Andean valleys, Central Andes, high elevations of the Andes including Eastern Andes and most of its western slope, Pacific region (excluding areas in the northwest with mid-high richness), Sierra Nevada de Santa Marta, and much of the Caribbean region (Fig. 4a). Interestingly, but with a lower richness compared to other areas, a local upper limit of high richness occurs at ~2000 m in Sierra Nevada de Santa Marta (Fig. 4a). The lowest richness (1 species) was found mainly in lowlands of the Orinoquia region, mid/low Magdalena river valley, Guajira, some areas of the Pacific region, the highest elevations of the Sierra Nevada de Santa Marta and lowlands of the caribbean region (Fig. 4b).

Of the total modeled areas, conservation within each species was highly variable, ranging from 23.5% in *M. germana* to 3.7% in *M. rubra*, and a median of 16.9% (Tab. 1). This shows that roughly 83% of all potential distribution areas for Marmosini lack effective protection. Of the total preserved areas for each species, areas with strict conservation preserved between 23.49% in *M. germana*, and 2.23% in *M. xerophila*, with a median of 13% (Tab. 1), with large unprotected areas for all species. The areas preserved under managed resources ranged from 7% in *M. isthmica* to less than 0.05% in *M. jansae*, *M. germana*, and *M. brevicaudata*, with a median value of 2.21% (Tab. 1). Human pressure within each species' area ranged from 68.4% to 0.08% (*M. robinsoni* and *M. brevicaudata*, respectively) and a median of 32.8% for high pressure, and from 96.7% to 32.1% (*M. brevicaudata* and *M. robinsoni*, respectively) and a median of 65.9% for low pressure (Tab. 1). No data values regarding pressure varied from a maximum of 3.2% in *M. brevicaudata* to 0.1% in *M. waterhousei* (Tab. 1).

Our conservation-only analysis based on IUCN criteria showed that most of the species had more of their potential area preserved under strict conservation (median of 13.05%) than area under managed-resources (median of 2.21%). Conservation based on governance showed that most protection comes from national governed areas (median of 12.83%), followed by sub-national governed areas (median of 2.97%), with private areas representing very little of the protected areas (median <0.1%) (Tab. 2). Among species, *M. germana* had the highest percentage of its area strictly protected while *M. xerophila* had the lowest, which were mostly under national governed areas. The percentage of sub-national governed areas was higher than national governed areas in *M. robinsoni* (Tab. 2). No protected areas of Indigenous territories and local communities were found throughout the potential distribution of Marmosini in Colombia.

Conservation-pressure analysis showed that regions within species ranges that are under strict-conservation have a lower area under high pressure (median of 1.66%) compared to areas under managed-resources (median of 33.81%) (Tab. 3). Within governance-types, the lower median values were for areas under national governance (3%), followed by sub-national areas (32.85%) and private areas (51.9%). This pattern is consistently found throughout all species of Marmosini analyzed (Tab. 3). These results show that Marmosini in Colombia are more exposed to higher human pressure in managed, sub-national and

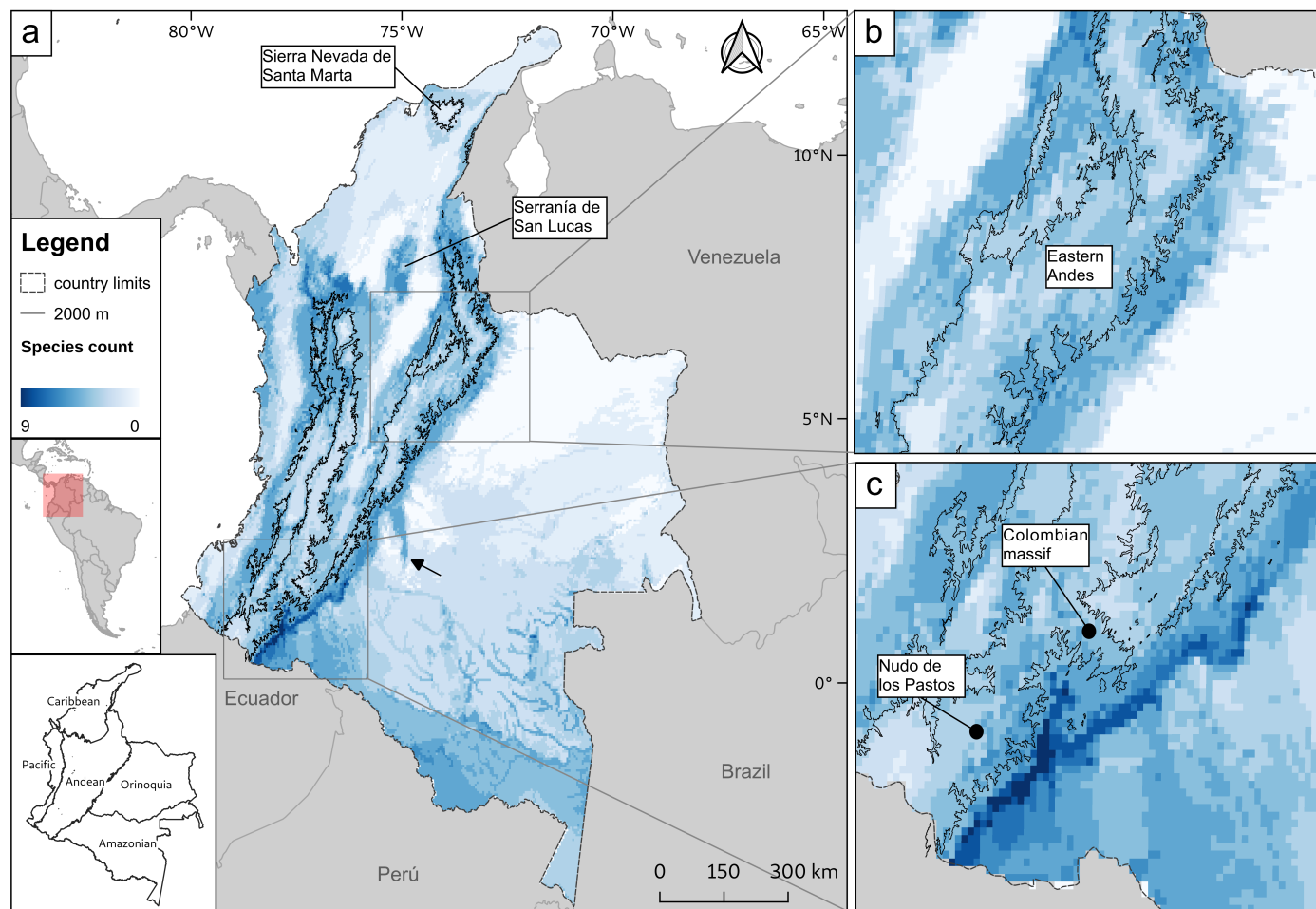


Figure 4 – Potential spatial richness of Marmosini species from Colombia at a 25 km² pixel-size (a), note that for the Andean region, especially for Eastern Andes, Marmosini richness has a sub-maximum value that follows an elevation belt of 2000 m (b), while maximum value is reached south of the country, east to the Nudo de Los Pastos formation (c). Black arrow signals Sierra de La Macarena. Map is depicted in a Mollweide projection.

private areas, while strict reserves and national governance areas have smaller percentages of areas under high pressure throughout the species' potential ranges.

Discussion

To our knowledge, this is the first time that the potential distribution and conservation of species of the tribe Marmosini were assessed specifically and at a national scale. Also, no other assessment of this kind was done within any other marsupial group in the country. In our study, we found that the species of Marmosini from Colombia have relatively few areas covered by the Colombian NPA network (Tab. 1). Moreover, only strict and national reserves represent desirable scenarios for their conservation, with most of their overlapped areas having low human pressure (Tab. 2). Regions identified in this work with the greatest richness of Marmosini are also known as important zones for threatened and endemic vertebrates in the country (Forero-Medina and Joppa, 2010; Kattan et al., 2004), giving support to the idea of Andean cordilleras as highly important spots for biodiversity and conservation in general (Myers et al., 2000), and for Marmosini species in particular.

Spatial patterns of biodiversity

Our finding of the highest potential richness concentrated at mid-elevations of the Andean region is a common pattern found in other groups of plants and animals (Rangel-Ch., 2015; Forero-Medina and Joppa, 2010; Kattan et al., 2004) but to our knowledge, this is the first time it is described for Marmosini (or any other New World marsupials). Yet, the prevalence of such richness in the eastern slope of the Eastern Andes needs to be explored and explained further on. This pattern is likely related to the many Cis-Andean taxa in this group (Voss

and Giarla, 2021; Gutiérrez et al., 2010), but also to other non Cis-Andean species contributing to this richness, which can be related to overlapping environments in western Amazonia (Supplement S3). Recently, Clerici et al. (2019) discussed the importance of the Páramo and Imerí provinces (sensu Morrone, 2014), with which our region of highest and mid-high Marmosini potential richness overlaps. These authors mentioned the area as a priority corridor to be preserved for Amazonian-Andean biodiversity in Colombia, especially within the current social context of the country (Clerici et al., 2019, 2016). This area could have played an important role in the diversification and distribution of this group of marsupials, as in other mammals (Patterson and Velasco, 2008).

Bax and Francesconi (2019) studied tropical Andean faunas, and found that areas in the Colombian Andes have high levels of irreplaceability and vulnerability. Forero-Medina and Joppa (2010) found that for mid-elevation biomes of the Andes ("Orobiomas medios de los Andes"), only 13% are covered by the NPA network. Moreover and specifically for marsupials, spatial data of conservation values (Martin et al., 2021) and phylogenetic diversity and taxonomic richness (Fergnani and Ruggiero, 2015) reinforce the idea of the Andes as a critical region for the conservation of New World marsupials (including Marmosini) in the country. Our results and those above strengthen the argument of the Andes, and specifically its mid-elevations habitats, as of crucial importance for the conservation of Marmosini (Fig. 4). However, it is also important to acknowledge other regions such as the Pacific, Serranía de San Lucas, Sierra de La Macarena, and Sierra Nevada de Santa Marta (Fig. 4), all of these with different potential richness values.

Our data shows that Marmosini is clearly restricted to low and middle elevations below 2000 m. Besides this, other natural limits identified

Table 1 – Range, conservation, and pressure areas for Marmosini species of Colombia based on Maxent models. All values are presented in km² and were calculated based on a geodesic approach in a WGS 84 projection. Area under protection categories (IUCN columns) are based on World Database on Protected Areas IUCN_CAT, while pressure categories are a discretization of pressure map for Colombia for the year 2015. Correspondent percentage of total range area is given in square brackets for pressure data. Area under pressure are based on Correa Ayram et al. (2020).

Species	Range area	IUCN		Area under pressure	
		Strict	Managed	High	Low
<i>Marmosa alstoni</i>	223 628	16 800	14 592	93217 [41.6]	133312 [59]
<i>Marmosa germana</i>	73 204	17 202	33	3125 [4.2]	69214 [94.5]
<i>Marmosa isthmica</i>	93 904	6917	6605	31297 [33.3]	62037 [66]
<i>Marmosa jansae</i>	138 798	27 496	42	10610 [7.6]	126481 [91.1]
<i>Marmosa lepida</i>	505 690	109 950	1999	46383 [9.1]	456494 [90.2]
<i>Marmosa phaea</i>	323 289	39 460	18 381	148768 [46]	175246 [54.2]
<i>Marmosa regina</i>	70 911	11 151	142	9783 [13.7]	61920 [87]
<i>Marmosa robinsoni</i>	213 643	13 506	12 925	146153 [68.4]	68539 [32]
<i>Marmosa rubra</i>	5347	145	55	2453 [45.8]	3072 [57]
<i>Marmosa rutteri</i>	74 932	15 683	114	3748 [5]	71317 [95.1]
<i>Marmosa waterhousei</i>	631 759	122 118	14 781	139608 [22]	491274 [77.7]
<i>Marmosa xerophila</i>	11 533	258	240	3712 [32.1]	7582 [65.7]
<i>Marmosa zeledoni</i>	90 293	8355	5140	33675 [37.2]	56999 [63.1]
<i>Monodelphis adusta</i>	330 140	45 870	21 496	142153 [43]	188887 [57.2]
<i>Monodelphis brevicaudata</i>	39 828	9101	19	33 [<0.1]	38502 [96.6]
<i>Monodelphis palliolata</i>	25 180	2619	718	13375 [53.1]	12201 [48.4]

in this report are worthy of mention, like mid-high richness areas at the Amazon which are bounded North by the Caquetá river (Fig. 4a). Similarly, two species in the Amazon presented complementary potential distributions (*M. germana* and *M. regina*), separated east and west between the Caquetá and Putumayo rivers, and many of the Amazonian species following river courses closely (Supplement S3). These results suggest an important role of rivers as natural barriers for these species, a hypothesis to be tested for this group of marsupials in Colombia. Different studies have shown the importance of rivers as barriers to the dispersion of New World marsupials (and other mammals), especially in forested habitats (Patton et al., 2000; Myers, 1982), in what is known as the “Riverine Barrier Hypothesis” (Wallace, 1854). Our results add support to this geographic hypothesis, especially for the Amazonian region, in which large and wide rivers occur.

Marsupials and environmental variables

The models we generated showed a higher relationship between precipitation variables and the distribution of Marmosini, with temperature variables only important in the models for a few species. This pattern of precipitation related variables as the most important in ENM was also

found in *Thylamys pallidior*, *Dromiciops gliroides*, and *Rhyncholestes raphanurus* (Martin, 2011, 2010, 2008), species from clearly different environments than those of Colombian Marmosini, and not close phylogenetically. Also, precipitation variables were found to be important in ENMs of the semiaquatic *Chironectes minimus* (Prieto-Torres and Pinilla-Buitrago, 2017), a tropical and subtropical species with an upper altitude limit of 2000 m. Although Birney and Monjeau (2003) described the mean minimum extreme temperature as a possible limiting factor for marsupial richness (especially outside the tropics), they acknowledged that precipitation differences could be a surrogate for habitat heterogeneity, thus supporting a higher richness in some latitudinal bands or areas. Our findings that ENM of Marmosini were mostly influenced by precipitation variables can be related to Colombia’s high environmental heterogeneity, especially in areas bounded by the different Cordilleras (Londoño-Murcia et al., 2010). These precipitation and geographic variations, and their consequence in the habitats/environments of Colombia, might help explain the high biotic richness, of which our findings of Marmosini richness is only an example.

Table 2 – Analysis of protection type areas for Marmosini species of Colombia based on Maxent models. Strict conservation category corresponds to Ia, Ib, and II, while Managed-resources corresponds to the remaining categories of the World Database on Protected Areas. All values are presented as percentages (%) of the total range area of each specie.

Species	IUCN		Governance		
	Strict	Managed	National	Sub-national	Private
<i>Marmosa alstoni</i>	7.51	6.53	7.71	6.26	0.06
<i>Marmosa germana</i>	23.5	0.05	23.54	0.00	0.00
<i>Marmosa isthmica</i>	7.37	7.03	8.60	5.84	0.05
<i>Marmosa jansae</i>	19.81	0.03	21.36	0.00	0.01
<i>Marmosa lepida</i>	21.74	0.40	26.99	0.54	0.02
<i>Marmosa phaea</i>	12.21	5.69	11.53	6.57	0.09
<i>Marmosa regina</i>	15.73	0.20	22.86	0.00	0.02
<i>Marmosa robinsoni</i>	6.32	6.05	5.95	6.34	0.08
<i>Marmosa rubra</i>	2.73	1.04	3.67	0.05	0.05
<i>Marmosa rutteri</i>	20.93	0.15	25.98	0.00	0.01
<i>Marmosa waterhousei</i>	19.33	2.34	23.49	2.46	0.05
<i>Marmosa xerophila</i>	2.24	2.08	2.24	2.08	0.00
<i>Marmosa zeledoni</i>	9.25	5.69	11.39	3.49	0.07
<i>Monodelphis adusta</i>	13.89	6.51	14.14	7.21	0.11
<i>Monodelphis brevicaudata</i>	22.85	0.05	22.85	0.00	0.05
<i>Monodelphis palliolata</i>	10.4	2.85	7.62	5.57	0.07

Table 3 – Analysis of conservation-pressure areas for the Marmosini species of Colombia based on Maxent models. For each species, values are presented as the percentage of the protected area of each protection category that falls under high (clean value) and low pressure (square brackets). Values that do not add up to 100% mean there are no data values for that category.

Species	IUCN		Governance		
	Strict	Managed	National	Sub-national	Private
<i>Marmosa alstoni</i>	5.07 [94.27]	34.86 [64.28]	5.29 [93.91]	35.47 [63.88]	41.16 [54.02]
<i>Marmosa germana</i>	0 [98.79]	4.67 [94.34]	0.01 [98.79]	0 [96.04]	34.86 [55.16]
<i>Marmosa isthmica</i>	4.27 [89.59]	32.76 [62.78]	7.8 [85.28]	32.9 [63.88]	51.99 [33.4]
<i>Marmosa jansae</i>	0.04 [98.8]	23.09 [75.91]	0.03 [99.13]	0 [97.84]	82.28 [14.26]
<i>Marmosa lepida</i>	0.51 [99.11]	24.87 [74.88]	0.4 [99.34]	17.13 [82.8]	49.27 [47.5]
<i>Marmosa phaea</i>	5.42 [94.36]	41.72 [58.08]	6.13 [93.7]	34.7 [65.09]	51.19 [43.3]
<i>Marmosa regina</i>	0.07 [99.9]	13 [86.91]	0.07 [99.9]	0	99.33 [0]
<i>Marmosa robinsoni</i>	7.29 [90.96]	48.11 [50.36]	7.1 [90.44]	45.63 [53.57]	68.79 [24.86]
<i>Marmosa rubra</i>	0.11 [97.47]	2.19 [97.38]	0.08 [98.12]	0 [98.35]	45.3 [47.68]
<i>Marmosa rutteri</i>	0.2 [98.19]	11.12 [88.62]	0.19 [98.7]	0 [98.49]	80.28 [16.91]
<i>Marmosa waterhousei</i>	0.42 [99.2]	41.77 [57.84]	0.7 [99.01]	35.06 [64.79]	62.16 [34.55]
<i>Marmosa xerophila</i>	17.14 [77.86]	74.49 [23.79]	17.14 [77.86]	74.49 [23.79]	0
<i>Marmosa zeledoni</i>	2.81 [95.99]	37.05 [61.63]	7.99 [90.96]	40.94 [57.29]	43.67 [49.44]
<i>Monodelphis adusta</i>	5.37 [94.06]	38.1 [61.08]	5.67 [93.69]	32.79 [66.69]	53.87 [41.97]
<i>Monodelphis breviceaudata</i>	0.01 [99.46]	1.32 [88.08]	0.01 [99.46]	0	1.32 [88.08]
<i>Monodelphis palliolata</i>	5.06 [93.03]	37.1 [60.68]	5.67 [92.94]	20.01 [77.24]	54.94 [41.05]

Colombian Marmosini richness, conservation, and pressure

We compiled information from 16 species of the 19 listed for the country (Voss and Giarla, 2021; Solari et al., 2013), which means that 15.78% of the species could not be evaluated due to lack of information. Importantly, species with no records in Colombia but that are cited in the current species’ list of the country (e.g., *M. rubra* and *M. palliolata*) were predicted to occur within the country’s limits (Supplement S3), adding support to the country’s currently recognized species richness. In the last national and global conservation assessment which included these species (IUCN, 2021; Rodríguez-Mahecha et al., 2006), only two were listed as globally threatened (*M. phaea* and *M. xerophila*) and only one nationally threatened (*M. xerophila*). Given that the last national assessment took place more than 15 years ago, we expect that the information provided here can be used in the upcoming and much-needed conservation reassessments.

Human pressure scenarios for the country are challenging. Correa Ayram et al. (2020), based on the Legacy-adjusted Human Footprint Index (LHFI), found that this index increased 50% from 1970 to 2015. Areas at the foothills of the Andes, especially in the eastern slope, are among the areas with the highest proportion of LHFI preserving less natural habitats. This is mostly related with deforestation fronts (Correa Ayram et al., 2020; Clerici et al., 2019) and their effects on habitat continuity and connectivity. This has a direct impact on the majority of species considered here due to their largely arboreal habits, except for the three species of *Monodelphis* (Astúa, 2015). Other regions such as the Pacific and Caribbean, that also present high levels of LHFI, are areas of high and mid-richness of Marmosini species (Fig. 4). What is more challenging in these areas, is that a variety of human activities affect marsupial species in different ways. For example, deforestation is the main cause of habitat loss in the Andean-Amazonian foothills (Dávalos et al., 2014, 2011), while illegal mining for gold and other metals is an important cause for habitat degradation and loss in the Pacific region (Correa Ayram et al., 2020; Servicio Geológico Colombiano, 2012). Illegal coca and the expansion of African oil palm plantations are among other important causes for habitat loss or modification (Dávalos et al., 2011).

In general, conservation-pressure scenarios for Marmosini species are complex, as is the case for many species in the country. Especially with the social and cultural context in which these problems are immersed. In particular, we suggest that species such as *M. xerophila* and *M. isthmica* (among others), with low percentages of their ranges covered by the NPA network and large areas of high pressure, should receive special attention in future conservation efforts.

There are many ways to study species distribution, as well as many algorithms among ENM methods (Peterson et al., 2011). In this study, we chose a widely used algorithm that we expect can be used to make direct comparisons, as more and better data become available and/or other groups are assessed. In this sense, we made a methodological framework that takes into account most of the discussed caveats of Maxent and ENM research (Zurell et al., 2020; Feng et al., 2019; Merow et al., 2013; Anderson and Gonzalez, 2011). Furthermore, other results from different models can be complementary and help clarify cases where our Maxent models seemed to have not performed appropriately (e.g., *M. phaea*). It is important to note that distribution maps from models are limited in their skill of predicting “true” species’ distribution, especially for recent events such as deforestation, fires, or other natural and human-related pressures affecting their distribution. It is then desirable that future field work corroborate or reject our final species range hypotheses.

Throughout this work, we highlighted the lack of studies on Colombian Marmosini in particular and marsupials in general, both at local and national scales. We expect to have shown one of the possibilities that arises from the current increase in taxonomic clarity within the group. A subject that we will keep working on and expanding for other related groups in the near future.

Conclusions

Although Colombia hosts a very high species richness within the tribe Marmosini, the distribution (and biology) of most species is poorly known. Also, the NPA network of Colombia preserves little of the overall species’ distribution. In this work, areas with the highest species potential richness for the tribe were identified, along with an upper limit of 2000 m, which should help maximize conservation efforts for these species. We hope our work can be included with other taxa to help prioritize the creation of new conservation areas in Colombia.

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Supplemental information

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

Table S1 Occurrences, model settings, and statistical results from MaxEnt modeling.

Supplement S2 Additional details on methods and results.

Supplement S3 Ranges and geographical barriers for *Marmosini* species of Colombia.