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Research article

Modelling 21st century refugia and impact of climate change on Amazonia's largest primates

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Edaphic and vegetation conditions can render climatically suitable sites inadequate for a species to persist, constraining the amount of suitable habitat and the possibilities of tracking preferred climatic conditions as they shift in response to climate change. We combined climatic and remotely sensed data to model current and future distributions of nine extant taxa of ateline primates across the Amazon basin. We used the models to identify and quantify potential range changes and refugia of suitable habitat from the present to the latter half of the 21st century. We applied an ensemble forecasting approach for species distribution models using 596 spatially rarefied occurrences. We parameterised these models combining reflectance data from a basin-wide Landsat TM/ETM+ image composite, and three sets of bioclimatic layers containing data for the current time period, and two different (moderate and worst-case) climate change scenarios for 2041–2070. Eight out of nine taxa are likely to experience pronounced range losses, with seven of them predicted to lose over 50% of their currently suitable habitats irrespective of climate change scenarios. Modelled ateline richness exhibited a broad decrease in high-richness areas, and a possible redistribution along the northernmost parts of western Amazonia. Refugia from 21st century climate change for the whole complex were mostly concentrated in western Amazonia, especially in its southern part. We identified hotspots of vulnerability to climate change and 21st century refugia for all Amazonian atelines while accounting for habitat characteristics that are important to guarantee the continued existence of suitable habitats for these strictly arboreal taxa. Increasing the understanding of climate change impacts on Amazonia's largest primates can help to inform spatial conservation planning decisions and management to sustain forest-dwelling biodiversity over large areas such as Amazonia.

Keywords: conservation biogeography, forest-dwelling biodiversity, habitat suitability, Landsat satellite, remote sensing, species distribution modelling

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Introduction

Climate change forecasts anticipate a massive redistribution of biota worldwide, with unprecedented negative consequences for ecosystem health and human well-being (Pecl et al. 2017). Studies attempting to predict climate-driven range shifts often rely only on predicted temperature increases and changes in rainfall patterns based on global emission scenarios (IPCC 2014). However, species distributions are also constrained by non-climatic environmental factors, such as soil characteristics that affect vegetation structure, plant species composition and primary productivity (Figueiredo et al. 2018, Van doninck et al. 2020). Unsuitable edaphic and vegetation characteristics can render climatically suitable sites inappropriate for the species continued survival, constraining both the amount of suitable habitat and the possibilities of tracking suitable climates as they shift to new locations (Sales et al. 2019, Zuquim et al. 2020). Broad-scale information concerning soil-related heterogeneity and vegetation characteristics can, therefore, make important contributions to understanding the potential synergistic effects of climate change and habitat constraints on species distributions.

Modelling species' environmental requirements and mapping geographic distributions through time and space by means of species distribution models (SDMs) is currently one of the most practical methods for assessing potential effects of future climate change on species ranges (Guisan and Thuiller 2005, Elith and Leathwick 2009). In recent years, SDMs have been greatly improved by the use of remote-sensing technology, which can provide continuous spatiotemporal information about key environmental factors, thereby improving their use and accuracy (Randin et al. 2020, Van doninck et al. 2020). Importantly, integrating remote sensing data into bioclimatic SDMs can improve spatial prioritization decisions for conservation planning, since effective habitat management needs to account for structural environmental variables other than climate to address appropriate habitat features for relevant management actions (Tuanmu and Jetz 2015, Randin et al. 2020). These habitat features are important to spatially-inform conservation planning decisions and management to sustain forest-dwelling biodiversity, especially when considering extensive areas such as Amazonia.

The use of Landsat surface reflectance data (i.e. the amount of light reflected by the Earth's surface as captured by a satellite sensor) to identify broad-scale habitat features such as local floristic and edaphic patterns within the hyper-diverse Amazonian forests have been previously explored (Tuomisto et al. 2003, Higgins et al. 2011, Zuquim et al. 2021). Landsat satellites are equipped with multispectral sensors that can capture images of the Earth's surface in multiple wavelength bands that carry essential information and environmental process that underlie the geographic distributions of species (e.g. vegetation phenology: Bobrowski et al. 2018, edaphic properties: Van doninck et al. 2020, canopy physiognomy: Chaitanya and Meiri 2021, land use change: Ma et al. 2021). A Landsat TM/ETM+ image composite, encompassing the entire Amazon biome, has been instrumental in identifying relatively stable habitat features in the region and enhancing the performance of SDMs (Van doninck and Tuomisto 2018, Tuomisto et al. 2019, Van doninck et al. 2020). These studies have demonstrated that Landsat surface reflectance data can predict field-measured concentration of exchangeable base cations and soil-related species compositional patterns across the Amazon basin with high accuracy. Plant nutrients concentrations and soil heterogeneity have direct impacts on overall plant physiology and growth, making Landsat composites important proxies for habitat features important to sustain Amazonian forest-dwelling taxa, such as primates.

The largest primates inhabiting Amazonian forests belong to the ateline clade, which consists of the genera *Ateles* and *Lagothrix* (Platyrrhini, Atelinae). Atelines are large-bodied highly frugivorous taxa, showcasing distinctively selective eating habits (Di Fiore and Campbell 2007). They have large home ranges, long reproductive cycles, and their combined geographic distribution captures the bulk of climatic and geological variability across the entire Amazon basin (Di Fiore and Campbell 2007). The extirpation of such large-bodied forest-dwelling animals from ecosystems could critically alter long-term forest dynamics, maintenance of above-ground biomass, and carbon storage (Peres et al. 2016). Atelines are among the most endangered and persecuted primates (Peres et al. 2016), exhibiting heightened sensitivity to deforestation and forest degradation (Rabelo et al. 2018, Cavalcante et al. 2020). They are considered keystone dispersers, providing essential ecosystem services, and their survival is intricately linked to intact and healthy forest ecosystems, making them valuable indicators of environmental change (Peres and Van Roosmalen 2002, Peres et al. 2016, Sales et al. 2020a).

Previous studies have also established that primates are highly sensitive to global climate change (Bernard and Marshall 2020), and that estimated rates of climatic niche evolution in primates are generally much slower than predicted rates of future climate change (Meyer and Pie 2021). Additionally, by 2050 temperatures in the Amazonian region may surpass the upper limits that primates can tolerate (Sales et al. 2020c). The Amazonian atelines can thus offer an especially robust and useful system for exploring the synergistic effects of climate and habitat constraints on species distributions.

In this study, we combined data on climatic variables and Landsat multispectral canopy reflectance via an ensemble forecasting approach for SDMs to project the distribution of nine extant taxa of atelines across the Amazon basin up until the mid-21st century (2041–2070). We used these projections to identify and quantify range changes and potential 21st century refugia at taxon level under two different scenarios of climate change, providing spatially explicit information on the extent to which potential ateline ranges can be expected to change in the near future. We also assessed spatial patterns and temporal changes in local species richness by stacking the SDMs obtained for all atelines for the present and for each future climate change scenario. Finally, we identified potential 21st century refugia for the whole complex while accounting for both scenarios of climate change.

Material and methods

Occurrence data

In this study, we adopted the taxonomic proposal of Fooden (1963), which is supported by molecular systematic studies (Di Fiore et al. 2014, Botero et al. 2015, Morales-Jimenez et al. 2015). Our focus was on nine extant taxa within six Amazonian species of the *Ateles*/*Lagothrix* complex (spider and woolly monkeys, respectively): *Ateles belzebuth*, *A. chamek*, *A. marginatus*, *A. paniscus*, *Lagothrix flavicauda*, *L. lagothricha cana*, *L. l. lagothricha*, *L. l. lugens* and *L. l. poeppigii*. We compiled geo-referenced occurrence data from online sources (Global Biodiversity Information Facility http://www.gbif.org; iNaturalist https://www.inaturalist.org/), and comprehensive peer-reviewed scientific literature. A total of 3297 occurrence records were found for all taxa combined. Following standard practices (Sillero et al. 2021, Sillero and Barbosa 2021), we carefully cleaned and spatially thinned our occurrence records in three main steps. First, we used an automated procedure to flag and exclude records with common georeferencing problems (‘CoordinateCleaner’ package: Zizka et al. 2019), such as occurrences assigned to open ocean, urban areas, administrative capitals or headquarters of the GBIF, as well as those with zero or identical latitude and longitude. Second, we carefully verified the remaining occurrences by corroborating these records with IUCN distribution maps and established literature, together with a careful visual inspection using interactive visualisations of spatial data. This step allowed us to identify major discrepancies, such as confirmed locality data outside IUCN range maps. Retention of these occurrence records was contingent upon confirmation through established peer-reviewed literature in the location (see the Supporting information for raw cleaned occurrence dataset). Finally, we thinned these raw occurrence records using a 5-km thinning distance to avoid spatial sampling bias from highly sampled areas, and to reduce the clustering of species occurrence points. For subsequent analysis, we used a final dataset consisting of 596 spatially rarefied occurrences (Supporting information).

Climatic data and multispectral canopy reflectance

When calibrating and projecting the SDMs, we aimed to take into account both the climatic niches of the primate taxa and their possible associations with forest habitat characteristics. The climatic niche was modelled using the nineteen bioclimatic layers available from CHELSA V2.1 (www.chelsa-climate.org, Karger et al. 2017) at a spatial resolution of 2.5 arc-minutes (~ 5 km at the Equator). Three sets of bioclimatic variables were used: one containing data for the current time period (1981–2010), and two providing predictions based on different climate change scenarios for one future time period (2041–2070).

To model forest habitat characteristics, we used surface reflectance data from a Landsat TM/ETM+ image composite (Van doninck and Tuomisto 2018) that covers the entire Amazon biome (Fig. 1). The compositing procedure used all Landsat images available for the dry season months of the years 2000–2009 (16 000 individual image acquisitions) and derived a reflectance value for each pixel that was representative of average conditions during the 10-year period (see Van doninck and Tuomisto 2017a, b, 2018 for technical details). Here we used only the red, near-infrared, and shortwave

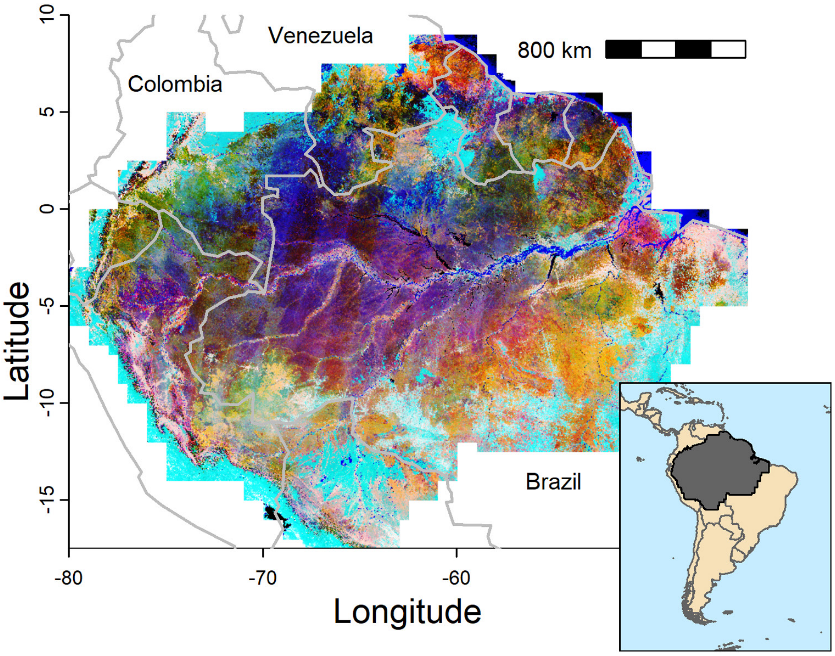

Figure 1. Landsat TM/ETM+ false color composite image depicting our study area across the Amazon basin. Red, green, and blue channels were assigned to bands 4, 7, and 3, respectively. Map projection WGS84.

infrared wavelengths (bands 3, 4, 5 and 7), because the blue and green bands had significant amounts of residual atmospheric contamination (Van doninck and Tuomisto 2018). We decided to use the raw spectral bands because it has been shown that SDMs built on unclassified remote-sensing imagery outperforms models built on single-summary transformations or classified land cover data (Shirley et al. 2013, Cord et al. 2014, Hopkins et al. 2022). Landsat TM/ETM+ variables were upscaled by resampling to a spatial resolution of 2.5 arc-minutes using the bilinear interpolation method (*resample* function in 'raster' package: Hijmans et al. 2018).

We evaluated the multicollinearity between all 23 variables using a variance inflation factor correlation analysis (*vifcor* function in the 'usdm' package: Naimi et al. 2014), setting the Pearson correlation coefficient threshold to 0.5 and VIF criterion lower than 3. Following this, we retained seven variables that were then used to model species distributions. Five of these were climatic variables: mean diurnal air temperature range (bio2), temperature seasonality (bio4), mean daily mean air temperatures of the wettest quarter (bio8), mean monthly precipitation of the warmest quarter (bio18), and mean monthly precipitation of the coldest quarter (bio19). Two were derived from the Landsat TM/ETM+ composite: band 3 (red) and band 4 (near infrared).

We carefully examined the bioclimatic variables bio8, bio18 and bio19 due to artificial discontinuities documented in Booth (2022). We reclassified these variables using the 0.01 and 0.99 quantiles, visualized this information over our study area, and applied the procedures outlined by Booth (2022). Specifically, we conducted visual inspections using the 'mapview' R package (Appelhans et al. 2022) and Google Earth Engine. We also used climate diagrams from https://climate.mapresso.com/ to analyze monthly data on precipitation and temperature at selected locations near potential zones of discontinuities, but found no artefacts within our study region.

Species distribution models

We modelled the distribution of each taxon based on environmental conditions represented by the selected five bioclimatic variables and two Landsat TM/ETM+ bands. We used three algorithms available in the 'biomod2' package (Thuiller et al. 2016) to produce the SDMs. Generalized additive models (GAMs) use nonparametric smooth functions to model nonlinear relationships between response and explanatory variables. Random forests (RFs) is an ensemble learning model based on regression trees that recursively partition the predictor space into sections to select influential predictors and automatically fit interactions. Boosted regression trees (BRTs) is another tree-based ensemble learning model that sequentially combines hundreds to thousands of regression trees. In BRTs, the trees are fitted in a forward stagewise fashion to minimize residuals in the prediction. At each step, the algorithm focuses on the weakest parts of the model (observations not accurately predicted) by fitting each new tree to the residuals of the previously fitted trees. The main difference between the two machine-learning methods is in the ensemble creation process: BRTs uses a stagewise approach, while RFs uses bootstrap aggregation (bagging) to combine multiple trees (Breiman 2001, 2002). We altered model settings from default parameters following benchmark studies (Breiman 2001, 2002, Valavi et al. 2021a, b). For GAM, we used *GCV* as the smoothing parameter estimation method; for RF, we used the square root of the total number of environmental variables as the number of variables sampled at each split (*mtry* = 3); and for BRT, we set the total number of trees to fit to 1000 (*n.trees* = 1000), and the k-fold cross-validation to five (*n.folds* = 5).

Since our SDMs were based on presence-only data, it was important to define an appropriate reference area from which the background points representing environmental variation would be selected (Soberón and Peterson 2005, Soberón and Nakamura 2009, Valavi et al. 2021a). We used as reference area the available Landsat composite covering all Amazonia (Van doninck and Tuomisto 2018). We aimed to consider species' accessible areas in an evolutionary context, accounting for the biogeographic history of both genera to capture the full potential extent of their niches (Di Fiore et al. 2014, Morales-Jimenez et al. 2015). This decision aligns with the use of biotic regions (i.e. regions where organisms share significant environmental adaptations and history) as effective geographical domains in ecological niche modelling (Barve et al. 2011). We extracted the values from samples of 1000 randomly chosen points within the reference area. We ran six different background selections for each taxon (two per algorithm) to allow for a robust estimate of model accuracy (total: 54 different background datasets), and to avoid the influence of the background-sample selection on the results of the accuracy measures (Guisan et al. 2017).

To assess the overall predictive capabilities of the SDMs, we calculated the true skill statistic (TSS) and area under the receiver operating characteristic curve (AUC) values for each model. We divided the data for each taxon such that 75% of the occurrence points were used as the training set and 25% as the testing set. We used both metrics together because they offer complementary insights into the two key aspects of predictive performance in SDMs: classification and discrimination (Sillero et al. 2021), providing a holistic evaluation of overall predictive capabilities. All models with a TSS value greater than 0.6 were retained and ensembled using the weighted average method to obtain the final probabilistic predictions (Araújo and New 2007).

We obtained taxon-specific variable importance values for each variable and modelling technique using the *get_variable_importance* function in the 'biomod2' package. The process of determining the importance of a variable for a particular modelling method involves shuffling a single variable of the given data set, creating model predictions with this shuffled data, and then calculating the Pearson's correlation between the reference and shuffled predictions. The final score is determined by subtracting this correlation value from 1. We calculated the ensemble variable importance of climatic vs reflectance variables as the average of the variable importance values of all models with the respective cross-validated TSS value above 0.6. We generated a total of 351 models (13 for each taxon for the present and 13 × 2 for the future).

Mapping potential ateline distributions in the future

Future predictions consisted of downscaled climatologies available from the CHELSA V2.1 database for 2041–2070 under two combined emission scenarios from the Earth System Model GFDL-ESM4, phase 6 of the Coupled Model Intercomparison Project (CMIP6): 1) the SSP3-RCP7, a moderate-to-high radiative forcing scenario (hereafter moderate scenario) depicting a future with low levels of economic growth but relatively high levels of greenhouse gas concentrations; and 2) the high radiative forcing scenario SSP5-RCP8.5 (hereafter worst scenario), with extremely high levels of greenhouse gas concentrations in a highly industrialized and fossil fuel-based future. The CHELSA database uses GCMs from the Intersectoral Impact Model Intercomparison Project (ISIMIP3b) protocol, which ranks models according to their performance (see technical specifications at Karger et al. 2017 for more details). These models are prioritized according to their ranking, with the highest-ranked model having the highest priority. We chose to use the GFDL-ESM4 model in accordance with these recommendations.

Given our primary focus on the impacts of climate change, only climate layers were projected into the future, while the two Landsat TM/ETM+ variables were held constant. Although these variables are dynamic entities, the biogeographic patterns in them primarily reflect geological and soil heterogeneity, which are relatively stable features of the landscape (Van doninck and Tuomisto 2018, Tuomisto et al. 2019). Therefore, it can be inferred that despite the potential impact of climate on soil formation, the slow and gradual nature of this process and their consequential effects on vegetation properties is unlikely to alter broad biogeographical patterns during the time period considered here.

To evaluate the proportional change in range size in the future compared to the present, we used the pixels for each taxon with predicted habitat suitability above and below the threshold where the sum of model sensitivity and specificity is maximized (max SSS: Liu et al. 2005). Pixels predicted above and below the max SSS will hereafter be referred to as suitable and unsuitable habitat, respectively. Using this cut-off from the ensemble models, we identified areas of range contractions (i.e. grid cells that were modelled as currently suitable but predicted to become unsuitable), range expansions (i.e. grid cells that are currently not suitable but were predicted to become so in the future), refugia (i.e. grid cells that were modelled as currently suitable and predicted to remain so in the future), and absence (i.e. grid cells unsuitable in both time periods).

We considered range changes under two alternative dispersal scenarios: 1) assuming that a taxon would be able to completely disperse into any new suitable grid cells in the future (full dispersal) and 2) assuming that a taxon would be unable to disperse from currently suitable grid cells (no dispersal). We quantified overall future projection outcomes by subtracting the proportional amount of range contractions from the proportional amount of range expansions.

To assess spatial patterns and temporal changes in local species richness, we stacked the probabilistic forms of the SDMs obtained for all taxa for the current period and for each of the two climate change scenarios, using the following equation:

$$E\left(S_j\right)=\sum_{k=1}^{K} p_{j,k}$$

where $E(S_j)$ is the expected species richness (S) at site j, K is the number of taxa in the dataset (n = 9), and $p_{j,k}$. is the occurrence probability prediction for taxon k at site j. The sum of the taxon-specific probabilities provided an estimate of the expected species richness in each grid cell, following the 'predict first, assemble later' principle (S-SDM: Guisan and Thuiller 2005, Guisan and Rahbek 2011, Peyre et al. 2020). We used the same max SSS threshold as in the taxon-specific range analysis and stacking approach to identify and quantify the potential refugia for the whole complex up until 2070.

Results

Modelled distributions of most woolly monkeys (*Lagothrix)* were restricted to the northwestern part of the Amazon basin, except for *L. l. cana* and *L. flavicauda* whose predicted distributions extended towards the southeastern and southwestern edges of the Amazon basin, respectively (Fig. 2). Spider monkeys (*Ateles)* were more widely distributed, occupying large areas across Amazonia, although *A. marginatus* and *A. paniscus* were restricted to the eastern part. The distributions of the nine taxa were largely controlled by climatic variables, but with important idiosyncratically differences (Fig. 3). Reflectance variables were particularly important for *L. l. cana*, *A. marginatus* and *A. paniscus*.

Mean TSS and AUC values were considered acceptable overall for individual models, with the ensemble approach prioritizing models with high discrimination and classification capacities for accurate predictions (Supporting information). We did not find any significant issues with using AUC and TSS in terms of their sensitivity to prevalence (Leroy et al. 2018), as the taxa with the highest and lowest sample prevalence in this study (*A. paniscus* and *L. l. lugens*, respectively) had consistently high values for both metrics (Supporting information). Across all taxa, the BRT and RF algorithms performed better than the GAM algorithm, with approximately 33% of the BRT and RF models retained in comparison to 21% retention for GAM models.

The surface areas of currently suitable habitat greatly varied among taxa, from 49 325 km^2 *L. l. lugens* to 874 025 km^2 *A. chamek* (Table 1, Supporting information). The SDMs of eight taxa predicted extensive range contractions under both climate change scenarios and dispersal assumptions, while only one taxon *L. l. lugens* was predicted to increase its spatial distribution (Fig. 4). As for the overall future projection outcomes, three of the nine taxa were predicted to lose more than 80% of their currently suitable habitat under both climate change scenarios, with one of them *L. l. lagothricha* becoming virtually extinct from the studied area under the worst-case scenario (Table 1, Supporting information). Two

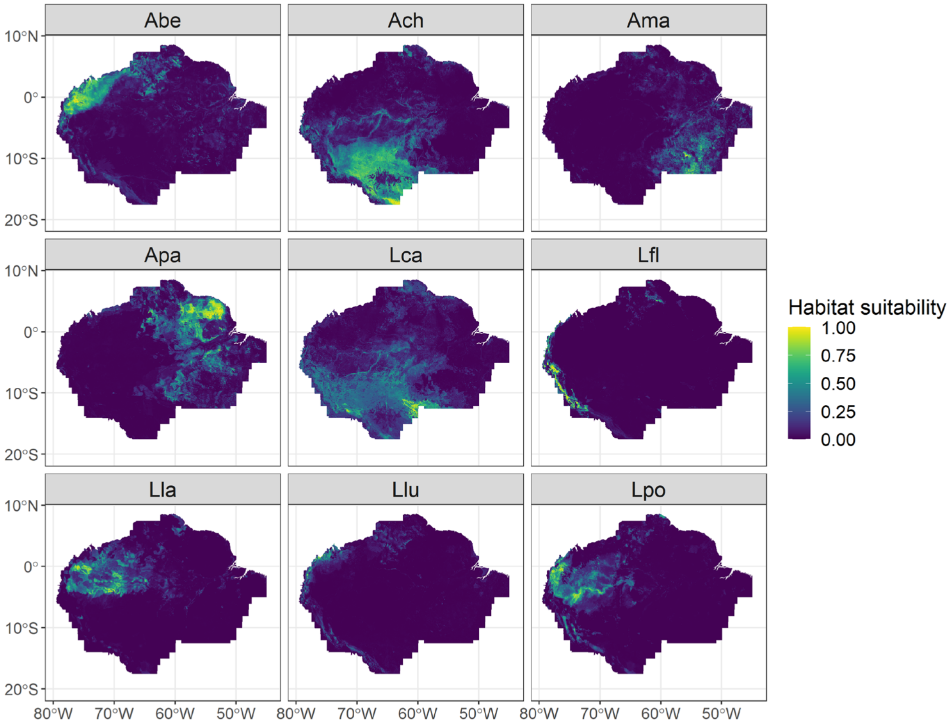

Figure 2. Current habitat suitability modelled for the nine taxa of atelines (Platyrrhini, Atelinae) across the Amazon basin. Taxon name abbreviations: Abe – *Ateles belzebuth*, Ach – *Ateles chamek*, Ama – *Ateles marginatus*, Apa – *Ateles paniscus*, Lca – *Lagothrix lagothricha cana*, Lfl – *Lagothrix flavicauda*, Lla – *Lagothrix lagothricha lagothricha*, Llu – *Lagothrix lagothricha lugens*, Llp – *Lagothrix lagothricha poeppigii*.

spider monkeys (*A. marginatus* and *A. paniscus*) were predicted to lose most of their original suitable habitat in eastern Amazonia, with the former virtually disappearing from the southeastern Amazon basin in Brazil under the worst-case scenario (Supporting information).

The amount of area identified as refugia varied among taxa and climate change scenarios (Table 2, Supporting information). *Ateles marginatus*, *L. l. lagothricha* and *L. l. lugens* had the smallest refugia in all climate change scenarios. Under the moderate climate change scenario, three of the nine taxa

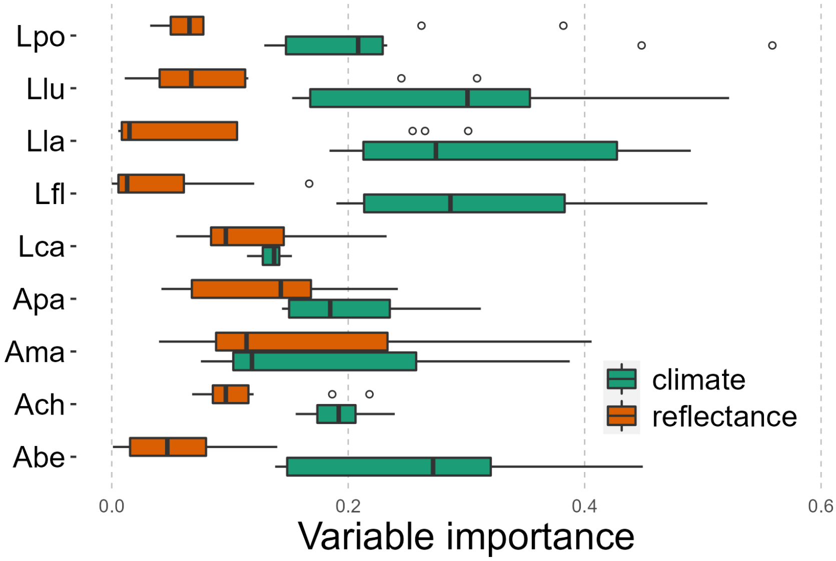

Figure 3. Ensemble variable importance of climatic vs reflectance variables used to fit the SDMs of the nine taxa of Amazonian atelines (Platyrrhini, Atelinae). The lower and upper hinges represent the 25th and 75th percentiles respectively, while the whiskers depict 1.5 times the distance between the first and third quartiles. Data beyond the end of the whiskers are displayed as individual dots. Taxon name abbreviations: Abe – *Ateles belzebuth*, Ach – *Ateles chamek*, Ama – *Ateles marginatus*, Apa – *Ateles paniscus*, Lca – *Lagothrix lagothricha cana*, Lfl – *Lagothrix flavicauda*, Lla – *Lagothrix lagothricha lagothricha*, Llu – *Lagothrix lagothricha lugens*, Llp – *Lagothrix lagothricha poeppigii*.

Table 1. Currently suitable habitat areas and overall future projection outcomes for the nine taxa of atelines (Platyrrhini, Atelinae) across the Amazon basin as estimated from SDM results. Positive and negative values refer to increase and decrease in suitable areas, respectively.

	Currently suitable habitat (km²)	Moderate scenario (%)	Worst-case scenario (%)
Ateles belzebuth	486 950	−68	−71
Ateles chamek	874 025	−22	−31
Ateles marginatus	300 275	−51	−78
Ateles paniscus	432 375	−91	−94
Lagothrix flavicauda	125 775	−42	−26
Lagothrix lagothricha cana	420 325	−64	−74
Lagothrix lagothricha lagothricha	371 450	−85	−98
Lagothrix lagothricha lugens	49 325	56	131
Lagothrix lagothricha poeppigii	351 700	−81	−91

had less than 10% of their currently suitable habitat predicted as stable (Table 2). Under the worst-case scenario, this was the case for six taxa. On the other hand, *A. chamek* was the species with the largest predicted refugia, encompassing 407 425 and 349 950 km² under the moderate and worst-case scenario, respectively.

For the current time period, our models estimated between 0.05 and 3.21 taxa per pixel (0.66 ± 0.39; mean ± SD), while for the future time period, the predicted range was 0.07–2.96 (0.65 ± 0.32) under the moderate scenario and 0.08–3.31 (0.70 ± 0.32) under the worst-case scenario. Areas with the highest predicted richness were mostly distributed in western Amazonia, especially in Peru, northeastern Ecuador, and southern Colombia (Fig. 5). The estimates for the moderate and worst-case scenarios of climate change exhibited a broadly similar spatial pattern of species richness, with a visual decrease in areas with higher predicted richness, and a possible redistribution/migration along the northernmost parts of western Amazonia.

Refugia for the whole complex were mostly concentrated in the western part of the Amazon basin, especially southwest (Fig. 6). Under the worst-case scenario, refugia were mostly absent from eastern Amazonia. We identified refugia areas in at least seven countries, irrespective of climate change scenarios (both scenarios in Fig. 6). Peru and Bolivia were the countries with the largest areas covered by refugia when both climate change scenarios were considered simultaneously. In Brazil, refugia were distributed in the southernmost part of Amazonas state, west of the Madeira River, and along the southern-most border of the country's Amazon rainforest. Colombia, Ecuador and Guyana also had important refugia areas irrespective of climate change scenarios.

Discussion

Spider and woolly monkeys

Ateles marginatus and *A. paniscus* were predicted to lose most of their original area of occurrence in southern and northeastern Amazonia, respectively. These results are in agreement with previous forecasts for other primate species from eastern Amazonia. For example, 11 out of 12 endemic primate species from eastern Brazilian Amazonia could have their distribution area reduced, with over 30% of these species predicted to lose more than 90% of their climatically suitable area by 2050 (da Silva et al. 2022). When considering climate change and deforestation scenarios simultaneously, da Silva et al. (2022) found that *A. marginatus* could suffer a loss of more than 98%

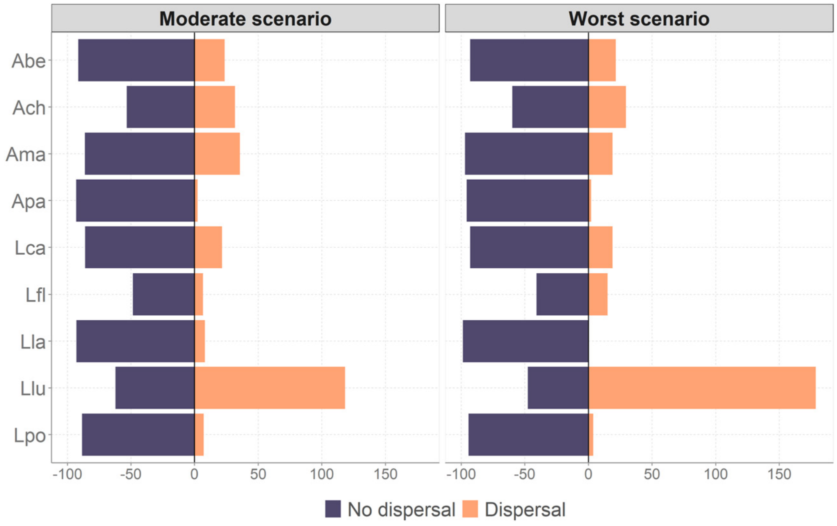

Figure 4. Predicted percentage change in Amazonian ateline (Platyrrhini, Atelinae) ranges under the moderate and the worst-case scenario of climate change (2041–2070), assuming either no dispersal or full dispersal. Taxon name abbreviations: Abe – *Ateles belzebuth*, Ach – *Ateles chamek*, Ama – *Ateles marginatus*, Apa – *Ateles paniscus*, Lca – *Lagothrix lagothricha cana*, Lfl – *Lagothrix flavicauda*, Lla – *Lagothrix lagothricha lagothricha*, Llu – *Lagothrix lagothricha lugens*, Llp – *Lagothrix lagothricha poeppigii*.

Table 2. Twenty-first century refugia size in comparison to currently suitable habitat areas for each Amazonian ateline taxon (Platyrrhini, Atelinae) under the moderate and the worst-case scenario. The '%' values represent the proportion of currently suitable habitat that were predicted to remain suitable in the future.

	Moderate scenario		Worst scenario	
	km²	Proportion (%)	km²	Proportion (%)
Ateles belzebuth	41 325	8	34 375	7
Ateles chamek	407 425	47	349 950	40
Ateles marginatus	41 375	14	8950	3
Ateles paniscus	29 950	7	18 525	4
Lagothrix flavicauda	64 750	51	74 325	59
Lagothrix lagothricha cana	58 625	14	29 250	7
Lagothrix lagothricha lagothricha	26 225	7	4900	1
Lagothrix lagothricha lugens	18 650	38	25 825	52
Lagothrix lagothricha poeppigii	40 250	11	19 900	6

of its suitable area of occurrence in the eastern part of the Brazilian Amazonia. We did not explicitly account for deforestation in our study, but the use of remote sensing data would have caused the already deforested areas to be identified as unsuitable habitat, which can explain the similarities between our pessimistic forecasts and the results cited above.

The results we obtained for woolly monkeys distribution models agree well with previous results (Linero et al. 2020), with both showing consistent range contractions across climate change scenarios. However, the previous country-level study may have underestimated climate change impacts on woolly monkeys, especially because it used only bioclimatic variables and combined all recognized sub-species of *L. lagothricha* to build SDMs, thereby obtaining a larger estimate of the realised niche. Incorporating variables derived from remote sensing into the woolly monkeys' habitat suitability models and considering taxonomic resolution below the species level led to narrower niche estimates, a greater decline in suitable conditions, and smaller refugia in our study. In addition, differences in habitat suitability between sub-species of *L. lagothricha* suggest that they are locally adapted, which is expected for species with distributions that span a wide range of environmental gradients (e.g. soils and climate) (Ikeda et al. 2017, Zhang et al. 2021). Reflectance data played a crucial role in this context providing information on a different niche axis than climatic data, and capturing canopy properties and vegetation characteristics that can vary dramatically with soil heterogeneity, even within climatically uniform areas (Higgins et al. 2011, Tuomisto et al. 2019, Van doninck et al. 2020, Zuquim et al. 2020).

Of all Amazonian atelines, the only taxon with a positive overall projected future outcome was *L. l. lugens*. This taxon had the smallest area of currently suitable habitat, matching previous studies reporting its distribution restricted to the eastern and central cordilleras of the Colombian northern Andes and adjacent lowlands (Botero et al. 2010, Mantilla-Meluk 2013). *Lagothrix l. lugens* is also historically documented in Venezuela, yet the lack of recent reports on its populations implies a possible extinction scenario in the country (Botero et al. 2010). However, patches of currently suitable habitat were predicted by our models in Venezuela, and these areas are expected to increase under both climate change scenarios, extending into the country's western and central high elevation areas (southeast of the Orinoco River), and along the border with Brazil (Supporting information). Anticipating potential shifts in the distribution of suitable habitat is particularly important for the appropriate reintroduction of populations for effective long-term conservation. We thus suggest that these areas should be targeted for future research, reintroduction and translocation plans, and also to further field-proof the purported extinction scenario for *L. l. lugens* in the country.

Assessing 21st century refugia and climate change impacts on strictly arboreal taxa

The outcomes of climate change on ateline distributions modelled in this study will likely have deleterious effects on their populations, since the distributions of the nine taxa

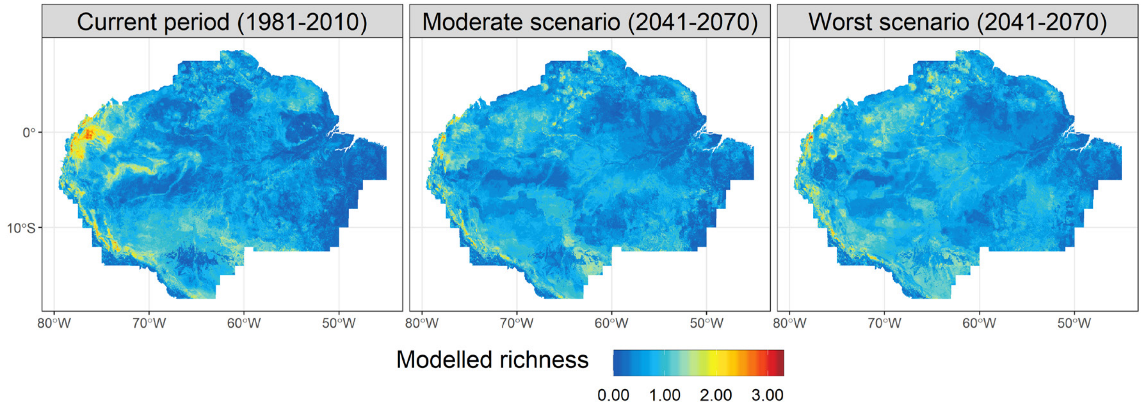

Figure 5. Modelled richness for the Amazonian ateline complex (Platyrrhini, Atelinae) across the Amazon basin for the present, and for the moderate and worst-case scenario of climate change.

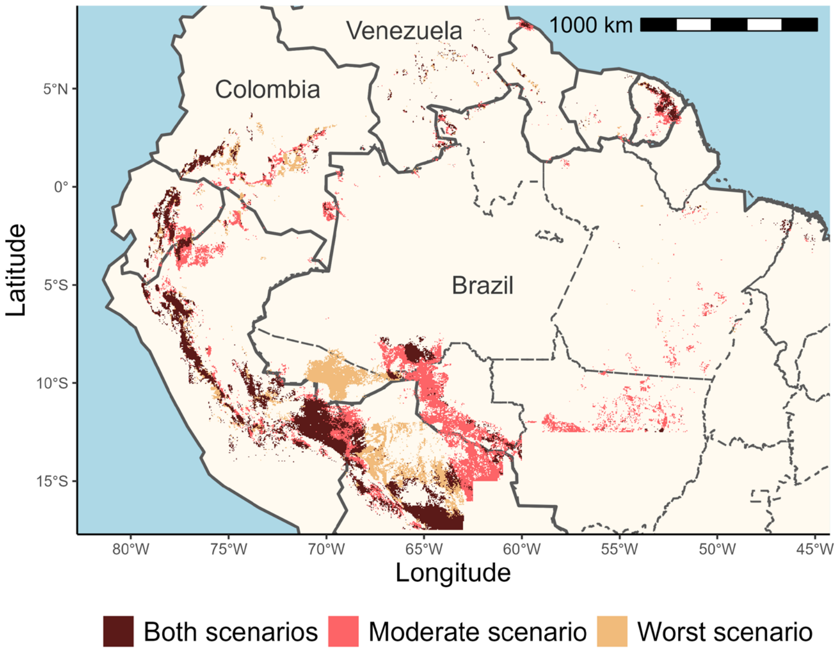

Figure 6. Refugia from 21st century climate change for the Amazonian ateline complex (Platyrrhini, Atelinae) across the Amazon basin under the moderate and worst-case scenario of climate change. Map projection WGS84.

were largely controlled by climatic variables (Fig. 3). In light of these forewarning scenarios and recognizing the large potential for lagged primate responses to climate change (Sales et al. 2020c), the identification of 21st century refugia that contain critical habitat features is a crucial step towards effective conservation and management of these strictly arboreal taxa. Suitable habitat physiognomy in terms of vegetation and soil conditions needs to remain coupled with suitable climatic conditions to guarantee the continued existence of colonizable habitats (Chaitanya and Meiri 2021). In addition, our results suggest a potentially extensive and significant mismatch between the climatic and the edaphic/vegetation niche dimensions of the ateline habitat in the near future. This mismatch may confine populations of atelines to non-analogue climates or to non-analogue habitat physiognomies, i.e. regions climatically suitable but with unsuitable edaphic and vegetation conditions (or vice versa).

These findings provide crucial insights that enhance our understanding of the atelines' vulnerability and contribute to more accurate conservation status evaluations in the face of climate change. Given the projected decline in both the extent and quality of habitat for Amazonia atelines in the coming years, we strongly advocate for the integration of climate change impact data derived from our study into future IUCN Red List evaluations. For instance, we propose that *Ateles paniscus* and *Lagothrix lagothricha* should be categorized as Engangered on the IUCN Red List. The Endangered status of *A. belzebuth*, *A. chamek* and *Lagothrix lagothricha poeppigii* should also be revised accordingly.

Modelled richness pointed to parts of western Amazonia, especially Peru, northeastern Ecuador, and southern Colombia, as centers of species richness for the study group. We also found a general agreement between patterns of current species richness and refugia. Although regions with high species richness are widely used to establish conservation objectives, there is a surprisingly low overall congruence between hotspots of species richness, threats, and endemism at larger scales (Orme et al. 2005), which are also key components to be considered when setting conservation priorities. Our SDMs predict extensive range contractions in regions with low ateline richness, especially in eastern Amazonia, where only two atelines are predicted to occur. Additionally, refugia were mostly absent in this region, especially under the worst-case scenario. The eastern Amazonian forests are experiencing rapid climate change in addition to other anthropogenic disturbances, such as deforestation and forest fires (Soares-Filho et al. 2006, Brando et al. 2020). These factors need to be invoked for priority-setting purposes, focusing on key elements such as irreplaceability and vulnerability. The Brazilian Amazonian endemic *A. marginatus*, the largest arboreal mammal inhabiting the highly-threatened eastern limits of Amazonia, should be a focus of particular attention.

Determining which conservation strategy will be best for mitigating climate change impacts on biodiversity represents one of the major tasks for conservation planning, and achieving it will usually depend on the ability of conservation managers to identify areas at higher risk and areas of climate refugia. Here we have provided decision makers with the necessary information to evaluate tradeoffs when considering different strategies by identifying and quantifying hotspots of vulnerability to climate change and refugia across the whole Amazon basin, considering both climatic and local habitat constraints. As conservation planning involves an interactive process (Margules and Pressey 2000), decision makers can use our results to develop more dynamic conservation strategies, identifying different adaptation needs for different taxa and areas towards which conservation efforts should be targeted to mitigate climate change in the Anthropocene.

Limitations of SDMs and future directions

Forecasting species risks to global climate change carries with it a number of assumptions and uncertainties (Wiens et al. 2009, Thuiller et al. 2019). We attempted to address some potential sources of uncertainty in our SDMs by using a rigorous data cleaning process, two different climate change scenarios, two dispersal assumptions, and an ensemble forecasting approach using highly important predictors of Amazonian ateline distributions. However, our current models do not consider other factors that could influence the modelled impacts of climate change, such as genetic limitations, adaptive responses, and more accurate dispersal models (DeMarche et al. 2019, Hu et al. 2021).

More specifically, due to simplifications in our dispersal scenarios (full dispersal versus no dispersal), it is crucial to underscore certain limitations in our conclusions. Firstly, we recognize that dispersal constraints are more likely to play a role lying somewhere between the two extremes considered in this study. Secondly, we assumed an isotropic dispersal, meaning that colonization would be contingent upon achieving a balance between climatic and edaphic/vegetation conditions; thereby overlooking other ecological aspects of primate dispersal dynamics, such as river barriers (Sales et al. 2019). It is also likely that forest dynamics, biotic interactions with other forest-specialist species, and other potential barriers such as deforested areas (Esquivel-Muelbert et al. 2019, Sales et al. 2019, 2020b) will limit species' abilities to occupy the full extent of the predicted suitable space, hindering the species' expansion towards refugia areas.

The use of alternative approaches explicitly integrating more accurate dispersal constraints into models, such as cellular automaton (Engler et al. 2012, Machado-Stredel et al. 2021) or stochastic migration models (Nobis and Normand 2014) might allow more accurate predictions. Future studies may also consider incorporating multiple GCMs and land use/land cover (LULC) change into new integrative approaches (Ma et al. 2021). This would enable a more comprehensive understanding of how the synergistic effects of global climate and LULC changes are expected to impact ateline populations and habitats.

Conclusions

Our results corroborate the findings of other recent studies showing that Amazonian primates and their habitats are being (and will continue to be in the near future) drastically affected by climate change and habitat loss (Sales et al. 2019, 2020c, Cavalcante et al. 2020, da Silva et al. 2022). By incorporating information about vegetation- and soil-related forest heterogeneity by means of remotely sensed data, our study goes beyond previous work and contributes to understanding the potential synergistic effects of climate change and other habitat constraints on future species distributions. Additionally, considering taxonomic resolution below the species level can be expected to reveal more accurate habitat suitability projections, especially when local adaptation has caused niche differences to emerge between taxa (Hu et al. 2021, Zhang et al. 2021). Increasing the understanding of climate change impacts on Amazonia's largest primates helps to plan actions to mitigate climate change and to improve effectiveness of conservation efforts. Atelines can serve as an indicator group when identifying hotspots of vulnerability to climate change and refugia for conservation, thereby providing vital information for prioritizing conservation efforts in Amazonia.

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Author contributions

Thiago Cavalcante: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Adrian A. Barnett:** Writing – review and editing (supporting). **Jasper Van doninck:** Writing – review and editing (supporting). **Hanna Tuomisto:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data and R script with the complete parameter implementation settings are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6hdr7sr7q (Cavalcante et al. 2024), together with interactive maps of hotspots of vulnerability to climate change and 21st century refugia for all taxa and climate change scenarios.

Supporting information

The Supporting information associated with this article is available with the online version.

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