A review of taxonomic history and phylogeography for the spider monkeys (genus *Ateles*), with habitat suitability modelling for Amazonian *Ateles*

Chloe Eve Grant

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Supervised by Professor Jean P. Boubli

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Abstract

The spider monkeys (genus *Ateles)* (É. Geoffroy Saint-Hilaire, 1806) are one of the most widespread platyrrhine primates, ranging from the tropical and subtropical rainforests of the Yucatan peninsula and coastal regions of Vera Cruz state in Mexico, through central America, from the Pacific coast of Ecuador to Guyana and Suriname in the north-eastern region of South America, all the way to northern Bolivia. They are primates that belong to the family Atelidae (Gray, 1825), and sub-family Atelinae (Gray, 1825), the prehensile tailed monkeys. The genus encompasses broad species richness with 16 currently recognised *Ateles* species and subspecies (PSG, 2022), and are considered key indicator species in the forest who have a large impact on ecosystem health and stability. They are severely threatened by deforestation, habitat degradation, and climate change as they have restricted habitat preferences facilitated by their specialist frugivorous diet and fission-fusion social system. Although multiple authors have debated and revised *Ateles*' taxonomy, evolutionary relationships, and biogeography, the main outcome has been confusion, which impedes the ability to implement conservation actions. This dissertation provides a comprehensive review of information and studies concerned with the taxonomic and biogeographic history, as well as the distribution and conservation status of the spider monkeys. It does this in an attempt to exemplify the decades of research the genus has been subjected to, and act as an inclusive source of knowledge for academics and students interested in such topics. Additionally, it explores the genetic relationships of the *Ateles* where mitochondrial DNA (mtDNA) sequences were available using the maximum likelihood (ML) method of phylogenetic inference. We created two phylogenetic trees using (1) whole mtDNA sequences and (2) sequences from the cyt-B gene region of mtDNA. A map was created of both trees to show the geographic information attached to the sequences to try and observe if location was a factor in the phylogenetic delineation and topology of the tree. It was found that mtDNA sequences construct a clearer and more well supported tree by using the bootstrap (BS) nonparametric method of reliability. Monophyletic clades were identified in both trees, as well as a visible distinction of two separate *A. chamek* clades, of which the geographical information attached supports the recognition of a new taxa possibly due to a speciation event that reproductively isolated the two clades. Withal, the cyt-B tree only represents 12 out of the 16 currently recognised *Ateles* species and subspecies (PSG, 2022) and the mtDNA tree only includes sequences from five species, no subspecies are represented in this tree. This fact may impede the results of the phylogeny. I recommend a full taxonomic revision of the genus with

each species accounted for and geographically labelled. Finally, this dissertation uses species distribution modelling to assess habitat suitability for Amazonian species of *Ateles,* while trying to uncover the true area of occupancy (AOO) within the predicted IUCN extent of occurrence (EOO). A Pearson's correlation was evaluated between variables used to measure habitat suitability in accordance with the distribution data to determine which environmental variables were the most important in the different regions inhabited by the separate species. The maximum entropy algorithm (MAXENT) (version 3.4.3) with "dismo" (version 1.3-5) in the statistical computer program RStudio (version 4.1.1) (RStudio Team, 2022) was used to create the models. I discovered that the AOO is substantially smaller for each Amazonian *Ateles* species than that suggested by the IUCN, and habitat suitability is often poor (<0.5) in these regions. High habitat suitability zones (>0.7) are scattered across the landscape and are not always governed by protected areas. The results show that precipitation and temperature related variables had the greatest influence on the outcomes of the MAXENT models. The priorities for conservation of the Amazonian *Ateles* lies in the successful development and expansion of protected areas (PAs), specifically in the regions occupied by *A. marginatus* and *A. hybridus* where the majority of suitable habitat falls outside of the jurisdiction of PAs, and hence these forests will be the first to be fragmented and depleted. I recommend that the conservation status of the *Ateles* be re-assessed by the IUCN based on these models, and propose that assessments of all spider monkey species be carried out more frequently due to the rapid transformation and degradation of the tropical rainforests of Central and South America.

Chapter 1: A review of the taxonomy, distribution, and biogeographic history of spider monkeys (genus *Ateles*)

1.1. Introduction

Spider monkeys, classified within the genus *Ateles*, inhabit the tropical forests of Central and South America, representing one of the most critically endangered primate groups within the region. They are part of the Atelidae family, sharing this classification with howler monkeys (*Alouatta*), woolly monkeys (*Lagothrix*), and muriquis (*Brachyteles*). Atelidae is recognised as being the largest bodied Platyrrhine family and the only with prehensile tails. The taxonomic classification, phylogenetic relationships, and biogeographic history of *Ateles* have been subjects of extensive discussion and revision by numerous researchers. However, these efforts have created considerable uncertainty, impeding the effective implementation of conservation strategies (Froehlich et al., 1991; Hernandez-Camacho, 1976; Kellogg & Goldman, 1944; Kunkel et al., 1980; Medeiros et al., 1997; Morales-Jimenez et al., 2015; Cortés-Ortiz et al., 2015; Rylands et al., 2006). Currently, there are 15 recognized species, including subspecies, of spider monkeys (PSG, 2022), with their distribution spanning a broad geographical range from Mexico in the north to Bolivia in the south. This extensive geographic coverage has led to great morphological diversity among spider monkey populations, prompting some researchers to employ variations in pelage color and patterns for taxonomic identification (Kellogg & Goldman, 1944; Campbell, 2008). This method of classification has faced scrutiny, leading to an increase in taxonomic studies on spider monkeys utilizing molecular, cytogenetic, and morphological data to resolve their systematics. Despite these efforts, consensus has been elusive, resulting in unalike phylogenetic trees, varying patterns of relatedness, and multiple hypotheses concerning the biogeographic origins of the family (Morales-Jimenez et al., 2015).

This cloud of confusion around the genus elicits challenges within scientific communication and sets back any progress in their conservation and survival. Each species of spider monkey, spanning from Central America to the southern reaches of the Amazon, confronts a severe risk of extinction, as stipulated by the International Union for Conservation of Nature (IUCN, 2022). The foremost threat looming over spider monkeys is the substantial reduction of their habitats, attributed to land clearance and the relentless expansion of agricultural activities (Campbell,

2008). The once-intact forests that house spider monkeys are now increasingly fragmented and susceptible to human encroachment, ushering in industries with significant ecological ramifications, such as wildlife trade, logging, mining, and colonization (Scherer, 2018). Given the gravity of these threats, it is imperative to address the prevailing ambiguity enveloping critical aspects of *Ateles* taxonomy, biogeography, ecology, behavior, and evolution. The aim of this dissertation is to critically review the entire spectrum of research literature, encompassing both historical and contemporary works. The knowlege gained from this research seeks to provide an updated and comprehensive reference on the genus *Ateles*. In doing so, it aspires to alleviate uncertainties of prior research, thus paving the way for the formulation and implementation of more precise and effective conservation strategies.

1.2. Taxonomic History

1.2.1. Review

Kellogg and Goldman (1944) conducted a pioneering systematic investigation, marking a significant milestone in the taxonomic study of *Ateles*. Their research was predominantly centered on the examination of morphological attributes, notably pelage coloration and limb dimensions, as the primary criteria for species delineation. Cranial measurements were also included in their analysis; however, they posited that external characteristics offered more dependable indicators of subspecific relationships due to the observed inconsistencies in cranial features. The outcome of their research led to the proposal of four distinct allopatric *Ateles* species. These species encompassed: (1) *Ateles geoffroyi*, distributed across Mesoamerica and delineated into nine subspecies, namely *A. g. geoffroyi, A. g. azuerensis, A. g. grisescens, A. g. frontatus, A. g. vellerosus, A. g. ornatus, A. g. pan, A. g. yucatanensis*, and *A. g. panamensis*; (2) *Ateles fusciceps*, inhabiting the Pacific coast of northwest South America and classified into two subspecies, *A. f. fusciceps* and *A. f. robustus*; (3) *Ateles belzebuth*, found within the Amazon basin and northern Colombia, with three subspecies identified as *A. b. belzebuth, A. b. marginatus*, and *A. b. hybridus*; and finally, (4) *Ateles paniscus*, distributed across the Guianas, central and southwestern regions of the Brazilian Amazon, Bolivia, and Peru, categorized into two subspecies, *A. p. paniscus* and *A. p. chamek*. In 1976, Hernandez-Camacho and Cooper conducted another taxonomic review also rooted in morphological analyses. Their proposal

challenged the previously established taxonomic framework by suggesting that all spider monkeys spanning central and South America should be consolidated into a single, albeit highly variable, species, *Ateles paniscus* (Hernandez-Camacho, 1976).

The first phylogenetic investigation of *Ateles* was conducted by Froehlich et al. (1991). This analysis used 50 cranial and dental characters derived from seven putative *Ateles* taxa. The study's findings led to the proposal of three distinct clades through the merging of certain previously recognized taxa outlined by Kellogg and Goldman (1944). These clades were identified as follows: (1) *Ateles paniscus*, consolidating the subspecies *A. p. paniscus;* (2) *Ateles belzebuth*, encompassing *A. b. hybridus, A. p. chamek*, and *A. b. marginatus*; and (3) *Ateles geoffroyi*, uniting all nine *A. geoffroyi* subspecies, *A. fusciceps, A. f. fusciceps*, and *A. f. robustus*. The authors also put forward the existence of a morphological cline among spider monkeys extending from the Guianas to Venezuela, suggesting that all South American forms collectively constituted an interbreeding ring species characterized by substantial phenotypic variation (Froehlich et al., 1991).

Since the first publication using phylogenetics by Froehlich et al. (1991), subsequent research endeavors have used various genetic data sources to explore the taxonomy, systematics, and evolutionary history of *Ateles*, transcending reliance solely on morphological data. The first exploration into *Ateles* taxonomy via chromosomal analysis was undertaken by García et al. (1975) and Kunkel et al. (1980). Their investigations centered on karyotype bands C and G within five species, following the nomenclature established by Kellogg and Goldman (1944), namely, *A. f. robustus, A. b. hybridus, A. b. belzebuth, A. geoffroyi*, and *A. p. chamek*. The authors proposed that their analyses lent support to the taxonomic framework delineated by Kellogg and Goldman (1944). However, they concurrently noted that the findings could align with the single-species hypothesis advanced by Hershkovitz (1968, 1969). This discrepancy arose from the detection of intraindividual heteromorphisms in the analysis, which contradicted the taxonomy proposed by Kellogg and Goldman (1944) and instead suggested a closer relationship between *A. b. belzebuth* and *A. p. chamek* (García et al., 1975; Kunkel et al., 1980).

It was noted that *A. paniscus* has a different diploid chromosome number than all other spider monkeys (Pieczarka et al., 1989). With this discovery, de Boer and de Bruijn (1990) determined that *A. paniscus* and *A. b. chamek* represent evidently separate species based on karyotypic evidence.

In 1993, Sampaio et al. conducted a taxonomic investigation of *Ateles* employing protein variance analysis as their methodological approach. They looked at the taxonomic relationship between subspecies *A. p. paniscus* and *A. p. chamek,* as per Kellogg and Goldman's 1944 nomenclature, utilizing isozyme analysis. This examination encompassed the assessment of 20 genetic loci, resulting in the identification of four polymorphic loci. The ensuing genetic distance computed between these two populations amounted to 0.149, a divergence level notably higher than that observed among other platyrrhine primate subspecies (da Cunha Sampaio et al., 1993). The considerable degree of genetic differentiation found aligns with the extended period of geographic isolation facilitated by the presence of the Rio Amazonas. Consequently, the integration of these findings with chromosomal data resulted in the recognition of two distinct species within the *Ateles* genus: *A. paniscus* and *A. chamek*.

In 1997, Medeiros and colleagues published the first complete taxonomic review of *Ateles* using karyotype data. They divided the genus into four karyomorphs: (1) *A. geoffroyi* and *A. hybridus;* (2) *A. fusciceps* and *A. rufiventris;* (3) *A. belzebuth*, *A. chamek,* and *A. marginatus;* and (4) *A. paniscus.* In this review, it was argued that *A. chamek* is the most basal form of the genus, originating in the southwestern Amazon basin and later extending to give rise to *A. marginatus* in the central Amazon and *A. belzebuth* in the northwest Amazon (Medeiros et al., 1997). The authors also suggested that *A. geoffroyi* and *A. hybridus* are reproductively isolated from *A. fusciceps* and *A. f. rufiventris* and therefore are possibly separate species.

Collins & Dubach (2000) added to the taxonomic debate by recognizing four monophyletic species of *Ateles* founded on mitochondrial DNA (cytochrome c oxidase subunit II (COII)) variation: (1) *Ateles geoffroyi* (including >2 subspecies) (all haplotypes found in the Choco region of South America and throughout Central America); (2) *Ateles hybridus* (all haplotypes found in the Magdalena River valley of Colombia); (3) *Ateles belzebuth* (all haplotypes found in the southern and western Amazon basin) and (4) *Ateles paniscus* (all haplotypes found in the northeast Amazon basin). Their phylogeny supports the notion that *Ateles paniscus* is the basal

clade among all *Ateles* and shares a last common node with all other spider monkeys. When comparing these four forms to Kellog and Goldman's (1944) previously recognized taxa, form one (*A. geoffroyi*) comprises all nine recognised *geoffroyi* sub-species and the former species *A. fusciceps robustus*. Form two (*A. hybridus*) is the former *A. belzebuth hybridus*. Form three (*A. belzebuth*) is the former *A. b. chamek* and *A. b. marginatus*. Form four (*A. paniscus*) is the former *A. p. paniscus* (Collins and Dubach, 2000).

To delve further into the intricacies of *Ateles* taxonomy, Collins and Dubach conducted a subsequent investigation in 2001. This time, they scrutinized the phylogenetic relationships within the genus by examining DNA variation in the aldolase A intron V nuclear genomic region and compared these findings to their earlier study , which was based on mitochondrial DNA sequences (Collins & Dubach, 2000; Collins & Dubach, 2001). Employing a multifaceted approach that encompassed maximum-likelihood, parsimony, and genetic distance analyses, the authors constructed phylogenies and assessed them using bootstrap support and confidence probabilities. Their results revealed that nuclear DNA analysis failed to resolve interspecific relationships within *Ateles* clades. Nevertheless, they posited that *A. paniscus* represents the most basal form, suggesting it closely resembles the ancestral type of spider monkey (Collins and Dubach, 2001; Morales-Jimenez et al., 2015).

Another taxonomy for *Ateles* was published by Groves (2001), who proposed a complete taxonomy for all extant primates after reviewing recent phylogenetic and molecular research. Groves recognized seven species of spider monkey: (1) *A. paniscus*; (2) *A. belzebuth*; (3) *A. chamek*; (4) *A. hybridus*; (5) *A. marginatus;* (6) *A. fusciceps* and (7) *A. geoffroyi* (with only five subspecies: *A. g. yucatanensis, A. g. vellerosus (synonym A. g. pan), A. g. geoffroyi (synonym A. g. frontatus), A. g. ornatus (synonyms azuerensis and panamensis), and A. g. griscescens*) (Groves, 2001). The classifications that Groves proposed has been considered as one of the better reflections of the true *Ateles* taxonomy (Morales-Jiménez, 2015).

Then in 2003, Ruiz-Garcia and Alvarez attempted to unravel six new world primate genera taxonomies, including *Ateles*, by using RFLPs (restriction fragment length polymorphisms) from mtDNA to infer the phylogenetic histories of the families. They uncovered two haplotypes within

the mtDNA of *A. fusciceps* and suggested that this may indicate two subspecies with distinct evolutionary lineages: *A. f. rufiventris* and *A. f. robustus*. They also proposed that gene flow may occur between *A. fusciceps* and *A. hybridus* as microsatellite alleles were detected (unpublished data) between northern populations of the two taxa (Ruiz-Garcia & Alvarez, 2003). Following this in 2005, Nieves et al created two phylogenies to explore *Ateles* taxonomy, one using molecular and the other using cytogenetic data. To construct the chromosomal tree, the authors used samples from six reputed *Ateles* taxa (*A. hybridus, A. geoffroyi spp, A. marginatus, A. belzebuth, A. chamek and A. paniscus*), the tree indicated that *A. hybridus* and *A. geoffroyi* formed separate clades and a monophyletic group was formed by species *A. chamek*, *A. belzebuth* and *A. marginatus* (Nieves et al., 2005). When constructing the mtDNA phylogeny, samples from three species were used: *A. chamek*; *A. geoffroyi* ssp and *A. paniscus*. Some of the individuals from these species were captive, and geographic information on the samples was limited (Nieves et al, 2005). When building the tree, the authors also included DNA sequences from GenBank. The results of this phylogeny showed *A. hybridus* placed in a different clade than *A. geoffroyi*. Their limited mtDNA-based results were coherent with those of Collins and Dubach (2000) yet contradictory of Medeiros et al. (1997), and their cytogenetic-based results indicated that *A. chamek, A. marginatus, A. belzebuth* and *A. geoffroyi* form a single homogeneous clade separate to *A. hybridus*.

Morales-Jimenez et al. (2015) conducted a recent taxonomic reassessment employing mitochondrial DNA (mtDNA) analysis on samples obtained from recognized *Ateles* species. Their study aimed to elucidate the phylogenetic relationships among various *Ateles* forms, evaluate whether presently recognized species formed reciprocally monophyletic groups consistent with current classifications, and estimate divergence times across *Ateles* lineages. To achieve this, the researchers sequenced 3.5 kilobases of coding sequence from an extensive dataset of genomes. Their findings revealed that, for all species for which they had samples from multiple localities, these species indeed formed monophyletic groups. According to their maximum likelihood taxonomy, *A. marginatus*, situated in northeast Brazil, emerged as the sister taxon to all other spider monkey species. Subsequently, the South American forms were the first represented on the phylogenetic tree, with *A. belzebuth* and *A. chamek* clustering into one clade, while *A. hybridus* and *A. paniscus* occupied separate clades. The Mesoamerican forms were the most recent to diverge in this tree, encompassing two species, *A. fusciceps* and *A.*

geoffroyi. Notably, the maximum likelihood taxonomy did not include any subspecies. Bayesian dating analysis suggested that the majority of species-level divergences within the genus transpired during the late Pliocene, with the most recent common ancestor of extant *Ateles* dating back to 6.7 million years ago, during the late Miocene. These findings collectively imply that the contemporary diversity of spider monkeys cannot be primarily attributed to the isolation and divergence of populations in forest refugia during the Pleistocene (Morales-Jimenez et al., 2015).

Janiak et al. (2022) provided a comprehensive phylogenetic tree of platyrrhine primates, including *Ateles*. In this study, they used 205 new mitochondrial genomes to construct a phylogenetic tree. This tree is most similar to that created by us in Chapter 3 of this dissertation, as a large portion of the samples used were taken from this study. Although not discussed in that paper, in their tree we can see that *A. geoffroyi* and *A. paniscus* are the first lineages to diverge in the taxonomy. Followed by a clade including both samples labelled as *A. marginatus* and *A. chamek*. Three samples of *A. belzebuth* are next to diverge, succeeded by a large number of samples of *A. chamek* as the last to diverge. In this phylogeny, there is a clear division in the *A. chamek* lineage, creating two distinct lineages. The geographic information in these samples shows that both of these clades exist in different geographic locations. The primary objective of their study was to ascertain whether the riverine barrier hypothesis aligns with the speciation patterns of Amazonian primates, although their findings yielded conflicting evidence in support of this hypothesis (Janiak et al., 2022).

1.2.2. Conclusion

The analysis of multiple taxonomic studies aligns with the following taxonomic arrangement. *Ateles paniscus* is consistently upheld as a distinct monotypic species by Groves (1989), Froehlich et al. (1991), Sampaio et al. (1993), Medeiros et al. (1997), Collins and Dubach (2000, 2001), and Nieves et al. (2005), supported by various systematic methodologies. *Ateles belzebuth* is recognized as a valid species with three subspecies: *A. belzebuth marginatus*, *A. belzebuth chamek*, and *A. belzebuth belzebuth*, in studies by Froehlich et al. (1991), Medeiros et al. (1997), and Nieves et al. (2005). However, Collins and Dubach (2000, 2001) detected substantial genetic diversity within this species and were unable to distinguish the specific

geographic ranges of the individual subspecies. Notably, Sampaio et al. (1993) advocate for the elevation of the subspecies *A. paniscus chamek* to the status of a distinct monotypic species, *A. chamek.*

A distinct monotypic species, *A. hybridus*, is recognized by Collins and Dubach (2000, 2001), Rylands et al. (2000), and Nieves et al. (2005), employing different systematic approaches. Nevertheless, it has been classified as a subspecies of *A. belzebuth* by Groves (1989) and as a subspecies of *A. geoffroyi* by Froehlich et al. (1991). The amalgamation of the two species, *A. geoffroyi* and *A. fusciceps*, into a single polytypic species, *A. geoffroyi*, garners support from Froehlich et al. (1991), Collins and Dubach (2000, 2001), and Rylands (2000). For practical purposes, the four-species taxonomy backed by Collins and Dubach (2000, 2001) has been adopted by the American Zoological Society in the management of captive *Ateles* populations, as it appears to be the most suitable arrangement for spider monkey research and conservation until a more refined taxonomic framework is universally accepted (Campbell, 2008).

This review demonstrates unequivocally that spider monkeys do not fit within the still widely accepted taxonomy of Kellog and Goldman (1944). Rather, a consensus based on the taxonomic relationships observed through various systematic studies of morphological, molecular, and cytogenetic variation should be used. As of yet, spider monkey taxonomy would benefit from further research, especially with regard to subspecies status and variation.

Rylands (PSG) 2021 provides the most recent taxonomic review of spider monkeys. He recognized a total of 15 taxa, with 7 species and 8 subspecies.

Table 1: Species list of spider monkeys (Ateles) currently recognised by PSG (2021).

Common Name	Scientific Name
Central American Spider Monkey	*Ateles geoffroyi* (Kuhl, 1820)

Geoffroy's Spider Monkey	*Ateles geoffroyi geoffroyi* *(Kuhl, 1820)*
Azuero Spider Monkey	*Ateles geoffroyi azuerensis* *(Bole, 1937)*
Black-browed Spider Monkey	*Ateles geoffroyi frontatus* *(Gray, 1842)*
Hooded Spider Monkey	*Ateles geoffroyi grisescens* *(Gray, 1866)*
Ornate Spider Monkey	*Ateles geoffroyi ornatus* *(Gray, 1870)*
Mexican Spider Monkey	*Ateles geoffroyi vellerosus* *(Gray, 1866)*
Brown-headed Spider Monkey	*Ateles fusciceps* *(Gray, 1866)*
Brown-headed Spider Monkey	*Ateles fusciceps fusciceps* *(Gray, 1866)*
Colombian Black Spider Monkey	*Ateles fusciceps rufiventris* *(Sclater, 1872)*
Black Spider Monkey	*Ateles chamek* *(Humboldt, 1812)*

Red-faced black Spider Monkey	*Ateles paniscus* *(Linneaus, 1758)*
White-whiskered Spider Monkey	*Ateles marginatus* *(É. Geoffroy, 1809)*
White-bellied Spider Monkey	*Ateles belzebuth* *(É. Geoffroy, 1806)*
Variegated Spider Monkey	*Ateles hybridus* *(I. Geoffroy, 1829)*

1.3. Geographic distribution

Spider monkeys have one of the largest geographical distributions of any Central or South American primate genus. They are distributed in the tropical and subtropical rainforests from the Yucatan peninsula and coastal regions of Vera Cruz state in Mexico, through central America, from the Pacific coast of Ecuador to Guyana and Suriname in the north-eastern region of South America, all the way to northern Bolivia (Kellog and Goldman, 1944). Spider monkeys can be found from the Tropic of Cancer almost all the way to the Tropic of Capricorn. As a result of their wide distribution, data collection has proven difficult, and it is an ongoing challenge to figure out the specific geographic ranges for the different species. Despite their large range spider monkeys have restricted habitat preferences, favouring the high canopy layers of lowland humid rainforests, selecting primary, evergreen, upland forest (Eudey, 1984; Campbell, 2008). These habitat preferences are attributable to the spider monkey's specialist frugivorous diet of soft-fruits, supplemented with flowers and young leaves (Hernandez-Camacho, 1976); Klein and Klein, 1977; van Roosmalen, 1985), and its fission-fusion social system with female dispersal upon maturation (van Roosmalen, 1985; Fedigan et al., 1988), and it is these actualities that affect the large distributions of these species.

Knowledge of the geographic distribution of *Ateles* is an important aspect of understanding their taxonomy, as the environments that they utilise influence gene flow and taxonomic relationships (Campbell, 2008). Geographic range can influence a species in a variety of ways, from ecological pressures, to behavioural characteristics and morphological traits. For example, South American species of *Ateles* are mostly black with differences only on the facial markings, yet there is an exemption to this pattern in *Ateles hybridus* which exhibit brown colouration with a cream/white belly and inner legs. Mesoamerican species of *Ateles* show highly variable morphology ranging from blonde, to red, to dark grey. The following section will briefly overview the current information we have on the different geographic distributions of separate *Ateles* species according to Ryland's taxonomy (PSG, 2021).

Figure 1: The geographic distribution of seven Ateles species. The black dots represent coordinate points of known sightings of these species (see supplementary material).

1.3.1. Ateles geoffroyi

Ateles geoffroyi and all six currently recognised subspecies (Table 1) (PSG, 2021) are found distributed throughout central America in the Mexican states of Veracruz, Tabasco, Oaxaca, Campeche, Chiapas, Yucatan, and Quintana Roo and expanding south to Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and Panama (Canales-Espinosa et al., 2020).

Ateles geoffroyi geoffroyi has been observed in Martina Bay in south-eastern Nicaragua and the species' range extends through to the Pacific coast in the areas of Lake Managua and Lake Nicaragua. They have also been observed in the coastal zone around San Juan del Norte (Kellogg & Goldman, 1944). There is a chance that the range of this species might extend south into northern Costa Rica as multiple sightings have been reported to the Global Biodiversity Information Facility (GBIF). However, this has not yet been reviewed, meaning that the true distribution of this species is unknown. The type locality of this species was unknown, and the

type specimen was an individual gathered from a menagerie collection from Paris, thus increasing the challenges of uncovering its true range (Kellog & Goldman, 1944).

The region that is occupied by this species is made up of different habitats, including Petén-Veracruz moist forests and Central American pine-oak forests, but only parts of the forests here remain intact. Much of this area comprises tropical and subtropical moist broadleaf forests, with some areas classified as tropical and subtropical dry broadleaf forests. It typically experiences an equatorial climate with dry winters. According to data from the Global Forest Watch (2022), an area of around 74.55 million hectares (Mha) of the distribution of *A. geoffroyi* is located in predominantly lowland forests. Between 2001 and 2021, this region lost 8.28 Mha of tree cover with 2.24 Mha of this loss occurring in primary forests. The total area of primary forest lost in this time period is around 14%. Tree cover loss can take place as a result of deforestation and non-deforestation (i.e., fire, climate change), and these data include natural and planted forest tree cover within this region. The peak fire season in this territory typically begins in mid-March and lasts around 14 weeks. A total of 997 thousand hectares (Kha) of tree cover was lost as a result of fires in this time frame, and a further 7.28 Mha of tree cover was destroyed by other drivers of loss. The year with the most tree cover loss due to fires during this period was 2020, with 171 Kha lost to fires—30% of all tree cover loss for that year. Since 2021, 49 Kha of land has been burned so far, but this total is normal compared to the total for previous years going back to 2001. In 2003, 200 Kha of forest was burned, making it the year with the most fires ever recorded in this region. From 2013 to 2021, 98% of the tree cover loss in this species' distribution occurred within natural forests. The total loss within natural forests amounted to 2.05 gigatonnes (Gt) CO2e emissions (Global Forest Watch, 2022).

1.3.2. Ateles geoffroyi azuerensis

The Azuero spider monkey is endemic to the forests of the Azuero peninsula of south-west Panama. Population surveys between 2001 and 2009 show that the species occurs within the provinces of Los Santos and Veraguas but are already extinct in the Herrera territory (Méndez-Carvajal et al., 2013). Most of the population of this subspecies can be found in the Cerro Hoya National Park and La Tronosa Forest Reserve, but it is only the latter habitat that maintains protection and a healthy population due to forest continuity (Méndez-Carvajal, 2011; Méndez-Carvajal et al., 2013). Some small groups can be found in isolated fragmented forest patches outside of the reserves, in gallery forests and living fences south-east of the Azuero

peninsula. Some of these localities include: Restingue, Cerro Culón, Río Ventana, Tembladera, Punta Blanca, Cerro Hoya National Park, Cerro Moya, Jobero, Cambutal, Altos de Güera, Río Güera, La Tronosa Forestal Reserve, El Cortezo, Quema, Guánico, Tonosí, Cacao, Cañas, Venao, Los Pozos, Macaracas, Las Palmas, Llano de Piedra, Mogollón, Cerro Canajaguas, Cerro El Vijía, Valle Rico, La Miel, Valle de Tonosí, Flores (Los Santos), Oria, Río Purio, Los Ñopos, El Cacarañal, Macaraquitas, La Llanita, Buena Vista, Mariato, Arenas, and Flores (Veraguas) (Méndez-Carvajal & Ruiz-Bernard 2009). Kellogg & Goldman (1944) thought that the species occurred from the Azuero Peninsula west up to the Burica Peninsula of Costa Rica, but there have been no reported observations within that area.

The habitat this species inhabits consists of Isthmian-Pacific moist forests. It is part of the tropical and subtropical moist broadleaf forest biome and exists in an equatorial climate with dry winters. This region contains no intact forest. From 2001 to 2021, this region lost 23.5 Kha of tree cover with 2.65 Kha of this area being primary forest. 4.2% of all primary forests in this region were lost in this time period, and an 8.7% decrease in total tree cover has been recorded since 2000. Fires caused 974 hectares (ha) of tree cover loss from 2001 to 2021 in *A. g. azuerensis*'s distribution, and all other loss drivers combined caused 21.1 ha. During this time period, the year with the most tree cover loss due to fires was 2019, with 189 ha lost to fires—11% of all tree cover loss for that year (Global Forest Watch, 2022).

1.3.3. Ateles geoffroyi frontatus

The black-browed spider monkey's range is thought to have a narrow distribution through north-western Costa Rica and western and northern Nicaragua (Kellogg & Goldman, 1944). Specimens of this species have been gathered and sampled from the following localities: Río Yoya, Río Siquia, Lavala, Peña Blanca Uluce and Tuma (Kellogg & Goldman, 1944). In 2015, Morales-Jiménez et al. stated that individuals of this subspecies from Santa Rosa, Costa Rica and those from central and eastern Nicaragua form a monophyletic clade similar to this subspecies, and that individuals from El Salvador may also belong to this subspecies or to a divergent and formerly unknown subspecies (Morales-Jiménez, Cortés-Ortiz & Di Fiore, 2015).

The region contains a variety of habitats, such as Central American Atlantic moist forests and Central American dry forests. Some of the forest here is still intact. Most of the region has an equatorial climate with monsoonal rains and is included in the tropical and subtropical moist

broadleaf forest biome (with some small areas classed as dry broadleaf forest). 10.44 Mha of this area is lowland forest. Between 2001 and 2021, 1.27 Mha of tree cover was lost, and 419kha of that loss happened in primary forests. The total area of primary forest decreased by 28% in this time frame. Fires were responsible for 62.2 kha of losses, while 1.13 Mha of losses were not fire related. In 2020, 27% of all tree cover loss that year was caused by fire. In the total 20 year time period, fires caused 5.3% of all tree cover loss (Global Forest Watch, 2022).

1.3.4. Ateles geoffroyi grisescens

The hooded spider monkey is a subspecies with highly uncertain authenticity. There is insufficient information on its abundance or distribution. Kellogg and Goldman (1944) reported that it occurred in south-western Panama in the valley of the Río Tuyra and spread to north-west Colombia in the Jurado vicinity. The type locality of *A. g. grisescens* is unknown, and the type specimen is from a British museum collection. Hernandez-Camacho (1976) believed that the subspecies is present in Colombia near the Panamanian border on the Pacific coast and restricted to a narrow region by the Baudó Mountains. Yet, there have been no observations of this species in Colombia, so its presence in the country cannot be confirmed (Defler et al., 2003).

The habitats in this region include the Isthmian-Atlantic and Chocó-Darién moist forests, of which some are still intact. It is part of the tropical and subtropical moist broadleaf biome and has areas of equatorial humid climate with monsoonal rainfall. From 2001 to 2021, the distribution of *A. g. grisescens* has lost 104kha of tree cover, equivalent to a 10% decrease in tree cover since 2000. 27.7kha of this loss occurred in primary forests, making up 28% of its total tree cover loss in the same time period. The peak fire season in this region typically begins in late February and lasts around 12 weeks. Fires caused around 3.07kha of tree cover loss in this time (3.1% of all loss), however the majority of loss occurred from non-fire related deforestation. The most affected year by fire was 2019 with 687kha of forest lost (Global Forest Watch, 2022).

1.3.5. Ateles geoffroyi ornatus

The ornate spider monkey is reported to occur in central and western Costa Rica, and the east of the Canal Zone in Panama (Solano, Méndez-Carvajal & Cortes-Ortíz, 2022). It was suggested

that the eastern limit of *A. g. ornatus* is at San Juan, Cerro Azul, Cerro Brujo and Río Pequeñi (an average of 30 miles east of the Panama Canal) (Heltne & Kunkel, 1975). The true distribution of the subspecies in Costa Rica is unknown, but it is thought to occur in the Carara Biological Reserve, Osa Peninsula and Corcovado National Park and recent sightings in Costa Rica have been reported to GBIF between 2002-2021 (Solano, Méndez-Carvajal & Cortes-Ortíz, 2022). There is a population of this subspecies that occupy Barro Colorado Island that were introduced in the early 1960's as an opportunity for researchers to examine population growth within a reserve of a certain size with the research question "What rate of population growth can be predicted for spider monkeys and similar species reintroduced into suitable forest fragments?" (Milton & Hopkins, 2006). However, the definite taxonomic ranking of this sub-species of *A. geoffroyi* is not certain.

The area contains a variety of habitats, including Isthmian-Atlantic moist forests and Isthmian-Pacific moist forests in the tropical and subtropical moist broadleaf forest biome. Equatorial monsoonal rains are the most typical environmental conditions in this area, and some of this forest is still intact. Between 2001 and 2021, the distribution of *A. g. ornatus* lost 111kha of primary forest and had a total forest loss of 493kha. During this time, the region's total area of humid primary forest shrank by 4.1%, with fires being responsible for 5.8% of all tree cover loss (Global Forest Watch, 2022).

1.3.6. Ateles geoffroyi vellerosus

The Mexican spider monkey is found in the forests of the following provinces of Mexico: Yucatan, Qunitana Roo, Oaxaca, Tabasco, and Campeche. They can also be found in the Guatemala highlands (Baja Verapaz, Huehuetenango, Quiché, Totonicapan, Sololá), Belize's central and southern forests, and Honduras' lowland forests (La mosquita in Gracias a Dios) (Rosales-Meda et al., 2022).

The habitat of *A. g. vellerosus* falls in the Petén-Veracruz moist forests and Central American pine-oak forests. Some of the forest in this area is still intact. The majority of the region consists of tropical and subtropical moist broadleaf forests and endures an equatorial climate with dry winters. This region lost 6.99Mha of tree cover between 2001 and 2021, and 1.74Mha of this loss occurred in primary forests. In this time frame, 14% of all primary forest in this area was lost. In this distribution, the peak fire season typically begins in mid-March and lasts around

14 weeks. Fires were accountable for 910 kha of tree cover loss in this period. 31% of all tree cover loss was lost in 2020 with 152 kha lost to fires, making it the year most affected by fires in this period (Global Forest Watch, 2022).

1.3.7. Ateles fusciceps

The brown-headed spider monkey is endemic to north-west Ecuador from the west of the Andes, the Esmeraldas Province, to the north-west of the Santo Domingo and Pichincha Provinces. Their range also extends to the western borders of the Carchi and Imbabura Provinces (P. G. Méndez-Carvajal et al., 2020). There have been previous reports of this species in the south, in the Colon Colonche Mountain Range (within the provinces of Manab, Guayas, and Santa Elena), and in the Chimborazo Province to the west. Recent sightings of this subspecies have been made in Los Bancos, Pichincha Province (Moscoso, 2011; Shanee, S. unpublished data), and Flavio Alfaro, Manab Province (Cervera & Griffith, 2016). It's unclear whether *A. f. fusciceps* is present in Colombia.

This region falls under the tropical and subtropical moist broadleaf forest biome and is made up of different habitats, including Chocó-Darién moist forests, and Northwest Andean montane forests. Both have an equatorial, humid climate and contain some intact forest. Between the years 2001 and 2021, *A. fuscicep*'s distribution lost 820kha of tree cover, and 33kha of this loss occurred in primary forests. Deforestation was responsible for 738 kha of the total tree cover loss, while fires only reduced the forest by 51 kha in this time period. This region experienced an unprecedented loss in tree cover due to fire in 2016, with 20.2 kha being burnt, equaling 32% of all loss for that year (Global Forest Watch, 2022).

1.3.8. Ateles fusciceps rufiventris

The Colombian black spider monkey extends from the western cordillera of the Andes in south-western Colombia to eastern Panama (Cerro Pirre and the basin of the Rio Bayano on the Pacific coast) (Rylands et al., 2006), with the Río Tucutí marking the border of this species with *A. geoffroyi grisescens.* They are present throughout the Pacific lowlands of Colombia, with the exception of the Juradó and the northwestern Chocó. They also occur in regions of Urabá and in northern Bolívar, east to the lower Río Cauca. The southernmost record of this species in Colombia is Barabacoas, and the northernmost record is in Cartagena, near the southern bank

of the Canal del Dique. According to Hernández-Camacho and Cooper (1976), it had once been reported as far north as Pendales. Only a few records of this species have been reported in the Colombian Chocó in the last decade, even though its historical distribution comprised large areas in this region. This is due to the fact that these areas are now significantly defaunated, specifically in Montes de Maria, Bolivar, at Mutatá, Chocó, near Guapi, Valle del Cauca, and in the surroundings of Tatamá National Park at altitudes of 1,800 m asl. This species is not found in Ecuador.

The range of *A. f. rufiventris* contains some intact forest and encompasses different habitats, including Chocó-Darién moist forests and Northwest Andean montane forests. The area has an equatorial, humid climate, with some areas also experiencing equatorial dry winters. It belongs to the biome of tropical and subtropical moist broadleaf forests, and around 18.9 Mha is predominantly lowland. Between 2001 and 2021, this region lost 50.8 Kha of tree cover as a result of forest fires. During this period, the distribution was most affected by fires in 2016 with 20.2 Kha of tree cover loss (a total of 33% of all loss during that year) (Global Forest Watch, 2022).

1.3.9. Ateles chamek

The black-faced black spider monkey is found in Bolivia's northern and central lowlands, as well as north-eastern Peru and western Brazil. This species range extends to the south of the Rio Amazonas-Solimões, west of the Rios Tapajós-Teles and Pires, and to the Río Ucayali in Peru. It extends into the interfluvium of the Rios Ucayali and Huallaga and crosses the middle Ucayali south of the Rio Cushabatay (a left bank tributary of the Ucayali) (Konstant & Rylands, 2013). From here, it continues south into Bolivia along the eastern Cordillera, south of the Río Madre de Dios, and north-east through the Noel Kempff Mercado national park (Wallace *et al.*, 1998), into the states of Rondônia and Mato Grosso (to the left bank of the Rio Teles Pires and Rio Tapajós). In 2014, the species range was extended to the interfluvium of the Rios Solimões and Japurá as a result of observations in the Mamirauá Sustainable Development Reserve (Amazonas, Brazil) by (Rabelo et al., 2014). In 2020, (Rabelo et al., 2020) updated the extent of occurrence for *A. chamek* using species distribution modelling tools and found that around 23% of the forest within its distribution has been lost since 2003.

The region inhabited by this species is made up of Southwest Amazon moist forest habitat and Madeira-Tapajós moist forest habitat. It is part of the tropical and subtropical broadleaf forest biome, and typical environmental conditions are equatorial with monsoonal rainfall. A total area of 260.28Mha is located primarily in lowland forests. Between 2001 and 2021, 20.5 mha of primary forest was lost in this region, making up 76% of the total tree cover loss in this time period. 13% of the tree cover loss during this time was caused by fire, and 17.9 mha of the loss was caused by other drivers (Global Forest Watch, 2022).

1.3.10. Ateles paniscus

The red-faced black spider monkey can be found north of the Rio Amazon, east of the Rios Branco and Negro. It is known in southern and eastern areas near the Rio Essequibo (Sussman & Phillips-Conroy, 1995), and through Suriname and French Guiana (excluding the lowland coastal plains) to the states of Pará, and Amazonas, Brazil. In 1998, Linares claimed its inhabitance west of the Rio Essequibo and up to Venezuela, but this is a tentative proposal (IUCN, 2022).

This species' range is made up of a variety of habitats, such as the lowland moist forests of Guianan and the Uatumã-Trombeta moist forests. These forests are intact and form part of the tropical and subtropical moist broadleaf forest biome. The climate is equatorial, with monsoonal rains. The forest gained 213 kha of tree cover (or about 0.25% of its total extent) between 2001 and 2012, but when the numbers for tree cover loss between 2001 and 2021 are taken into account, the forest lost 1.77 Mha of cover due to drivers of loss and an additional 475 kha of cover due to fires (a total of 21% of all tree cover loss). The habitats this species inhabits are facing increasing climate pressure. There were 94,395 deforestation alerts reported in its distribution from October 4 through October 11, 2022 (Global Forest Watch, 2022).

1.3.11. Ateles marginatus

One of the least understood distributions of all the Amazonian *Ateles* taxa is that of *A. marginatus*, the only species in the genus *Ateles* without a multinational distribution. The white-cheeked spider monkey is endemic to the Brazilian Amazon. It occurs between the right bank of the Rio Tapajós (and its tributary), the right bank of the Rio Teles Pires, and the left bank of the Rio Xingu, south of the Rio Amazonas (Kellogg & Goldman 1944; Buss et al., 2019).

There are unconfirmed records of sightings along the right bank of the Rio Xingu, whose reliability should be investigated. I believe this species to be one of the worst affected by Amazonian deforestation, with their southern range falling directly within the boundaries of the arc of deforestation.

The majority of the region inhabited by this species comprises Tapajos-Xingu moist forests, but some areas fall under the tropical dry forests of Matto Grosso, both within the tropical and subtropical broadleaf forest biome. This region generally has an equatorial climate with monsoonal rainfalls, though it can also have dry winters. It mostly occurs in lowland forest areas. *A. marginatus*' distribution lost 1.18Mha of tree cover due to fires and 5.09Mha due to all other loss-causing factors between 2001 and 2021. The most tree cover was lost to fires in 2017 (242 kha), accounting for 45% of the total loss of tree cover for the year. Between October 4 and October 11, 2022, there were 176,539 deforestation alerts reported here, spanning a total of 2.16 kha (Global Forest Watch, 2022). I believe this species to be one of the worst affected by Amazonian deforestation.

1.3.12. Ateles belzebuth

The white-bellied spider monkey lives in the lowland forests of Ecuador, Peru, the northern Amazon in southern Venezuela, the western Amazon in Colombia, and as far north as the Rio Branco in northwest Brazil. *A. belzebuth*'s distribution is known in at least three discontinuous areas, making a simple description challenging. The first of these distinct areas of occurrence is the northwestern Amazonian rainforests in Colombia. The second area is the western Amazonian rainforests in eastern Ecuador (south of the Rio Napo) and northwestern Peru. The final, and easternmost, region is in Venezuela and northwestern Brazil. Savannas, which are made up of low, sparsely spaced-out shrubs, may help to explain some of the gaps in the distribution of this species.

Although widely distributed in Brazil, the species does not occur continuously, with large areas being absent or very rare in the campina and campinarana habitats in the westernmost part of the state of Amazonas and savannas in the northeast of the state of Roraima. The species is present throughout the northern region of the Rio Negro and in Roraima, on the western side of the right bank of the Rio Branco. From Brazil, it extends into Venezuela north towards to Rio

Orinoco and Rio Caura, but this range is limited by the llanos/forest interface (Bodini & Pérez-Hernández, 1987)

This species has been observed in Colombia, in the piedmont and Cordillera Oriental, as far north as the Rio Upia drainage in the province of Boyaca, according to Defler (2003;2004). Though this species is usually found in lowland areas below 1,000m altitudes, a population was recently discovered in a forest patch in Yopal from 1,000 m to 1,800 m. There have been confirmed sightings of populations of A. belzebuth in the Sierra de La Macarena region, eastern Caqueta, and the Coehmani rapids in the department of Caqueta's southeast. It was reported from the upper Rio Mesay, the right bank of the Rio Apaporis across from the mouth of the Rio Pirá-Paraná, and a salado (clay-lick) site close to the Estrella rapids (Defler, 2003; 2004). Notably, it is rare to see this species west of the Rio Yari, and there is no evidence for its occurrence between the Rios Caqueta and Putamayo (except on the most western, upper reaches). Additionally, it is not present south of the middle and lower Putumayo and only occurs south of the Rio Napo (Mourthé et al., 2019). From there, it spreads throughout the Amazon region of Ecuador and into northern Peru.

According to a distribution map published by (R Aquino & Encarnacion, 1995), *A. belzebuth* can occur throughout northern Peru, between the Rio Putamayo and Rio Amazonas, along the left bank of the Rio Ucayali, including the basins of the Rios Napo, Tigre, Maranon, Pacaya, Pastaza, and Samiria, and as far south as the Rio Cushabatay, where it is replaced by *A. chamek*. Its presence between the Putumayo and Amazonas Rivers in Peru would suggest that it occurs in the Colombian Trapezium, but this needs to be confirmed, according to Defler (2003; 2004). It appears that there are no known locations that link the populations of south-western Colombia, Ecuador, and northern Peru with those of Brazil and Venezuela. Further fieldwork is necessary to fully understand the presence of this species between the Amazonas-Napo and the Rios Putumayo (IUCN, 2022).

Napo moist forests and Guianan piedmont moist forests make up the habitat of this region. The region, which is mostly equatorial and humid, belongs to the biome of tropical and subtropical broadleaf forests. Between 2001-2021 a total of 3.37mha of tree cover was lost, and 471khha of this was due to fires. The year 2016 saw 235 kha lost to fires, or 57% of all tree cover loss for that year, which was the year with the most tree cover loss due to fires over this time period (Global Forest Watch, 2022).

1.3.13. Ateles hybridus

Brown spider monkeys can be found in the Perija Mountains in north-eastern Colombia, the western bank of the Magdalena river (in the provinces of Bolivar, Antioquia, and Caldas), the eastern bank of the Magdalena river (in the provinces of Magdalena and Cesar), the Sierra Nevada de Santa Marta's southern portions, and across the Andes into western Venezuela. On the eastern side of the Andes mountains, this species can be found in the Río Catatumbo watershed in the department of Norte de Santander and in the north-east piedmont forest of the department of Arauca (Hernández-Camacho & Cooper 1976; Defler 2003;2004). An isolated population of *A. hybridus* is located in the Parque Nacional Guatopo, in north-eastern Venezuela. Their Venezuelan distribution is disrupted, they are found in the north, along the south-eastern part of the Central Mountain Range (Cordillera de la Costa) in the state of Miranda, and possibly the state of Vargas. They are also located on both sides of the Venezuelan Andean Mountains (states of Zulia, Táchira, Mérida, Trujillo, Portuguesa, Apure and Barinas) Most wild populations can be located in lowland forests below 1,000m, though recent observations have been reported in higher altitudes of 1,780m (Duque, 2012). In the eastern portion of its distribution, they occur in the piedmont forest along with the severely threatened San Camilo and Ticoporo lowland forests. In the western portion, it also occurs from the piedmont of the Andes throughout the lowland areas surrounding the southern region of Lake Maracaibo (Bodini & Pérez-Hernández 1987; Cordero-Rodríguez & Biord 2001; Duque 2007).

Magdalena Valley montane forests and Magdalena-Urabá moist forests make up the habitats of this region. The most common environmental conditions of the area are equatorial with dry winters. The region is divided into two biomes: tropical and subtropical moist and dry broadleaf forests. 1.43 Mha of tree cover was lost in this distribution between 2001 and 2021, 125 kha of this loss was due to fires. Between the 4th of October 2022 and the 11th of October 2022, 1,104 deforestation alerts totaling 13ha were reported in the hybridus distribution (Global Forest Watch, 2022).

1.4. Biogeography and speciation

Understanding the various processes that could account for the presence of a large number of species in a single location, and for the extensive turnover of species between habitats and regions, is necessary to explain the astounding diversity of species found in tropical forests. This

enormous diversity found in tropical forests is frequently attributed to various ecological processes that enable species coexistence as well as to various historical, evolutionary, and biogeographical processes that drive diversification over time and space (Ricklefs, 2004). Many authors have concentrated on the context of allopatric speciation models and on the natural causes of population isolation when discussing the biogeographic mechanisms underlying this diversity (Link et al., 2015).

One of these biogeographic hypotheses is known as the "refugium hypothesis" proposed by Jurgen Haffer (1969), who postulated that the Amazon was divided into a number of smaller forests isolated by parcels of savannah-like open vegetation during several dry climatic periods in the Pleistocene and post-Pleistocene. The author claimed the remaining forests served as "refuge areas" for various populations of forest-dwelling organisms, which diverged from one another during periods of geographic isolation. During periods of humid climatic conditions, the isolated forests were again united when the region became forest-covered, allowing the refuge-area populations to expand their ranges (Haffer, 1969). The refugia hypothesis gained popularity due to its applicability to a wide variety of taxa, the clear connection it established between biogeographic history and evolutionary mechanisms, and the variety of questions it raised for future research. However, it contained some integral assumptions which we presently know are not-so valid: (1) species' geographic distributions were valid for hypothesis generation; (2) Amazonia experienced drier conditions during glacial periods due to reductions in annual precipitation; (3) forest-dwelling species underwent rapid speciation centred on ice ages; and (4) the main mechanism that originated most Amazonian species was allopatric speciation (Bush & Oliveira, 2006; da Rocha & Kaefer, 2019)

The riverine barrier hypothesis, which proposes that major Amazonian rivers substantially reduce, or prevent, gene-flow between populations inhabiting opposite river banks, thereby promoting speciation, is another early explanation of Amazonian high species diversity and biogeographic history (Wallace, 2009). The importance of this theory lay in its attempt to locate discontinuities, such as rivers, in the formerly thought of as largely homogeneous Amazonian landscape that could not account for breaks in species distribution (Boubli et al., 2015; Janiak et al., 2022).

Numerous endemicity zones have been proposed based on consistent species distribution patterns, all delineated by the Amazon River and its primary tributaries (e.g., Haffer, 1974;

Cracraft, 1985; da Silva et al., 2005; Borges & da Silva, 2012). In parallel, Hershkovitz's (1968) model invokes the isolation of modern, shifting river systems, with only sporadic waifing, to elucidate the peripatric speciation of primates. Conversely, Endler's (1982) parapatric model posits that speciation naturally arises due to clinal variation in a predominantly stable mosaic environment, with transitions occurring at locations of rapid environmental change or partial geographic barriers. The latter two theories both rely on an anticipated association between taxonomic constraints and contemporary geography in the form of environmental barriers (Froelich et al., 1991).

Janiak et al. (2022) conducted a mitogenomic phylogenetic analysis of New World primates to evaluate the support for the riverine barrier hypothesis in neotropical primate diversification. Their findings provide limited or mixed evidence for the global applicability of this theory, suggesting that it may not universally hold true that rivers act as vicariant agents. While they identified primate divergences occurring at or near river barriers, only a few of these events were synchronous and coincided with proposed river formation dates. They advocate for a more species-specific interpretation of the impact of riverine barriers and advocate for increased consideration of the role of sympatric speciation, speciation driven by sexual selection, ecological factors, and biotic interactions in elucidating the factors that have shaped Amazonian primate diversity (Boughman, 2001; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000; Gutiérrez et al., 2014; Maan & Seehausen, 2011). Additionally, they observed that some primate species do not perceive even the largest rivers as insurmountable barriers, as at least some platyrrhine species are proficient swimmers (Barnett et al., 2012; Benchimol & Venticinque, 2014; Gonzalez-Socoloske & Snarr, 2010; Lynch Alfaro et al., 2015), and that floating islands and meandering rivers may offer alternative means for primates to traverse major rivers (Ali et al., 2021; Ayres & Clutton-Brock, 1992; Gascon et al., 2000). Nunes (2014) reported instances of A. chamek observed swimming in large rivers in central-western Brazil.

A more recent historical revision of these theories, known as the Tierra Firme model, postulates that meandering flood plains in the Andean forelands served as greater geomorphic barriers during wet cycles of the Pleistocene than they do in the present (Silva et al., 2019). For instance, in the Maranon-Pastaza Basin of northern Peru, Quaternary sediments reached a thickness of 1,500 m, and because of Andean tectonics, this massive flood plain migration was largely unidirectional, leading to the creation of a much wider barrier (Räsänen et al., 1987).

This model suggests that undisturbed upland rainforests served as isolating environments for the biological differentiation of upland organisms, resulting in species dynamics similar to those predicted by the refuge model. It is suspected that the high site-turnover and forest succession will result in great beta diversity and high alpha diversity from the subsequent mixing of flood plain fauna (Salo *et al.*, 1986). However, this hypothesis predicts that taxonomic boundaries will exist at some river barriers today, in contrast to the refuge model (Froehlich et al., 1991).

Almost all crown platyrrhine primates are hypothesised to have origins in the southern Amazon basin (Kinzey, 1997). Hartwig (1995) supports this scenario with fossil evidence from *Ateles*-like ancestors, claiming that spider monkeys evolved around 15 million years ago (mya). However, molecular data has been used to support more recent evolution hypotheses, which contend that *Ateles* originated around 5mya (da Cunha Sampaio et al., 1993; Porter et al., 1997). Biogeographic reconstructions indicate that the river draining the Amazon basin was not as large as it is today at the beginning of the Pliocene (Brown, 1986; Colinvaux, 1998). Additionally, the Andes mountains were still rising and had not yet reached significant heights in many regions, particularly in the northern Colombia of today (Van der Hammen, 1989; Haffer, 1987). The older, then-existing mountains of the Guianan Shield, with their high elevation and unsuitable habitat, would have likely served as a dispersal barrier through this area. And at this time, the Central American isthmus was still a collection of islands (White, 1986).

Ateles could have migrated across this landscape by crossing the Amazon directly via substrate contact or by being effectively transported when an oxbow in the river was cut off, isolating the monkeys on one side. According to Haffer (1982), it is plausible that *Ateles* maintained gene flow in the southern and western Amazon Basin for a significant portion of the Pliocene up until the start of the Pleistocene. It appears possible that *Ateles* could have traversed the northern Andes cordillera before these mountains grew and began to obstruct gene flow as they do today. The modern Central American isthmus formed between 3.5 and 3.1 mya, so *Ateles's* colonisation of this area is unlikely to have started until then (Coates & Obando, 1996). Since then, this area has undergone continuous modification, and *Ateles* would have had to vie with its climatic changes ever since its formation (Campbell, 2008).

The majority of spider monkey speciation events were caused by biogeographical mechanisms, such as the continuous uplift of the northern Andes and the formation of the Amazon River as

the basin's primary drainage, that took place in the middle to late Pliocene and early Pleistocene (Collins & Dubach, 2000). The findings of Collins and Dubach (2000) are similar to those reported for other tropical taxa using molecular phylogenetic studies and provide little evidence in support of Pleistocene refugia formation or riverine barriers (with the exception of the Amazon) as primary mechanisms in *Ateles* speciation (Smith & Patton, 1993; Riddle, 1996; Engel et al., 1998).

The diverse genus *Ateles* provides several advantages for testing the various biogeographical models that have been proposed to date. Due to their specialised habitat needs and large territorial requirements, spider monkeys may not have been able to survive in smaller, less stable refugia created during Pleistocene habitat fluctuations. Because of their fission-fusion social organisation (augmented by female emigration), intergroup animosity, and broad foraging range in search of a highly selective ripe fruit diet, they have a high dispersal potential (Klein & Klein, 1973; Fedigan & Baxter, 1984; Mcfarland, 1986; Symington, 1990; Symington, 1988a, 1988b). This would imply that in the theorised refugia, only large populations with high levels of genetic diversity survived. It is possible that speciation did not occur when populations from large refuges were connected; their gene pools had not diverged enough to prohibit interbreeding (Campbell, 2008).

On the basis of morphological data, Froehlich et al (1991) state that the Rio Marañon and Rio Tapajos form the species boundaries between *A. belzebuth*, *A. marginatus,* and *A. chamek.* However, they believe that a second biogeographic scenario could explain the speciation of *A. hybridus* and *A. belzebuth*, the Pleistocene forest refugia hypothesis (Haffer, 1969), as there is no other apparent geographic barrier to the integration of these species. They also theorised that *A. geoffroyi* speciated due to an isolated population in a northern forest refugium that migrated to Central America and dispersed towards Mexico.

On the basis of cytogenetic data, Medeiros et al. (1997) proposed that *Ateles* originated in the southwest Amazon basin from populations of *A. b. Chamek*, where some populations then migrated east towards Brazil, forming *A. b. Marginatus*, and some populations migrated to the northwest, forming *A. b. belzebuth*. Additionally, they suggested that a single population (possibly *A. b. belzebuth*) that migrated from the Amazon basin was the source of *A. hybridus, A. geoffroyi,* and *A. fusciceps.* According to the karyotype analysis done in this study, *A.*

paniscus was found to be the most distantly related species. The authors suggested that it may have descended from *A. hybridus'* ancestors, who migrated along South America's northern coast.

On the basis of phylogenetic data, Collins and Dubach (2000) found information parallel to that of Medeiros et al. (1997) in that *A. paniscus* is the most distantly related and most similar form to the common ancestor of *Ateles*. They also put forth that the first species to be isolated by the separation of the Guianan region from the Amazon (around 3mya) was *A. paniscus*, followed by *A. b. belzebuth*, *A. b. chamek*, and *A. b. marginatus*. They hypothesised that *A. geoffroyi* and *A. hybridus* split off from a single population of spider monkeys in northern Colombia between 3.1 and 2.0 mya. And that *A. fusciceps* may have originated from some of these primates that initially dispersed into Central America and then returned to South America via the Pacific coasts of Colombia and Ecuador.

1.5. Status

1.5.1. Conservation Status

The IUCN SSC Primate Specialist Group has examined 14 out of the 15 recognised spider monkey species and subspecies, with the exception of one species (*Ateles geoffroyi grisescens*) due to taxonomic disagreement and ambiguity about its existence (Cortes-Ortíz & Méndez-Carvajal, 2020). Table 3 demonstrates that four taxa are vulnerable, five are endangered, and four are critically endangered, indicating that all species are classified as being at high risk, very high risk, or extremely high risk of extinction. Per the IUCN's recent report "The World's 25 Most Endangered Primates: 2018-2020," *Ateles geoffroyi* and its six subspecies are some of the world's most threatened primates and are in pressing need of conservation measures (Schwitzer et al., 2019).

Table 2: IUCN red list status of spider monkey described as data deficient (DD), vulnerable (VU), endangered (EN) and critically endangered (CR) (IUCN, 2022). For definitions of categories and the criteria used to assign them (in parentheses), see IUCN (2022). For definitions of CITES categories, see UNEP-WCMC (2022)

Species and subspecies	IUCN category	CITES category
Ateles geoffroyi	EN (A4cd)	II
Ateles geoffroyi geoffroyi	CR (A4cd)	II
Ateles geoffroyi azuerensis	CR (A2acd; C2a(i))	II
Ateles geoffroyi frontatus	VU (A4cd)	I
Ateles geoffroyi grisescens	DD	-
Ateles geoffroyi ornatus	VU (A4cd)	I
Ateles geoffroyi vellerosus	EN (A4cd)	-
Ateles fusciceps	EN (A4cd)	II
Ateles fusciceps fusciceps	CR (A4cd)	-
Ateles fusciceps rufiventris	VU (A4cd)	-
Ateles chamek	EN (A2acd+3cd+4acd)	II
Ateles paniscus	VU (A4cd)	II
Ateles marginatus	EN (A4cd)	II

Ateles belzebuth	EN (A4cd)	Ⅱ
Ateles hybridus	CR (A4cd)	Ⅱ

The most recent summary of IUCN and the Convention on International Trade in Endangered Species (CITES) categories of each recognised *Ateles* taxon is presented in Table 2. The majority of spider monkey species were last assessed by CITES in 1975 (category Ⅰ) or 1977 (category Ⅱ). Considering the speed of habitat loss and land change in recent years, we believe these classifications to be too old to be accurate. The IUCN statuses also change very rapidly throughout the *Ateles* genus (thus are assessed regularly), and not all recognised species have even been assessed by CITES. The main recommendation I put forth is that the eastern Amazonian species *A. marginatus, A. paniscus* and central/western Amazonian species *A. chamek* be categorised as category Ⅰ, as they remain the most threatened taxa in the genus, with there ranges bordering on the arc of deforestation (Boyle, 2008).

The status of spider monkeys has changed considerably in recent years. Most species' population trends are decreasing and continuing this way. In the span of five years, *A. geoffroyi* changed from least concern (LC) in 2003 to endangered (EN) in 2008. It is suspected that in the next ~50 years, the population will see a 50% decrease (Canales-Espinosa et al., 2020). After being considered LC since the species' last review in 1996, *A. g. geoffroyi* jumped straight to critically endangered (CR) in 2008 (Solano et al., 2020). *A. g. azuerensis* has been considered CR since the species' first IUCN assessment in 1996. The species' population has seen a >80% reduction over the last 45 years, leaving fewer than ~74 mature individuals in the wild (IUCN, 2022) (PMéndez-Carvajal & Cortes-Ortíz, 2020). Again, in only half a decade *A. g. frontatus* went from LC in 2003 to vulnerable (VU) in 2008. It achieved this status as a result of a population decline of at least 30% over a period of 45 years (roughly three generations). The continuing decline of this subspecies coincides with the Global Forest Watch (2022) data that shows close to 20% of their suitable habitat, including the Costa Rican provinces of Punta Renas and Guanacaste as well as the Pacific Coast forest regions of Nicaragua, is likely to be

lost by 2063 (Solano et al., 2020). *A. g. grisescens* was classified as EN in 2000, but there was no justification for this assessment. In 2020, it was classified as data deficient (DD) as there is still uncertainty about whether this species does, in fact, exist. There have been no known sightings of the species in the wild since the original description by Kellogg and Goldman (1944) (Cortes-Ortíz & Méndez-Carvajal, 2020). The status of *A. g. ornatus* has fluctuated over the years, going from VU in 2000, to EN in 2003, and back to VU in 2020. There is no justification shown by the IUCN for the lowering of the risk status for this species. Significant fragmentation exists in four of the five regions where they occur and an annual decline rate of 4.2% a year is predicted for the population, which is a 71% decrease over 30 years (Sánchez-Azofeifa et al., 2005). *A. g. vellerosus* has been classed as EN since its first assessment in 2020. By 2063, 40% of the habitat for the species is likely to be lost, according to forest data for Mexico, Guatemala, Belize, El Salvador, and Honduras, where they are currently found (Global Forest Watch, 2022). This figure combined with pressures of hunting for bushmeat and the pet trade pushes this subspecies above the threshold for EN (Mittermeier et al., 2020).

Despite the increasing rate of forest loss and fragmentation in the home range of *A. fusciceps* (Ecuador, Colombia, and Panama), it was recognised as EN in 2020 after being classed as CR since 2008 (Méndez-Carvajal et al., 2020). Since the recognition of the subspecies *A f. fusciceps* by the IUCN in 2008, it has been credited as CR. Based on Global Forest Watch data, a population reduction of >80% is predicted over the next 45 years, and the species' final strongholds (the Ecuador regions of Eloy Alfaro and San Lorenzo) could lose more than a third of their inhabitable forests by 2063 (Moscoso et al., 2020). The status of the subspecies *A. f. rufiventris*, since its recognition by the IUCN, has changed from CR in 2000 to EN in 2020. The reason for the reassignment of the status of this species is unclear, as the population trend is still decreasing. In 2008, a long term population study in Panama found that there were fewer than 2,000 individuals left in the wild (Mendez-Carvajal et al., 2019).

The South American species *A. chamek* jumped from LC to EN in the space of 5 years (2003-2008) and maintained this assignment after its last IUCN assessment in 2020. It is suspected that over the past three generations, 50% of the population is now extinct. The southern part of this species' range is in the 'arc of deforestation' which has devastated the southern Brazilian Amazon habitats (Rabelo et al., 2015). *Ateles paniscus* is currently recognised as VU after its last two assessments in 2008 and 2019. This status is an increased risk level

from LC, which it was classified as in 2003. The population of *A. paniscus* has decreased by 30% in just one generation as a result of severe hunting pressure and significant habitat loss, which are the causes of this status change (Régis et al., 2019). *Ateles marginatus* has always been considered EN since the species' first IUCN assessment in 1994. This is based on the assumption that there will be a population decline of up to 50% in the next 25 years due to habitat loss in both protected and unprotected regions of its range, as well as associated declines and population extirpations due to ongoing intensive hunting (Buss et al., 2019). *Ateles belzebuth* was considered VU between 1982-2007 until its reassessment in 2008, changing the risk level to EN. A 30% decline of the species' population in the last three generations can be attributed to extensive deforestation and intense hunting pressure in its range in Ecuador. These decline's root causes still exist, and the species is scarce in Brazil and is heavily hunted in the northwestern Amazon, ensuring the maintenance of the EN status until present day (Mourthé et al., 2019). The first assessment for *A. hybridus* was applied in the year 2000, assigning the species an EN status. Shortly thereafter, this status changed to CR in 2003. It achieved this status due to a predicted 30% reduction in the population over the next 45 years, including the current generation between 2018-2033 (Stevenson et al., 2020). Additionally, and perhaps more significantly, this species is actively hunted for both its meat and for the pet trade. Population densities of heavily hunted Ateles species can drop by as much as 80% or more over several generations, according to research by (Peres & Palacios, 2007).

1.5.2. Conservation value

Spider monkeys, as predominantly frugivorous creatures, occupy a vital ecological niche within the intricate web of interactions among plants, animals, and their environment. For pollination and seed dispersal, plants rely on outside factors like wind, water, or interactions with other moving species. These interactions are pivotal for plant survival since seeds that remain in proximity to the parent plant face risks such as predation, infection, and competition for vital nutrients and space. Additionally, the densely layered forest canopy, which obstructs up to 98% of sunlight from reaching the forest floor (Gentry, 1983), underscores the importance of seed dispersal away from dense plant populations. Large seeds are not easily dispersed by the environment, yet most tropical canopy plants are under selective pressure to produce large seeds (as the seedlings often require large energy reserves to survive in the understory of the forest) (Lawrence & Dew, 2008). This energy reserve comes in the form of fleshy and nutrient

dense fruit, of which the spider monkeys specialise in consuming and successfully defecate and disperse around their large home ranges. This dispersal strategy is known as endozoochory (van der Pijl, 1982).

Primates are regarded as one of the most successful dispersers of large seeds generated by tropical trees, specifically the spider monkeys with their exceedingly long day ranges and intensely specialised diet of ripe fruit (Mittermeier & van Roosmalen, 1981; Chapman & Chapman, 1987; Nunes, 1998; Di Fiore & Campbell, 2007). Thus, there could be serious deleterious community-level effects if these important seed dispersing taxa are removed from the ecosystem. This has been documented across the *Ateles* genus, in Guatemala (see Cant, 1977; Muskin & Fischgrund, 1981), Costa Rica (see Chapman, 1989), the Guianas (see van Roosmalen 1985; Zhang & Wang, 1995), Ecuador (see Dew, 2001 & 2005; Link & Di Fiore, 2006), Colombia (see Klein & Klein, 1977), and Peru (see Russo et al., 2005). A study by Di Fiore et al. (2008) demonstrated that the reason the *Ateles* are considered one of the best neotropical seed dispersers is because they prey upon very few seeds but ingest them in large quantities and of a variety of sizes, and they deposit most of these seeds in locations far away from the parent trees (Hulme, 1998). Following the pathways left by the seedlings, this study discovered that a large portion of the seeds disseminated by spider monkeys are successfully sprouted *in situ* and survive the establishment stage (Dew, 2008). There are probably no other neotropical mammals with longer mean seed dispersal distances than *Ateles*, nor any that disperse more seeds from huge canopy plants per kilogramme of biomass (Knogge & Heymann, 2003). Many Amazonian flora would lose their sole known means of distribution without spider monkeys. These plants may provide food for a variety of animals, but only spider monkeys have been observed to distribute them. Wherever it is located, the spider monkey is probably the most significant disperser of large fleshy-fruited seeds. Due to its crucial ecological function and vulnerability to hunting pressure, this threatened genus can act as an indicator species for the neotropical forest, whose decline or extinction would indicate an unbalanced environment and damaged ecosystem, meaning that frugivore population density is a crucial component to conservation biology (Dew, 2008).

1.6. Threats

1.6.1. Habitat Loss, Alteration and Deforestation

A well-known problem facing the rainforests of South America is presented in the form of deforestation as a result of the growth in cattle-ranching, agricultural practices, and resource extraction industries (i.e., timber). These rainforests are also facing scourge due to non-deforestation threats such as climate change, forest fragmentation, the selective extraction of plants and animals (i.e., hunting for food, pet trade, and medicinal uses), biological invasion, the changing of atmospheric composition, and tree turnover rates (Phillips, 1997). Each of these threats, whether directly or indirectly, poses a monumental threat to forest ecology and spider monkey survival. As forests cover nearly half of Latin America's land surface, spider monkeys can be found there in higher densities where the forests are still intact. But in the regions where spider monkeys can be found, deforestation rates are rising (0.51% annual from 2000-2005, compared with 0.46% from 1990-1999; FAO, 2007). The majority of the distribution ranges for the South American *Ateles* are found in the Brazilian Amazon, the largest and least disturbed tropical forest in Latin America. It was estimated that the Brazilian Amazon loses 1-3 mha of forest per year (FAO, 2006), but this estimation has probably grown since that date. The eastern and southern portions of the forest show the highest rates of deforestation, (Soares-Filho et al., 2006) suggested that primate species whose distribution falls heavily within the Brazilian Amazon would lose 60-100% of their range by 2050. The forests of Colombia are also important for Ateles conservation, containing a large portion of *A. hybridus*' range and 90% of *A. g. robustus*' range (Ramos-Fernández & Wallace, 2008). Although Colombia's deforestation rates are generally lower than those of the Brazilian Amazon, the species that live here are still extremely vulnerable due to their small geographic ranges.

Numerous studies have demonstrated the genus' susceptibility to habitat disturbance, failure to persist in sparsely populated forest areas, and lower numbers in logged and disturbed areas (Freese et al., 1982; Lovejoy et al., 1986; Michalski & Peres, 2005). Johns and Skorupa conducted a study in 1987 to identify the ecological factors that are most significant in indicating the severity of the responses of various primate species to logging operations. They discovered that larger frugivorous primates are typically more vulnerable, particularly if their primary route of movement is through the forest canopy because logging might damage aerial

paths ((Johns & Skorupa, 1987). The spider monkeys' population densities are seriously threatened by both forest fragmentation and vegetation disturbance, but neither an undisturbed tropical forest with naturally varying environmental conditions, nor a partially disturbed tropical forest, can be assumed to have a constant population density. A forest that appears to be a continuous extension is, in reality, uniquely heterogeneous from natural and anthropogenic causes (Turner et al., 2001). Gonzalez-Kirchner. (1999) studied populations of spider monkeys in the Yucatan Peninsula (Mexico), of which appeared to have high population densities. They discovered that these populations actually correspond to isolated, less sustainable populations as a result of the 'crowding effect' of habitat fragmentation, in which a population that once occupied a vast region now persists in high densities in isolated forest remnants (Meffe & Carroll, 1994; Lovejoy et al., 1986; Gonzalez-Kirchner, 1999). Temporarily high densities are frequently followed by abrupt drops in density because the forest remnants are too fragmented to support healthy populations (Ramos-Fernández & Wallace, 2008).

A synthesis of the threats facing the rainforests inhabited by spider monkeys are contributing to a decline in the role of these rainforests in acting as carbon sinks. Forests play a key role in the global carbon cycle, they keep the levels of carbon dioxide (C02) in the atmosphere at manageable/safe levels, and are globally respected for the services they offer to society. Without the presence of these carbon sinks, the severity of the climate breakdown will worsen and have damaging impacts on society. The Amazon rainforest accounts for 50% of all carbon stored in tropical forests (Pan et al., 2011). As the Amazon is exposed to disturbances such as deforestation, droughts, and climate change, these disturbances have the ability to shift forests into earlier succession rates and influence the forests' species composition and structure (Dubayah et al., 2020; Gatti et al., 2014; Rödig et al., 2018).

Within the distribution of Amazonian spider monkeys, the forests are changing, along with the amount of CO2 absorbed and released in these areas. Data from the Global Forest Watch (2022) shows that between 2001 and 2021, the forests encompassed in *A. chamek's* distribution emitted 608MtCO$_2$e/year, and removed -542MtCO$_2$e/year. This represents a net carbon flux of 65.3MtCO$_2$e/year. Tree cover loss resulted in an average annual release of 608Mt into the atmosphere, and regions where deforestation was one of the main loss drivers saw an increase in CO2e of about 10.6Gt. This means that the forest is releasing more carbon than it is absorbing. The same pattern is also present in the forests that make up *A. marginatus's* range.

In the same time frame, the forest emissions were around 199MtCO₂e/year, and they removed -110MtCO₂e/year. This represents a net carbon flux of 88.8MtCO₂e/year. And as a result of tree cover loss, an average of 199Mt of CO2e was released into the atmosphere each year, and the range's deforested regions are responsible for approximately 3.85Gt of CO2e emissions. Fortunately, this pattern changes in the rest of the Amazonian species ranges. Between 2001 and 2021, the forests in *A. paniscus*'s distribution emitted 71.4MtCO₂e/year, and removed -193MtCO₂e/year, representing a net carbon flux of -122MtCO₂e/year. In the range of *A. hybridus* a carbon flux of -7.34MtCO₂e/year was reported within the same 20 year timeframe, and in the range of *A. belzebuth* a carbon flux of -87.5MtCO₂e/year was reported (Global Forest Watch, 2022). The fact that large areas of Amazonian spider monkeys are still absorbing carbon is auspicious, but the continuous exploitation of these areas means these figures could change very quickly. In the collective distribution of these species, around 154.1MtCO₂e/year has been released into the atmosphere for 20 years, while around -216.84MtCO₂e/year has been absorbed. Upon examining the climatic information for each species' inhabited forests, it is apparent that carbon emissions are much higher in areas where deforestation is the dominant driver of tree cover loss. This represents how important the conservation of spider monkeys is. With enforced protection of these areas, reforestation, and the reduction of damaging industries, these areas could heal and resume their role as significant carbon sinks once again. The conservation of *Ateles*' home ranges will benefit all species in the biodiverse hotspot that is the Amazon.

1.6.2. Hunting and Pet-Keeping

Due to their substantial size and the perceived tastiness and palatability of their meat, spider monkeys (*Ateles*) rank among the most coveted primate hunting targets in rural Neotropical communities (Kellogg & Goldman, 1944; Peres, 1990). This heightened demand for their meat intensifies the hunting pressures that spider monkey populations face. The peril posed by hunting cannot be overstated, particularly given that overhunting stands as a primary driver of catastrophic faunal extinctions following human settlement in previously pristine areas (Ramos-Fernández & Wallace, 2008). In undisturbed tropical forests across Guyana, Suriname, French Guiana, and northeast Brazil, hunting emerges as the gravest threat to primates (Takahashi, 2008). For example, within central Amazonia, *Ateles paniscus* stands as the most frequently hunted mammal by five Waimiri Atroari villages, with a staggering 421 individuals

hunted in one year, constituting 8% of the total harvest weight. It is notable that approximately 80% of the hunted individuals are females, a matter of concern given the spider monkeys' female-biased sex ratio and relatively low reproductive rate (De Souza-Mazurek et al., 2000). Moreover, the increased rates of logging further compound hunting threats to Ateles by rendering forests more accessible to hunters through the construction of roads (de Thoisy et al., 2005).

The primary adverse impact of hunting on spider monkeys pertains to its profound influence on population densities. An extensive survey conducted across 45 locations in the Brazilian Amazon reveals that the densities of *Ateles* species dwindle by as much as 83% in regions subject to high hunting pressures compared to those with minimal hunting activities (Peres & Dolman, 2000). Peres' (2000) seminal study on the hunting of *Ateles* in the Brazilian Amazon yielded several key outcomes that shed light on the gravity of this issue. One of the most striking findings was the widespread prevalence of hunting across the Amazon region, with around 300,000 animals estimated to be harvested annualy. This extensive form of subsistence hunting affects vast tracts of tropical wilderness, which otherwise remain structurally unaltered. However, distinguishing hunted from nonhunted tropical forests presents a difficult problem because this diffuse resource extraction leaves few visible signs of its occurrence. They found that crude vertebrate biomass (highly correlated with hunting pressure) gradually declined from nearly 1200 kg km2 at nonhunted sites to less than 200 kg km2 at heavily hunted sites. This significant reduction in biomass had a negative effect on the total biomass and relative abundance of vertebrate species in different size classes at these forest sites, particularly for large bodies vertebrates like spider monkeys. The study also estimated that as many as 23.5 million game vertebrates, equivalent to 89,224 tons of bushmeat with a market value of US$190.7 million, are consumed each year by the rural population of Brazilian Amazonia, illustrating the enormous socioeconomic value of game resources in the region (Peres, 2000). These findings show the urgent need for conservation measures to protect *Ateles* populations and preserve the ecological and economic integrity of the Amazon rainforest.

Despite their ecological significance, spider monkeys are hunted less for pet-keeping, as their large size, arboreal lifestyle, reliance on forested habitats, and vital role in seed dispersal render them ill-suited for captivity. Nevertheless, in Mexico City, *Ateles* remains the most frequently kept monkey species as pets, with individuals fetching prices of approximately 500 USD. These

illicit transactions take place in markets and along highways in the southern part of the city, in defiance of regional laws (Silva-Lopez, 1988). Female spider monkeys also become targets, as hunters seek to capture their infants for higher profits, a practice that exerts additional pressure and can disrupt spider monkey population dynamics.

Moreover, rumors of the medicinal benefits of spider monkey fat, purportedly used to alleviate neck pains and aches, have fueled hunting demand (Silva-Lopez, 1988). However, since the inception of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and with all Latin American countries becoming CITES members by 1991, the trade in primates and other wild animals has seen a decline (CITES, 2008). CITES, in effect, has played a pivotal role in curbing the primate and wildlife trade in the region (Mittermeier et al., 1989). Despite the notable progress in regulating this trade, ongoing vigilance and conservation efforts are essential to safeguard spider monkey populations and their ecosystems.

1.6.3. Potential solutions to protect spider monkeys

The prima solution to protecting the spider monkeys is protecting the rainforest, but this task in itself involves numerous avenues of research and different aspects of conservation, while at the same time focusing on what's best for the people who live there, thus is not a simple task. The development, adequate maintenance, and administration of protected areas by national governments, as well as the participation of the international community, are necessary to stop or reduce deforestation rates in the Neotropics, which is essentially the highest priority in the conservation of spider monkeys. Increased protection and legislation against poaching and illegal trade is also necessary. Since these species are spread over large areas crossing frontiers, many countries will have to work together with conservationists to make this happen. The reality of accomplishing this task is far-fetched, as stopping the deforestation of the rainforest will require changes in the politics and economical interests of all countries involved (something that often favours rich profits over anything else), but it is not impossible!

The crucial function of the genus as indicator species and seed dispersers shows that it is insufficient to justifiably support conservation efforts solely on concerns faced by a specific population or taxon. It is important to mention the potentially long-term effects of their population declines on the variety of tree species and the structure of the ecosystem (Ramos-Fernandez & Wallace, 2008). The global recognition of the importance of this genus to

the rainforest, which in turn contributes to human wellbeing and economic prosperity, may be a way of gaining government and financial support for conservation. Getting the protection of spider monkeys acknowledged under the PES (payment for environmental services) scheme, payment incentives could be offered to farmers and landowners who agree to take certain actions to manage their land or watersheds in ways that would protect the genus. In PES initiatives, people are paid for managing their natural resources to safeguard watersheds, preserve biodiversity, and sequester carbon dioxide by planting new trees or adopting more environmentally friendly agricultural practices to stop deforestation and vegetation destruction (IIED, 2023). The beneficiaries of the environmental services, such as water consumers and hydropower corporations, could contribute to the expenses. Governments at the local and national levels, who are indirect beneficiaries, could also make payments on behalf of their citizens. Generally speaking, both at the global and regional levels of PES schemes, the private sector's role is expanding.

Another way to protect the spider monkeys could come in the form of community-based ecotourism, specifically, primate-watching tourism as a conservation solution. This would work similarly to how the bird-watching sector already operates, and most of South America already has the agroindustry infrastructure needed for this tourism to start. In some regions of Asia and Africa, primate watching tourism is already a well-established and successful industry, but in South America, where the greatest diversity of primates can be found, there are very few such ventures (Lebrão et al., 2021). Initiatives to promote primate tourism that target endangered species could aid in the creation of protected areas, provide income for locals, and maintain the ecosystem of the rainforest. These kinds of initiatives that guarantee local people's governance and the conservation of biodiversity are urgently needed given the current situation of political and economic instability in the Amazonian countries (Estrada et al., 2022). In order to establish a baseline model to be utilised for primate watching programmes, (Lebrão et al., 2021) et al. (2021) tracked the sighting rate of bald uakaris (*Cacajao calvus calvus*) in 2019. They did this by identifying the key factors that could affect the species' sightings. Local tourist guides reported information on 602 tourist expeditions over the course of 334 days, with 190 encounters with uakari groups (109 in the morning and 81 in the afternoon). Species sightings fluctuated each month; 73.4% of visitors said they saw uakaris at least once while they were there, while 26.6% reported they did not. The central finding was that seasonal variability in

food availability, water levels, and species-specific socioecological behaviours were the main elements that may have made these primates easier for tourists to detect (Lebrão et al., 2021). The success of this study, which only had a small number of dissatisfied visitors, demonstrates the tremendous potential for primate-watching to strengthen the collaboration between traditional and scientific knowledge, promote social and economic benefits for local communities, and support new primate conservation initiatives. Even though this won't address all of the issues that neotropical forests face, implementing tourism initiatives like this could present opportunities to help protect some areas and alter people's perceptions of forests as useless development land (Mobray, 2022) by highlighting the understanding and value of biodiversity, like spider monkeys, and allowing people to use the land for economic gain without endangering the forest.

Chapter 2: Molecular phylogenetic analysis

2.1. Introduction

The utilization of molecular genetics within conservation biology has emerged as a critical tool to combat the impending global extinction crisis and curb the alarming rates of biodiversity loss. An integral facet of this approach involves the application of mitochondrial DNA (mtDNA) in phylogenetic research. Recent advancements in phylogenetic methodologies, coupled with the increasingly accessible whole genomes of nonmodel organisms, have significantly broadened and simplified the practice of phylogenetics over the past two decades (Hebert & Gregory, 2005). This has allowed for a more comprehensive understanding of evolutionary relationships and the dynamics of biological diversification.

The foundation of phylogenetic theory is the assumption that all species share a single common ancestor and that closely related lineages have a more recent ancestor. Through this assumption, a phylogenetic tree can be built to locate these ancestors in evolutionary time and comprehend the relatedness between lineages (Baum & Offner, 2008). However, the classification of species remains a debated topic amongst taxonomists; there is no universally accepted species concept (Kress et al., 2015). The prognostic capabilities of phylogenetics using

mtDNA are crucial to helping resolve this debate and addressing biological questions concerning taxonomy, conservation, and evolution.

Early forays into phylogenetic reconstructions transitioned from morphological characters to DNA sequences, particularly in the early 1980s (Hillis, 1987). This shift was fueled by the clarity and simplicity offered by DNA sequences, composed of adenine, thymine, cytosine, or guanine. Sequence-based phylogenies enable a thorough examination of organisms across all taxonomic ranks, even in cases where morphological variation is limited (Ajawatanawong, 2016).The determination of evolutionary history relies on orthologous gene comparisons to reconstruct gene trees, a method considered highly accurate.

Recent years have seen an increase in phylogenetic and taxonomic study, particularly in regards to primates like spider monkeys (genus *Ateles*). The genus encompasses prodigious species richness and has occupied various positions in the taxonomic relationships among members of the Atelinae sub-family within the scientific literature. Researchers are still in debate on the number of extant taxa, classifications, and evolutionary relationships, demonstrating the necessity of phylogenetic assessment.

The threats that spider monkeys face are intensifying year by year, demonstrating the urgent need for conservation actions for their survival. Molecular phylogenetics can help in the precise targeting of resources for conservation because it enables us to understand species diversity within ecosystems and reveals data on species diet, which can help investigate the foraging ecology and habitat use of species. It can help to uncover more precisely the number of species within a taxonomic group, aid in the discovery of new species, or help delineate cryptic species. It can reveal data on competition and trophic interactions which helps in understanding how species interact within an ecosystem which helps in assessing and predicting its overall health and functioning. Additionally, data on trophic interactions can inform strategies to control invasive species and mitigate their impacts on native ecosystems and assist in habitat restoration and management. Studying trophic interactions can help the identification of indicator species, which can provide early warnings of environmental changes or disturbances. Conservationists can then take proactive measures to address threats and protect vulnerable ecosystems. It can reveal data on alpha and beta diversity which measures species richness within a specific habitat or area and provides us with a snapshot of the number of species present in this area, which is a fundamental component of biodiversity assessment. It can

reveal data on evolution and relatedness that have been obscured by morphological and behavioural analyses (Moritz & Faith, 1998). Reconstructing phylogenies can answer research questions to better comprehend lower-level relationships for species-specific conservation efforts, dispute theories regarding the geographic origins of particular groups (such as Templeton, 2004), or look at relationships between species complexes. The hypothesis that phylogenetically diverse congregations sustain higher functions and enhance ecosystem stability (Cadotte et al., 2008; 2009) provides good justification for conservation resources to be directed towards the genus *Ateles*.

In this study, I employ whole mtDNA genomes and the cyt-B gene region of mtDNA to construct two phylogenetic trees, meticulously evaluated using the bootstrap non-parametric method. My objective is to elucidate the intricate taxonomic questions surrounding the genus *Ateles* in order to promote a comprehensive understanding that could guide practical conservation actions to prevent the genus from the precipice of extinction. In making these efforts, I hope to eliminate past taxonomic discrepancies and enhance our understanding of this genus in order to inspire successful conservation strategies.

2.1.1 Maximum-Likelihood phylogenies and IQ-Tree

The phylogenetic trees created in this study were done so using the maximum likelihood (ML) analysis method within the IQ-Tree (Nguyen et al., 2015) platform. ML is a statistical technique developed from a character-based approach to molecular phylogenetics, that looks for the tree that increases the likelihood that the data is true. By identifying the tree that maximises the chance of observing the data, it aims to suggest an evolutionary tree (Lemmon et al., 2009). ML entails estimating branch lengths, tree topology, and substitution model parameters. These properties are generally calculated one after another, with the tree topology being the major parameter of concern. Although there are effective numerical techniques for calculating branch lengths and substitution model parameters on a fixed tree (Yang & Nielsen, 2000), determining the ideal tree topology is a complex computational problem (Chor & Tuller, 2005). To discover the "best" tree, one must therefore rely on search heuristics (Nguyen et al., 2015). Given its infamous reputation for being slow and complex, ML is usually only applied in the sciences of evolution, phylogenetics, and systematics (Sinclair et al., 2005). However, ML is not as complicated as its reputation would have you believe, and recent software developments have made it possible to overcome speed issues (Guindon & Gascuel, 2003).

In phylogenetic analysis, trees can be rooted or unrooted. Unrooted trees indicate topological interactions between sequences, while rooted trees show the evolutionary basal and derived associations between sequences. Though it is impossible to tell if a node represents a primitive or derived evolutionary state (Dopazo, 2009), knowing a tree's root allows us to observe the sequences' order of descent and evolutionary direction (Hall, 2008). But it is worth nothing that both rooted and unrooted trees offer the same data when employing ML analysis: the degree of evolutionary change (which is reflected in the branch lengths) and the relationships between the taxa. The output tree is called a phylogram.

In the tree generated in this chapter using the gene region cyt-B (fig. 2), I used the outgroup species *Alouatta belzebul,* which is known to have recently diverged from the remainder of organisms in the tree (Ajawatanawong, 2016). For the tree created using the whole mitogenome (fig. 4), I used the outgroup species *Alouatta seniculus and Lagothrix lagotricha* for the same reasons.

2.2. Methods

2.2.1 Data Collection

2.2.1a Sequence acquisition

For a comprehensive phylogenetic analysis of the *Ateles* genus, two distinct datasets were acquired, yielding separate sets of results. The initial dataset comprises complete mitochondrial genome (mitogenome) sequences, while the second dataset includes cytochrome-b (cyt-B) sequences. The genetic sequences for these analyses were sourced from GenBank®, an online genetic sequence repository maintained by the National Library of Medicine (NIH) through the National Center for Biotechnology Information (NCBI). GenBank® is an integral part of the International Nucleotide Sequence Database Collaboration, encompassing the DNA DataBank of Japan (DDBJ) and the European Nucleotide Archive (ENA) in addition to GenBank at NCBI.

The sequence retrieval process entailed the utilization of the Basic Local Alignment Tool (BLAST) within GenBank®. BLAST is used for identifying local similarities within sequences and comparing nucleotide (or protein) sequences with reference databases, thereby determining the statistical significance of matches. Sequences meeting the following criteria were gathered:

>80% query coverage, an E-value of 0, and sequence lengths exceeding 500 base pairs (bp) for cyt-B or 16,000 bp for the entire mitogenome. Furthermore, additional cyt-B sequences were extracted from the complete mitogenome sequences using Geneious Prime (Geneious, v.2022.2.1). In total, 38 sequences were incorporated into the cyt-B phylogeny, while 19 sequences were utilized in the mitogenome phylogeny. These sequences spanned 11 of the 15 recognized *Ateles* species and subspecies. To provide a geographical context for the sequence data, two outgroup species, *Alouatta belzebul* and *Lagothrix lagothrica*, were included in the phylogenetic analysis. These outgroup sequences were collected using the same methodology as the primary study species. All sequences used in this study were sourced from prior research on primate and Amazonian biodiversity phylogenetic studies (see supplementary material), with a significant portion originating from the most recent study by Janiak et al. (2022). Notably, the majority of the samples utilized in this study were obtained from wild individuals during various significant field surveys authorized by the Brazilian government between 2000 and 2017, with a limited number of samples originating from hunted individuals within local communities (Janiak et al., 2022).

2.2.2 Data analysis

2.2.2a Editing and alignment

Alignment of both the mitochondrial genome and cyt-B sequences was executed using the Geneious multiple sequence alignment tool within Geneious Prime (v.2022.2.1). The alignment settings encompassed a cost matrix of 65% similarity (5.0/-4.0), alignment type with free end gaps, a gap open penalty of 12, an extension penalty of 3, and two refinement iterations. Many of the cyt-B sequences obtained for the phylogenetic analysis contained additional gene regions, such as the ND-6 and ND-5 regions, necessitating their removal. The coding sequence (CDS) of the cyt-B gene region was extracted from the original sequences, forming a new matrix that underwent realignment in Geneious before further editing. Subsequently, the aligned sequences from both datasets underwent analysis and editing in Aliview, with sequence gaps, insertions, and deletions accounted for (Larsson, 2014). Duplicate records were removed to ensure the tree accurately reflected species delineation (Roy, 2009), and taxon labels were updated to align with the latest taxonomic nomenclature (see supplementary material). It is noteworthy that while the Geneious alignments exhibited large gaps, these sequences were retained, as this characteristic is indicative of rapidly evolving genes within divergent species. Additionally,

sequences with substantial gaps retained more present than absent data. The edited sequences were realigned in Aliview before being input into IQTree (IQ-TREE multicore version 1.6.12 for Linux 64-bit built Aug 15, 2019) (Nguyen et al., 2015) in preparation for tree building. The resulting alignment constituted of 25,000 base pairs (bp) for the cyt-B alignment, and 413,964 bp for the whole mitogenome alignment.

2.2.2b Phylogenetic tree construction

IQ-TREE is a fast and efficient stochastic algorithm for inferring phylogenetic trees using maximum likelihood. Through the Los Alamos Lab (USA) web server on the IQTree website, the nucleotide substitution model was set to algorithmically find the best nucleotide substitution model and apply it to the alignment. An SH-like aLRT test was done so that the relative support of internal nodes was assessed and optimised. The best model was TIM2+G4+F (Yang, 1994). This model compensates for the unequal and empirical base frequencies within the sequences and rates heterogeneity with a discrete gamma model. Estimated for the model parameters are, epsilon = 0.010, base frequencies A: 0.287, C: 0.290, G: 0.120, AND T: 0.303. Maximum likelihood was chosen as the parameterization method for the tree's state frequency. I selected the branch support of an ultrafast bootstrap with 1000 replicates, chose a tree search with 0.5 perturbation strength, and set a limit of 100 unsuccessful iterations to stop. The root of the tree was not pre-set; instead, I let IQTree compute the ancestral sequences of the maximum likelihood tree. The graphical viewing programme Figtree was used to visualise the output (Drummond & Rambaut, 2007) .

2.3. Results

2.3.1 Cytochrome-b tree results

The first phylogenetic analysis in this chapter was based on a dataset comprising a total of 38 cyt-B sequences for species of the *Ateles* genus, as illustrated in Figure 2. To provide a broader context, an outgroup sequence for *Alouatta belzebul*, a closely related species within the Atelidae family, was incorporated into the phylogeny. This comprehensive tree encompasses 12 out of the 15 most recently recognized *Ateles* species and subspecies, as outlined in Table 1 (PSG, 2022). Unfortunately, due to the unavailability of sequences, *A. f. fusciceps*, *A. g. geoffroyi*, *A. g. azuerensis*, and *A. g. grisescens* are not represented in this analysis. The

branches of the phylogenetic tree are color-coded to denote the delineation of predicted clades, each identified by letters A to J, along with the corresponding Genbank sequence ID prefixing the label nomenclature.

Inititating from the first break by the outgroup species in the phylogeney, *A. fusciceps* (including subspecies *A. f. rifiventris*) is the first to branch off within a clade supported by 95 bootstrap (BS). The second break in this clade includes the *A. geoffroyi* species along with the subspecies *A. g. ornatus, A. g. frontatus*, and *A. g. vellerosus*. This shows that the Central American Ateles species are identified as the sister to the rest of the spider monkeys with very high support. After the split of the sister taxa, *A. paniscus* is the first of the South American taxa to break off. This is followed by the break of *A. hybridus*, then a clade of *A. chamek* and *A. marginatus* sequences, then a split of a singular *A. chamek* sequence, proceeded by the break of the *A. belzubuth* in the tree. The remainding three splits in the tree all represent *A. chamek* and are randomly assigned.

Across the entire inferred phylogeny, clade support values (bootstrap support for the ML) offered dramatically different levels of support ranging from 40%-99% and the levels of support are scattered with no clear pattern through the clades. The Central American clades A and B have a high support, but the South American taxa that proceed drop support dramatically to 46% (clade C) and 40% (clade D). The next two clades, E and F, increase again to strong supports of 96% and 98%. The proceeding clade G decreases in support with 45% and is followed by slowly increasing supports in clade H (74%), I (98%), and J (99%). This fluctuating pattern of support across the phylogeny may suggest challenges in confidently placing certain clades and highlights potential limitations in the reliability of these placements.
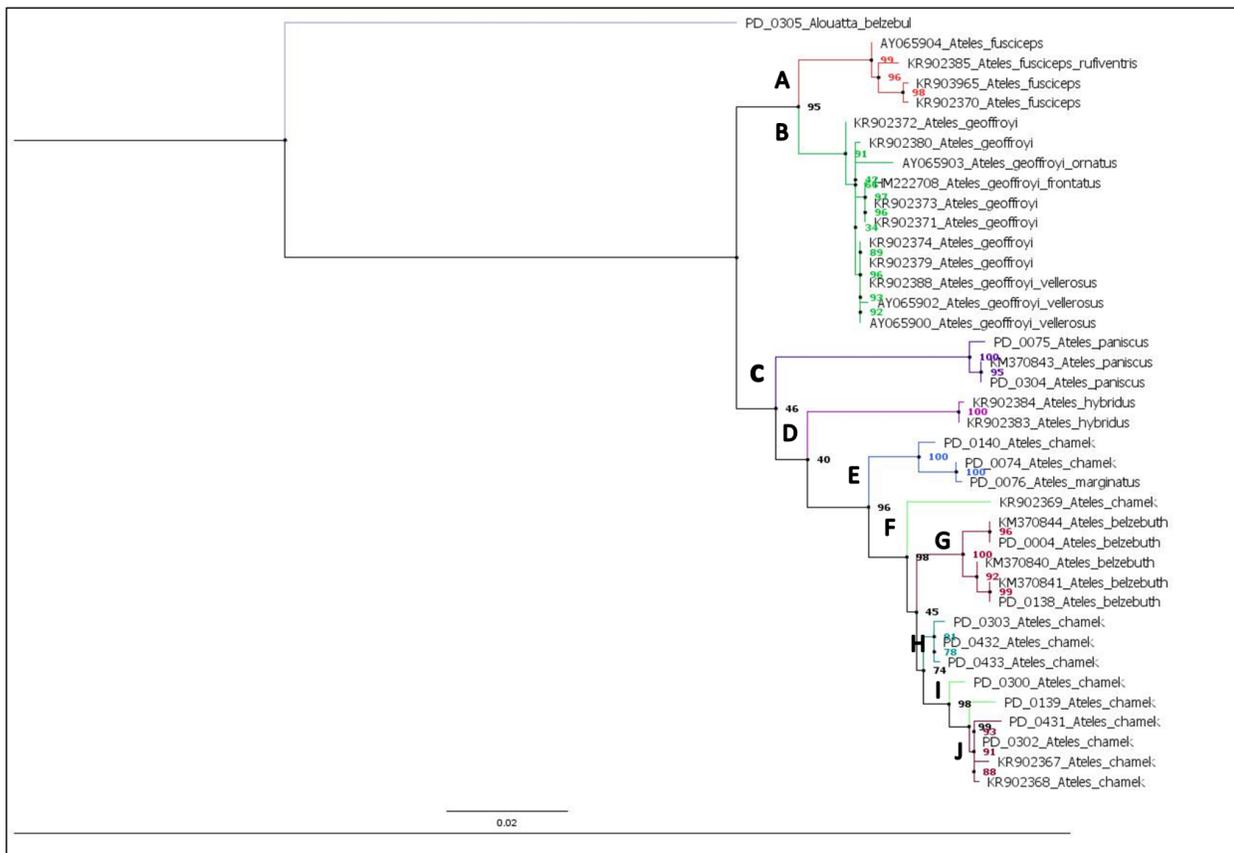
Figure 2: A maximum likelihood phylogenetic tree of the Ateles genus, constructed using the cyt-B gene region of mtDNA.
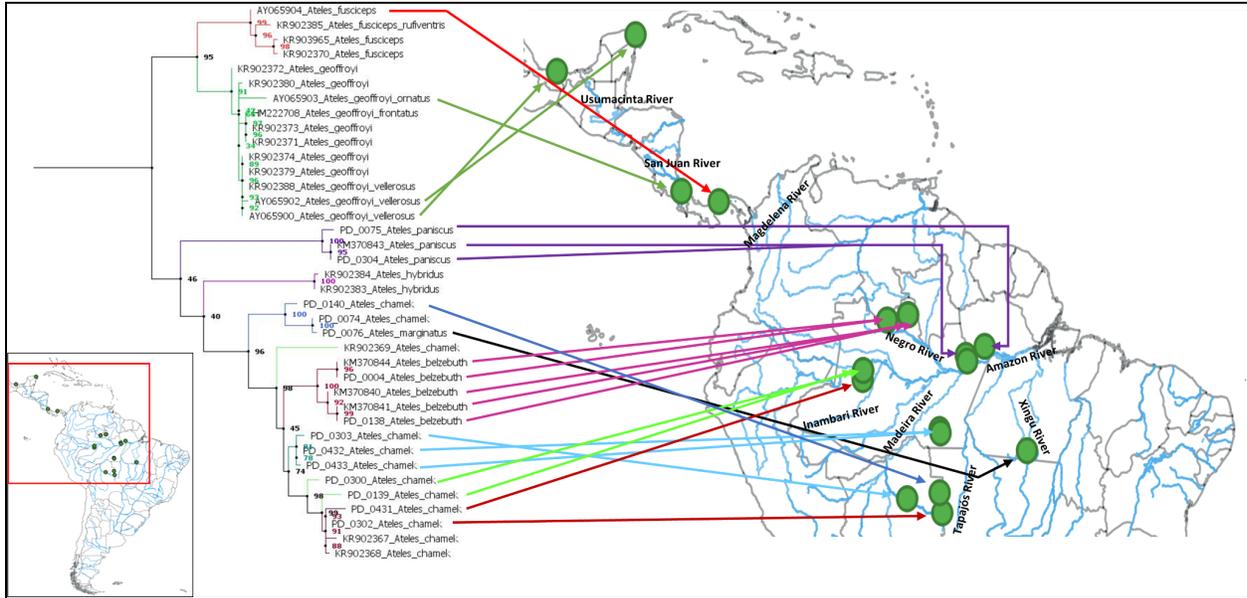
Figure 3: Sequence distributions for cyt-B sequences in geographical space.

2.3.2 Whole mitogenome tree results

The construction of the mitogenomic sequence-based phylogenetic tree employed the maximum likelihood method and utilized a dataset comprising 19 sequences, as visually represented in Figure 4. Inclusion of two outgroup sequences, *Lagothrix lagothrica* (OM328878) and *Alouatta seniculus* (OM329056), both belonging to the Atelidae family, was necessary to establish the root of the tree effectively. Attempting tree construction with only one outgroup sequence failed to resolve the tree's root. Within this phylogenetic representation, five distinct Ateles species were incorporated, whereas *A. fusciceps* and *A. hybridus* could not be included due to the absence of available sequence data. No subspecies are represented in this tree. Clades in the tree are distinguished by color-coding, and each clade is denoted by abbreviated labels A to F, accompanied by the respective Genbank sequence ID.

Proceeding the split of the two outgroup species in the tree, *A. geoffroyi* is the first of the *Ateles* species to branch off within a clade with low support of 47% BS. The second species to split within this clade is *A. paniscus*. This brings intrigue to the phylogeny straight away as there is both Central and Southern American taxa in this clade, which had been identified as the sister to the rest of the spider monkeys. Following the break of the sister taxa is a clade (C)

containing sequences for both *A. chamek* and *A. marginatus*. After this is the splitting of *A. belzebuth* (clade D). The remaining two clades on the tree, E and F, both represent the species *A. chamek*.

Across the entire inferred phylogeny, clade support values (bootstrap support for the ML) were mostly 100%. The exception is in the initial divergence of *Ateles* species within clades A and B, where support is comparatively lower at 47%. Interestingly, the split between clades E and F, despite involving the same species, also garners 100% support, reinforcing the robustness of this particular phylogenetic branching.
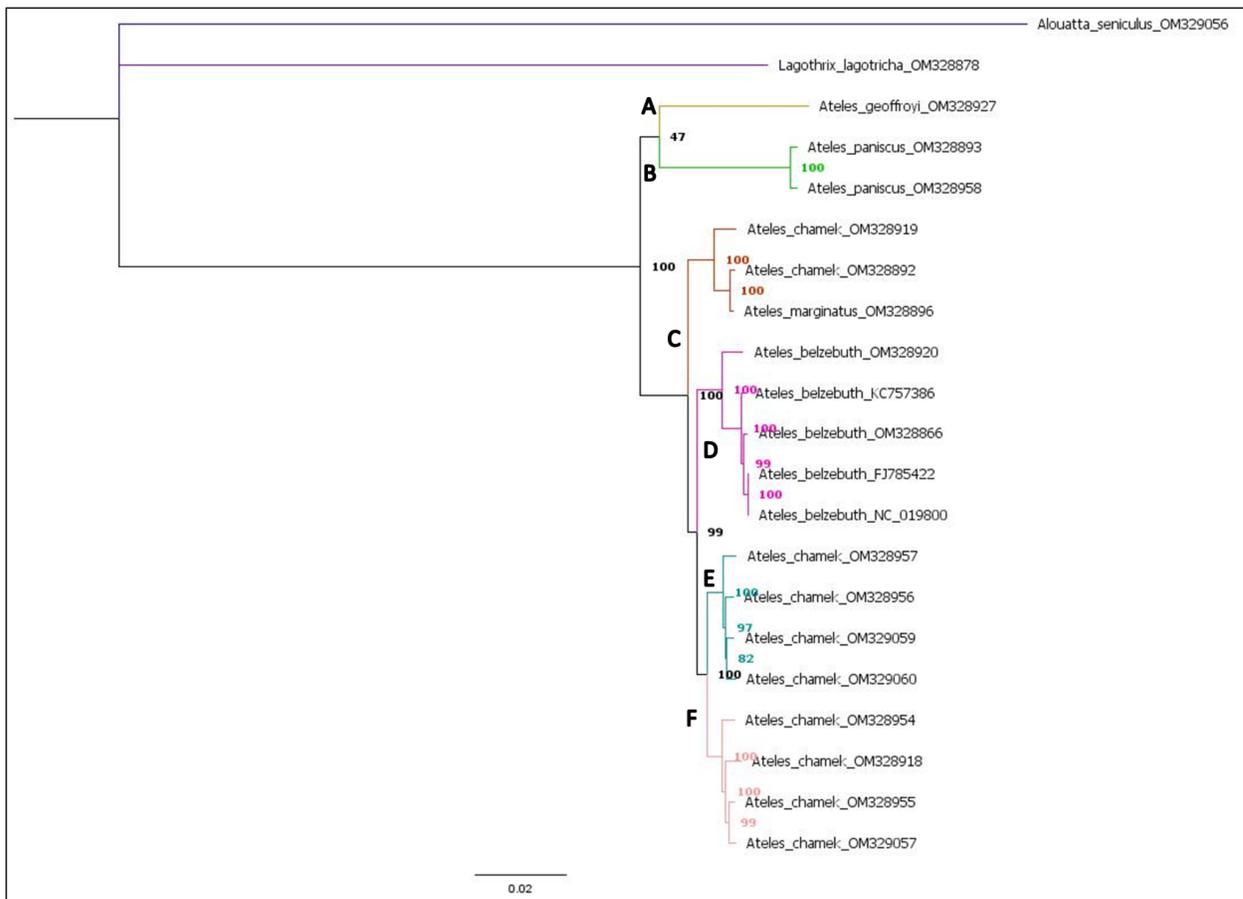
Figure 4: A maximum likelihood phylogenetic tree of the Ateles genus, constructed using full mtDNA genomes.
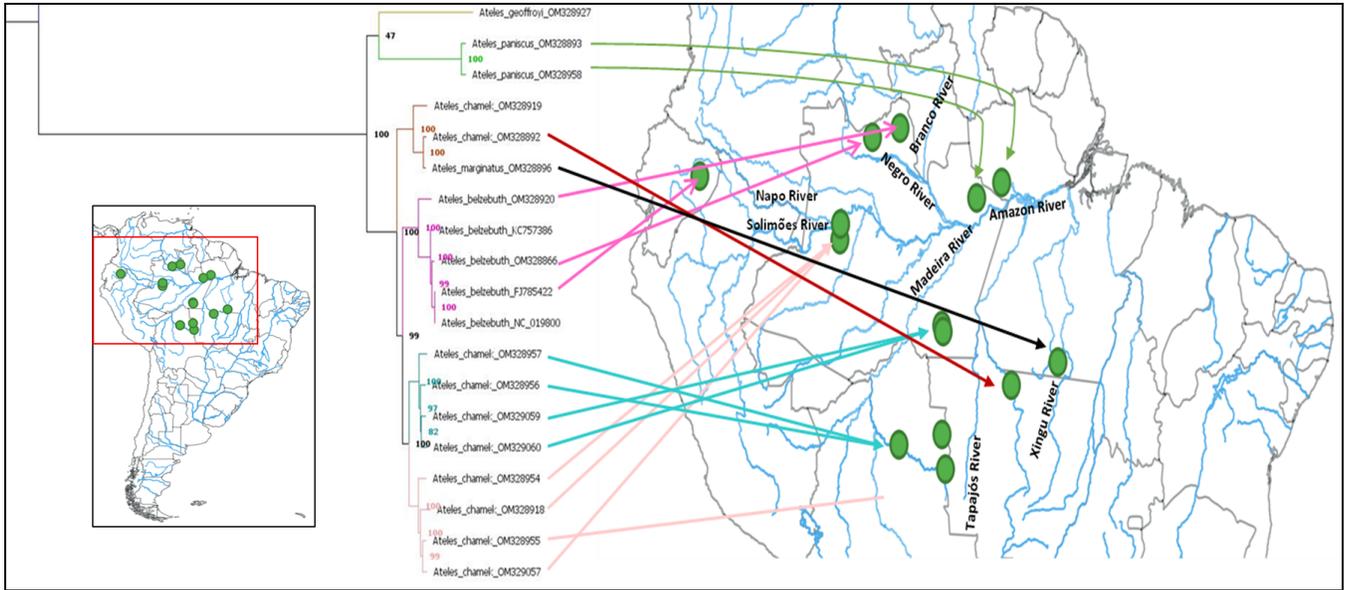
Figure 5: sequence distributions for full mtDNA genomes in geographical space.

2.4. Discussion

2.4.1 Cytochrome-b analysis

The initial tree observation reveals the Central American species *A. fusciceps* and subspecies *A. f. rufiventris* as the first to branch off within the same clade (A). This branch is accompanied by a robust bootstrap support (BS) of 95, with the inter-sequence splits consistently exhibiting high support values of 99, 96, and 98 BS. The subspecies *A. f. rufiventris* is embedded within the core of the clade. It's pertinent to mention that geographical data is available for just one sequence (AYO65904) hailing from eastern Panama. This particular sequence aligns with the IUCN-delineated distribution ranges for both *A. fusciceps* and *A. f. rufiventris*, raising the possibility of its true affiliation with the subspecies *A. f. rufiventris*, supported by a 99 BS between sequences AYO65904 and KR902385.

The second split from the inferred basal branch with 95 BS reveals clade B, encompassing another Central American species, *A. geoffroyi*, along with its subspecies *A. g. ornatus*, *A. g. frontatus*, and *A. g. vellerosus*. A total of 11 sequences constitute this clade, with a mere three containing geographical annotations. A3, representing the subspecies *A. g. ornatus*, is geographically positioned in western Panama. In contrast, sequences AYO65902 and AYO65900 signifying the subspecies *A. g. vellerosus*, are sourced from disparate locations: the Yucatan and

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Veracruz states of Mexico. Both of these localities fall within the IUCN-anticipated distribution range for this species.

The first two splits in this phylogeny (clades A and B) representing Central American *Ateles* species are unexpected. The results found here challenge conventional expectations that platyrrhine primates are believed to have originated in the Southern Amazonian basin before migrating northward into Central America. Speculatively, A. paniscus might have been the first species to diverge from the common ancestor of the spider monkey (Morales-Jimenez et al., 2015).

The third bifurcation in the tree introduces the Amazonian *Ateles*. Here, *A. paniscus* represents clade C with only 46 BS. But surprisingly, within the clade, the BS support between the sequences is notably high, ranging from 99 to 100. It is imperative to note that all sequences in clade C hail from the same geographic region, specifically the state of Para, Brazil (see Fig. 3).

Clade D is the fourth split in the tree, characterised by a low BS of 40 and representing *A. hybridus* with two sequences. Neither of these sequences have geographical information attached to them (see supplementary material), but both sequences exhibit a strong 100 BS, thereby confirming their conspecificity.

The fifth tree split, under the label "clade E" possesses a support of 96 BS, encompassing two *A. chamek* (PD_0140, PD_0074) and one *A. marginatus* (PD_0076) sequences. This finding engenders intrigue, as a re-analysis of the *A. marginatus* sequence through NCBI reveals a shared 100% query coverage with sequences labelled as *A. marginatus* and *A. chamek*. This discrepancy may be attributed to mislabeling in NCBI or could potentially signify a lack of distinct clades between these species. Notably, the *A. marginatus* sequence was obtained in the Brazilian state of Para, proximate to the Rio Xingu, coinciding with the species' IUCN-predicted distribution. Similarly, the *A. chamek* sequence (PD_0140) was collected in Rondônia, Brazil, left of the Rio Tapajos, aligning with the IUCN-predicted distribution. Though these rivers could serve as natural barriers, it's essential to acknowledge the inadequacies of the riverine barrier hypothesis for large-bodied primates like *Ateles*, as it fails to account for historical distributions, spatial limitations, and endemism areas (Smith et al., 2014; Santorelli et al., 2018).

The sixth split, labelled "clade F" features a solitary sequence for *A. chamek* (KR902369), which, when subjected to NCBI analysis, is identified under the previous nomenclature *Ateles belzebuth chamek* (Humboldt, 1812). This sequence exhibits 96% query coverage with *A. chamek*, *A. belzebuth*, and *A. marginatus* sequences in NCBI. Notably, prior research by Froehlich et al. (1991) suggests that these species once constituted an interbreeding ring species in central Amazonia, potentially elucidating the model tree's difficulties in taxonomic placement and the genomic similarities.

Clade G, the seventh split in the tree, comprises five sequences for *A. belzebuth*, displaying a low BS of 45. Intriguingly, within clade G, there exists a BS range of 96-100 among the individual sequences, endorsing their conspecificity despite the tree's uncertainty regarding clade placement. Geographic information is available for all these sequences, all originating from the State of Amazonas, Brazil, north of the Rio Negro.

Clade H accommodates three sequences of *A. chamek*. Two of these sequences (PD_0432, PD_0433) were collected in the state of Amazonas, Brazil, while the third (PD_0303) originates from Rondonia, Brazil. All three of these localities align with the IUCN-predicted distribution for *A. chamek.* The absence of an obvious geographic barrier between these sequences provides likely assurance that each sequence in clade H belongs to the same species. The remaining clades (I, J, and K) branching from the tree lack clear and explicit delineations. Curiously, each clade encompasses *A. chamek* sequences. It is notable that sequences PD_0300 (clade I), PD_0139 (clade J), and PD0431 (clade K) all stem from the same region in the State of Amazonas, Brazil, west of the Rio Inambari and south of the Rio Amazonas. The divergence of these sequences into different clades despite their shared sampling area is intriguing. Additionally, within clade K, sequence PD_0302 originates from the state of Rondonia, Brazil, in the same locality as sequences PD_0140 from clade E and PD_0303 from clade H. Since the other sequences in clade K (KR902367 and KR902368) lack geographic information, it remains challenging to determine their predominant distribution.

Using this phylogenetic approach with cyt-B, a discernible geographical partition within the currently recognised *A. chamek* species emerges, despite ambiguities regarding the placement of numerous clades containing this species within the tree. Sequence samples are distributed on

either side of the Rio Madeira, implying a potential taxonomic division despite the tree's lack of clarity in this regard. When the phylogeny is paired with the sequence locality information, a slight divide can be seen. In the Brazilian states of Amazonas and Rondonia, all three sequences (PD_0303, PD_0432, and PD_0433) in clade H are found to be grouped together in one region, left of the Rio Madeira. Both sequences (PD_0300 and PD_0139) observed in clade I are shown to be sampled from right of the Rio Madeira. In clade J, only two out of the four sequences have geographic information, and remarkably, one sequence (PD_0431) claims to originate with those of clade H on the left side of Rio Madeira. While the other sequence (PD_0302) is grouped with those from clade I on the left of the River. The incompleteness of sequence information, ie the lack of geographic data, has impeded the analysis of the predictions of this tree. Though there is not a perspicuous separation in the phylogeny, a slight taxonomic divide can be observed here, and this geographic information is an important feature to consider when trying to understand *Ateles* true taxonomy as this observation could represent a new clade in the genus never before observed.

2.4.2 Mitochondrial genome analysis

The initial branch of the mitogenome phylogeny segregates *A. geoffroyi* (clade A) and *A. paniscus* (clade B) as the sister taxa to the rest of the genus with a BS of 100. But despite this robust initial support, the subsequent separation between these two species exhibits a considerably lower BS of 46. Clade A, encompassing the exclusive representation of the Central American species within this tree, features a solitary sequence that has no geographic data. Contrarily, clade B, which contains a South American species, consists of two sequences that were sampled close to one another, within the species' estimated IUCN range of distribution, particularly in the Brazilian states of Para and Amazonas, which are located north of the Rio Amazonas.

The placement of these two species in this phylogeny raises certain suspicions, given that *A. paniscus* is traditionally positioned as the sister species to all others, while Central American species typically appear as the earliest divergence in cyt-B-based phylogenies (Fig. 2). This prevailing pattern is consistent across various phylogenetic analyses, encompassing morphological studies (Froehlich et al., 1991), cytogenetic investigations (Medeiros et al., 1997), and mitochondrial DNA studies (Collins & Dubach, 2000). An exception is found in the

phylogenetic analysis conducted by Morales-Jimenez et al. (2015), wherein *A. marginatus* is identified as a sister lineage to the remaining *Ateles* genus with 100% BS in the maximum likelihood analysis and 100% Bayesian posterior probability.

The division of these species in this phylogeny may have some evidence of support, but the predicted relatedness between these clades is questionable, warranting the relatively low BS. When comparing the findings of this tree (Figure 4) with those in Figure 2, the clade housing *A. paniscus* consistently emerges as the sister clade to *A. geoffroyi* in both phylogenies, supported by an identical BS of 46. It is noteworthy that the only instance of low support in this phylogeny is observed here, with subsequent branches exhibiting high BS values ranging from 82 to 100, affirming the overall reliability of the tree.

The third split in the tree delineates clade C, featuring two *A. chamek* sequences and one *A. marginatus* sequence supported by a 100 BS value. It is highly plausible that all three of these sequences belong to the A. marginatus species, given that the sequence data for two out of three falls within the same geographical region predicted within the IUCN distribution for the currently recognized A. marginatus. The alignment of these findings with the cyt-B phylogeny in Figure 2 confirms the congruence in placement for these sequences.

The fourth branch in the tree, representing clade D, is made up of five *A. belzebuth* sequences with reliable BS values of 99-100. Three of the five sequences in this clade (OM328920, OM328866, and FJ785422) contain geographic information and are distributed widely across the projected IUCN distribution, rather than clustering. This distributional diversity enables a more precise taxonomic reconstruction grounded in the true distribution of the species. Sequence FJ785422 is located in Ecuador, specifically the Yasuni National Park and Biosphere Reserve. Sequences OM328920 and OM328866 are both found in the state of Amazonas, Brasil, north of the Rio Negro and west of the Rio Branco. This is interesting, as the phylogeny predicts all of these sequences belong to the same species, but at the same time their distribution is extremely large with clear geographic barriers present between the localities. Yet, the populations represented here have not speciated and may act as proof that the riverine barrier hypothesis is not a valid biogeographic theory for this species.

The remaining two splits in this phylogeny (clades E and F) are of exceptional significance and intrigue. Both clades contain sequences belonging to the presently recognized *A. chamek* species (PSG, 2022). These clades constitute sister groups, firmly supported by a BS value of 100. Within clade E, high BS support levels ranging from 82-100 underscore the high accuracy of the predicted placement of this clade and affirm the conspecific status of its constituent sequences. This is the same for clade F; the prediction that the sequences in this clade belong to the same species but are different from those of clade E is very likely to be true, as a result of the extremely high maximum likelihood support of 99-100 BS. This taxonomic prediction receives further validation from the geographic information associated with these sequences.

Examination of Figure 5, which provides a geographic perspective, reveals distinct regional presence of each clade separated by geographic barriers. Clade E sequences OM328957 and OM328956 are situated in the state of Rondonia, Brazil, whereas sequences OM329059 and OM329060 originate from the southern region of the state of Amazonas, Brazil. Clade F, on the other hand, encompasses sequences (OM328954, OM328918, and OM329057) found in the central region of the state of Amazonas, west of the Rio Madeira and Rio Iramabe, south of the Rio Solimoes. A single sequence in clade F (OM328955) challenges the phylogeny's prediction of a new clade, as its locality is located in the state of Mato Grosso, in close proximity to the sequence localities in clade E. Despite this isolated exception, the collective information, in conjunction with geographic data and high-confidence bootstrap support values, substantiates the identification of a novel *Ateles* taxon within these clades. Importantly, these clades, despite their distinct geographic ranges, align with the projected IUCN distribution for A. chamek.

2.4.3 Comparative analysis

In the comparative examination of the phylogenetic outcomes derived from the mitochondrial genome tree (Figure 4) and the cyt-B tree (Figure 2), an intriguing and congruent pattern emerges. A clear division among the *A. chamek* sequences becomes evident in both trees, despite the somewhat less distinct topology in the cyt-B tree (Figure 2). This recurring pattern is also observed in the phylogenetic analysis conducted by Janiak et al. (2022). Such consilience may signify the recognition, or at least investigation, of a new taxa. This new taxonomic structure may be the result of allopatric speciation, which may have been facilitated by the existence of geographical barriers that have induced reproductive isolation among different

populations. Alternatively, this pattern could be indicative of parapatric speciation, wherein a portion of the species population has ventured into a new ecological niche, subsequently undergoing reproductive isolation within the adjacent niche.

It is noteworthy that this consistent pattern of divergence is robustly supported across three independent phylogenetic analyses (two of this study, and of Janiak et al. (2022)). If, indeed, clade E is confirmed as a distinct lineage, immediate and decisive conservation measures become imperative. This particular clade is geographically situated in Rondonia, Brazil, an area undergoing rapid transformation and extensive deforestation. Due to extensive government colonisation efforts, the state has seen an increase in rural migrants, leading to a significant increase in population and putting the forest under intense pressure from deforestation activities like logging and ranching (Pedlowski et al., 2005). The extent of deforestation in Rondônia is alarming, with a staggering 67,764 km2 of forest cleared by 2003, marking a substantial escalation from the 4200 km2 cleared in 1978 (Global Forest Watch Data, 2023).

The importance of this recently-recurring delineation is that extinction has a high probability of occuring before the recognition of a new species may occur. As with most species, spider monkeys are profoundly affected by extensive habitat loss stemming from land clearance and agricultural expansion (Mittermeier et al., 1989). Furthermore, habitat degradation in the form of selective logging and vegetation disturbance exacerbates their vulnerability (Michalski & Peres, 2005). The genus *Ateles*, characterized by low intrinsic rates of population increase, displays heightened susceptibility to ecosystem perturbations (Johns & Skorupta, 1987). The predicted phylogenetic distinction must be thoroughly investigated right away. This research requirement provides the rationale to advocate the disbursement of conservation funds and the creation of strict protected areas in locations where this clade is anticipated to occur.

Another noteworthy observation in the comparative analysis between the two presented phylogenetic trees is the apparent insignificance of the species *A. hybridus* within the taxonomic framework. This study identified only a single cyt-B sequence for this species. However, the overall topology and evolutionary chronology of the genus remain unaltered when *A. hybridus* is absent from the mitogenome model. This scenario is the same when considering the species *A. fusciceps*, in that the trees do not differ in the relative branching order among the taxa when

this species is absent in Figure 4. The Central American taxa are still identified as the sister to all other spider monkeys in both tree constructions.

I recommend a comprehensive taxonomic review of the *Ateles* genus. I advocate for the acquisition of new genomic data from various regions encompassing the genus's entire distribution, particularly in areas where current phylogenies suggest speciation or where sample records are lacking. To this end, I propose the initiation of further field research and sample collection across South America for *Ateles* species, especially into the recognised subspecies of this clade where the gaps in information are most severe. There are no available whole mtDNA sequences for any subspecies, as represented in Figure 4.

2.5. Implications for spider monkey taxonomy and conservation

2.5.1 Taxonomic implications

The analysis in this thesis reveals the presence of potential cryptic species within the *Ateles* genus, where morphologically similar individuals exhibit distinct genetic lineages. This observation challenges existing taxonomic classifications and suggests that some spider monkey populations may have been inaccurately grouped as a single species due to their physical similarities. Consequently, these results make a compelling case for a comprehensive taxonomic revision within the genus. This revision entails reevaluating current species and subspecies classifications, with the possibility of formally recognizing new, genetically distinct lineages as separate species. Geographic factors, particularly geographic isolation, are paramount in this consideration and may lead to the recognition of subspecies or entirely new species.

2.5.2 Conservation implications

The implications for spider monkey conservation are equally significant and multifaceted:
- Identification of a New Taxon: The findings of this chapter's phylogenetic analysis indicate the possible existence of a novel Ateles taxon in clades E and F (Figure 4), highlighting the immediate need for detailed taxonomic investigation in order to formally classify and preserve this recently observed potential lineage. Conservation efforts

should be faced towards safeguarding the unique genetic diversity represented by this taxon.

- Conservation Prioritization: Clades E and F are both situated in distinct South American geographic regions. This genetic divergence could be a result of geographic barriers, suggesting the potential existence of separate spider monkey populations adapted to specific ecological niches. Consequently, conservation priorities should be targeted to preserve the respective habitats and ecosystems, recognizing them as potential evolutionary significant units (ESUs) or distinct species.

- Habitat Protection: Regions inhabited by these potential new taxa, such as Rondonia and Amazonas in Brazil, are experiencing alarming rates of habitat loss due to activities such as logging, ranching, and deforestation. Urgent and robust conservation measures are imperative to shield these habitats from further degradation and loss.

- Ecosystem Integrity: Spider monkeys play a pivotal role in maintaining the ecological health of their habitats. Their role as seed dispersers contributes to forest regeneration and sustains biodiversity. Preserving spider monkey populations and their habitats is pivotal for the overall health and resilience of these ecosystems.

- Human Impact: Addressing human-induced threats, including hunting and habitat destruction, is paramount to spider monkey conservation. Collaborative initiatives with local communities can mitigate these threats while promoting sustainable coexistence.

- Genetic Diversity: Recognizing and safeguarding the genetic diversity within spider monkey populations are crucial for their long-term survival. Protecting distinct genetic lineages and preventing genetic bottlenecks are vital for maintaining healthy populations and their adaptive potential.

- Further Research: Ongoing research efforts, encompassing field studies and genetic analyses, are essential for a deeper understanding of spider monkey populations. This knowledge informs targeted and effective conservation strategies.

2.6. Conclusions

The spider monkey genus *Ateles* has achieved increased phylogenetic attention in recent years due to its remarkable species diversity and the intricate taxonomic questions surrounding it. These foundations must be understood if conservationists have any chance of determining if a taxon is genetically distinct enough from others to justify developing distinct and effective action plans to preserve and protect lineages, landscapes, and genetic diversity. This study has

unveiled compelling insights into the taxonomy, genetic diversity, and evolutionary relationships within the *Ateles* genus, which hold profound implications for conservation efforts.

In this study, two distinct clades were identified within the phylogenetic tree, both representing the Amazonian species *A. chamek*. The existence of these clades and their geographic segregation offers strong evidence in favour of speciation events occurring within this species. This discovery suggests the emergence of a new Molecular Operational Taxonomic Unit (MOTU) within the *A. chamek* complex. Additionally, the analysis revealed several monophyletic clades, each of which can be considered as autonomous management units.

These discoveries represent a considerable improvement in our understanding of the *Ateles* genus, necessitating a thorough taxonomic revision. The classification of *A. chamek*, in particular, emerges as a primary research concern. When dealing with similar evolutionary units within the genus, the development of a strong taxonomy based on phylogenetic links will enable ecologists, behavioural scientists, and other researchers to derive more insightful conclusions from their work. Furthermore, this taxonomic clarity will serve as a cornerstone for holistic conservation efforts.

In summary, this study has illuminated the intricate web of spider monkey taxonomy and genetic diversity, paving the way for more informed and targeted conservation measures. As we delve deeper into the complexities of this genus, we move closer to safeguarding not only the enigmatic spider monkeys themselves but also the rich tapestry of life they inhabit.

Chapter 3: Species Distribution Modelling for Amazonian *Ateles*

3.1. Introduction

The tropical rainforests of South America, inhabited by spider monkeys, are facing enduring transformation and degradation due to widespread deforestation and habitat loss. These threats are primarily driven by factors such as agricultural expansion, logging, mining, fossil fuel extraction, and over-hunting (Estrada et al., 2017). There is a concerning projection that by the year 2050, approximately 40% of the Amazonian forests will have been destroyed (Soares-Filho

et al., 2006). Spider monkeys are classified among the most endangered primates on earth, emerging as particularly vulnerable to habitat disturbance. They do not survive in small, fragmented forest patches (Michalski & Peres, 2005). Additionally, their population densities decrease substantially in areas subjected to selective logging or other forms of human-induced disturbance (Freese et al., 1982a).

One of the biggest threats confronting spider monkey populations, especially within the "arc of deforestation", arises from extensive deforestation driven by the exponentially increasing global demand for Brazilian beef. This has led to the conversion of vast tracts of forests into pasturelands. In 1995-96, the land area allocated for crops amounted to 5,608,000 hectares, while pastureland covered 33,579,000 hectares (Kaimowtiz et al., 2004). Moreover, a significant portion of crop production (70-75%) serves as livestock feed, pointing towards a continued and simultaneous expansion of both agricultural practices, further exacerbating deforestation trends (Barona et al., 2010). The surge in the cattle population from 26 million in 1990 to 57 million in 2002 is closely linked to this expansion, with 80% of the growth occurring in the Amazon, particularly in states like Mato Grosso, Pará, and Rondônia, which are subjected to substantial deforestation rates (Kaimowtiz et al., 2004). Logging activities pose another prominent threat and significantly impact spider monkeys as they are large frugivorous primates with preferences for living in the upper levels of the forest canopy. Logging disrupts their aerial pathways and diminishes the availability of essential food resources (Johns & Skorupa, 1987; Van Roosmalen, 1985).

Spider monkeys are extremely important to ecosystem health, serving as effective dispersers of large seeds produced by tropical trees due to their extensive home ranges and specialized diet. However, the degradation of their habitats has led to a reduction in the size of these ranges. This trend can be seen when looking at previous literature, such as Kellogg & Goldman (1944) and Collins & Dubach (2001), revealing a concerning decline in the predicted distribution of *Ateles chamek* over the last two decades. This decline primarily affects species inhabiting the southern Amazon region, often referred to as the "arc of deforestation," characterized by the highest rates of deforestation driven by Brazil's expanding agricultural frontiers.

Another problem driving the alarming rates of deforestation in spider monkey habitats is the establishment and "improvement" of transamazonian highways BR-230 and BR-319. These highways have heightened accessibility to these forests, attracting human population migration,

illegal colonization, wild-meat hunting, illegal wildlife trade, and an array of land and resource exploitation activities, including both legal and illegal logging and cattle ranching. These activities have raised substantial ecological concerns, as they advance northward, causing extensive forest loss and ecological shifts along their paths (Faleiros & Isensee, 2018). The potential repercussions extend to community-level impacts, affecting both flora and fauna (Campbell, 2008; Di Fiore et al., 2009). Hence, the conservation of *Ateles* species holds paramount importance for the preservation of the Amazon rainforests and their intricate biodiversity, including human communities intricately linked to these ecosystems.

Protected areas (PAs) are fundamental for biodiversity conservation. PAs help to maintain key habitats and ecosystem balance, provide refugia and allow for species migration and movement, build resilience to climate change, maintain water quality, and provide global food security to secure the wellbeing of all biodiversity and humanity (CBD, 2022). Globally, species richness and abundance are both 10.6% and 14.5% higher in PAs than they are outside of them, respectively (Gray et al., 2016). PAs are not just beneficial for wildlife, 1.1 billion people rely on PAs for their livelihoods, and over a third of the world's largest cities' primary source of drinking water comes from PAs (*Campaign for Nature*, 2023). When PAs are willingly and equitably governed, remarkable benefits can be attained far beyond their borders, advancing national economies and assisting in the fight against poverty and sustainable development. Ultimately, PAs offer a practical response to an unpleasant reality as the planet is threatened by the negative effects of climate change.

In this chapter, I employ species distribution modeling (SDM) to predict the distribution of South American spider monkey species, including *A. chamek, A. paniscus, A. marginatus, A. hybridus,* and *A. belzebuth*, as recognized by PSG (2021). I also construct a figure with PAs overlaid onto habitat suitability models for each species, highlighting where gaps exist and how much of the most suitable habitat for each species is actually protected, as well as highlighting which regions require PA expansion. The objectives of this study include identifying regions within the Amazon with the highest habitat suitability for these species, estimating current and future rates of habitat loss in these areas, and identifying priority zones for spider monkey conservation efforts. I illustrate the application of SDM as a valuable tool for assessing threats to species and providing guidance to decision-makers in implementing targeted conservation measures. My recommendations include the expansion of existing protected areas and the initiation of forest

restoration projects to enhance landscape connectivity and preserve these invaluable primates and their habitats.

3.2. Habitat suitability modelling and MAXENT

Habitat suitability modelling can help conservation by aiding endangered species, habitat management, and encouraging ecosystem reintroduction and restoration. It achieves this by forecasting and developing models of species distribution that assess the relationship between species occurrences and a set of spatially explicit environmental variables in order to evaluate the species' environmental requirements and project them in geographical space. The goal is to identify the areas within a region of interest that satisfy the species' ecological niche and form part of its potential distribution (Anderson & Martínez-Meyer, 2004). The potential distribution identifies the areas within the region where conditions are suitable for species survival, and helps to determine the realised distribution of the species by removing areas where the species is known to be absent (i.e due to some form of habitat destruction). These models have been widely used as decision-support tools to guide conservation efforts (see Villero et al., 2017). In this study, we use the maximum entropy (MAXENT) approach to species distribution modelling (Phillips et al., 2006) as we are using presence-only data (meaning we have data on occurrence localities from sightings/museum collections, but no data on where the species has failed to be observed), which is useful for species that inhabit poorly sampled tropical regions, such as spider monkeys. Maxent was chosen because, when using presence-only data, it outperforms comparable methods (Elith et al., 2006).

3.3. Methods

To construct species distribution models, assess habitat suitability, and estimate potential distributions, I employed MAXENT version 3.4.3 within the statistical environment RStudio version 4.1.1 (RStudio Team, 2022), supported by the "dismo" package (version 1.3-5). The concept of MAXENT is to estimate the target distribution by determining the distribution of maximum entropy (i.e., that is nearest to uniform), under the condition that each feature's expected value under this estimated distribution is equal to its empirical average. And under convex duality, this is the same as finding the maximum likelihood Gibbs distribution (Phillips et al., 2006).

MAXENT aims to construct models that depict the potential distribution and habitat suitability of the target species based on relevant environmental variables. The algorithm discerns non-random relationships between species occurrences and environmental factors to accomplish this (Rabelo et al., 2020). We adapted five RStudio scripts provided by Rabelo et al. (2020) for data preparation and manipulation, tailoring them to suit the requirements of this study. These procedures were replicated for each of the five distinct spider monkey species under study in this chapter.

3.3.1 Data Collection

Species occurrence data were gathered from various sources, including literature, online repositories like the Global Biodiversity Information Facility (GBIF, 2022) and INaturalist (2022), and the University of Salford laboratory records supplied by Prof. Jean P. Boubli (see supplementary material). Collection from community science project websites, such as GBIF and INaturalist, involved stringent criteria before being selected for use in this study, with a focus on research-grade quality. Observations meeting these criteria had to include valid dates, precise locations, photographic or auditory evidence, and exclusion of captive or cultivated individuals. Such observations underwent community review and required a minimum of two agreeing identifications by expert users to achieve research-grade status. Duplicate records were removed, and a further filtering step eliminated records within a 0.5 km radius of each other to mitigate sampling bias or overestimation of presence (Boria et al., 2014). A total of 714 occurrence records were initially gathered for *Ateles chamek, A. belzebuth, A. marginatus, A. hybridus*, and *A. paniscus*, with 599 records used in the model, after filtering. Geographic information system software, QGIS (version 3.16.11, QGIS Development Team, 2022), was used to spatially represent the species' data. In QGIS, I created a polygon layer encompassing all occurrence points. IUCN red list species distribution shapefiles (IUCN, 2022) were merged with the polygon of species locality records to delineate the species' extent of occurrence, which was used to parameterize the final model. A species' extent of occurrence is the area that is/has been accessible to the species, given its dispersal capacity over a specific time period (Soberón & Nakamura, 2009), while it is not expected that a species will occupy its entire extent of occurrence uniformly due to environmental or biotic constraints (Rabelo et al., 2020). In this situation, having established the habitat suitability threshold above which the species is anticipated to exist, it can be assumed that (a) the areas within the EOO with habitat suitability

> 40% equate to the species' AOO; (b) species records situated within the AOO indicate populations occurring in highly suitable habitats; and (c) records located outside the AOO constitute populations occurring in habitats with low suitability and environmental restrictions. This is empirical information and should be acknowledged for species conservation concerns. An adjustment was made to the IUCN shape for *A. belzebuth* to rectify its omission of locality areas in or near Ecuador, a region known to be inhabited by this species, particularly in Yasuni National Park (Cant et al., 2001; Blake et al., 2010; Spehar et al., 2010; Suarez, 2014). The shape was updated within QGIS to incorporate these well-studied *A. belzebuth* populations, and the IUCN has been notified to revise its information accordingly.

3.3.1a Protected areas

To create a figure representing the amount of a species IUCN predicted distribution that is recognised as PA's, data from the World Database of Protected Areas (WDPA)(2023) was downloaded online and layered over the distribution and predicted habitat suitability models created for this chapter (see Figure 11). The online data was converted into a polygon shapefile on QGIS, and using the overlap analysis function in the proccessing toolbox, the percentage of coverage over the shapefile of species IUCN predicted distributions could be calculated.

3.3.2 Data Analysis

3.3.2a Environmental variables

To select environmental variables for the species distribution models, a Pearson's correlation analysis was performed between the variables and species distribution data. This analysis was executed independently for each of the five species under study. For *Ateles chamek*, a correlation coefficient of 0.69 was identified through the pearsons correlation analysis. *A. belzebuth* showed as 0.86, *A. marginatus* was 0.64, *A. paniscus* was 0.95, and *A. hybridus* showed as 0.69. Correlation results were used to construct dendrograms, elucidating the importance of variables and revealing highly correlated variables. Variables displaying significant collinearity (>10) were subsequently excluded to prevent model distortions, as the ideal scenario for predictive modelling is to have the colinearity measure as close to one as possible. (de Carvalho et al., 2017).

Climatic variables were obtained from wordclim.org (2022), projecting a total of fifteen variables into the model. The use of climatic variables is important to SDM as it allows patterns of climate change to be visualised. Following correlation assessments only nine variables were retained (see supplementary Table 1). These environmental variables remained consistent across all species, providing a controlled setting while acknowledging that these species inhabit similar habitats, resulting in overlapping influential variables. The selected variables included isothermality, precipitation seasonality (coefficient of variation), precipitation of the coldest quarter, mean diurnal range, mean temperature of the wettest quarter, precipitation of the warmest quarter, annual precipitation, and precipitation of the wettest month. For *A. marginatus*, an additional variable, the mean temperature of the driest quarter, was incorporated into the model, as correlation analysis indicated its significance for this species but not for others.

To align environmental variables with the species' extent of occurrence polygon, I cropped the variables accordingly. Pair-wise correlation tests were conducted to validate the model. Utilizing the cross-validation technique with 500 randomly selected background records, the occurrence records were divided into subsets, reserving one for training and nine for testing (Phillips & Dudík, 2008). By establishing a habitat suitability threshold of >40% that determined occupied habitat areas (i.e., the species' area of occupancy), I converted continuous habitat suitability models into binary predictions. The overlap analysis tool in QGIS was used to calculate the percentage of habitat suitability. The MAXENT output polygon was converted into a vectorised layer by removing all cells in the shape with missing information (indicating non-appropriate habitat), resulting in a vectorised layer holding only suitable habitat cell information (the extent of occurrence). This vecorised layer was compared to the IUCN predicted distribution to see what percentage of the area of occupancy is compared to the extent of occurance. The percentage of occupancy could not be calculated for *A. belzebuth*, as the polygon used for the analysis was created by myself, and not the IUCN, so there was no geographic background data to compare the size of the vectorised layer to the original polygon.

3.3.1b Model evaluation

To measure model accuracy and evaluate its performance, a combination of threshold-independent and threshold-dependent metrics was employed. Threshold-independent

assessment was accomplished through the Area Under the Curve (AUC), a common measure used in receiver operating characteristic (ROC) analysis. An AUC value of 0.5 signifies that the model's predictions are no better than random chance, values below 0.5 indicate performance worse than random, while the range of 0.5–0.7 suggests poor performance. An AUC in the range of 0.7–0.9 indicates reasonable to moderate performance, while an AUC exceeding 0.9 is indicative of high model performance (Peterson et al., 2011). In this study, the mean AUC value across all five models stands at 0.842, with specific values for individual models detailed in the species-specific results sections.

Threshold-dependent evaluation involved sensitivity, specificity, and standard deviation calculations. Sensitivity measures the percentage of correctly classified presences, whereas specificity quantifies the percentage of correctly classified absences. Maximizing the sum of sensitivity and specificity is a robust approach for selecting an optimal threshold (Kong et al., 2019). These mathematical metrics sensitivity and specificity indicate the precision of a test in distinguishing true positives and true negatives, respectively, assuming regions with suitable habitat are considered "positive" and areas without suitable habitat are considered "negative" (West et al., 2016)

To ascertain the reliability of the models, the standard deviation (SD) was employed. SD quantifies the proximity of results to the estimated mean, thus offering insights into the experiment's accuracy. Notably, standard deviation and accuracy exhibit an inverse relationship: larger standard deviations correspond to reduced experiment precision. The mean standard deviation across all five models featured in this study is 0.083, with specific values for individual models elaborated upon in the respective species-specific results sections.

3.4 Results

3.4.1 Ateles chamek

The habitat suitability and predicted species distributions are shown in Figure 6. According to the model, the species has a reduced area of occupancy within its extent of occurrence, occupying only 74.9% of the IUCN predicticed range. I discovered that the species is more likely to occur in the central-southern region of its range, where habitat suitability is higher. The

model also predicts suitable habitats for the species in the northwestern part of its range, in Peru's Amazonas-Javary interfluvial region and along Brazil's Lower Jutai and Jurua rivers.

The most important variables in the model were (3) isothermality, (19) precipitation of the coldest quarter, and (18) precipitation of the warmest quarter, which jointly contributed 60.3% to the model gains in all iterations (28.7, 15.3, and 16.3%, respectively; Supplementary Table 3) and were concurrently responsible for 46.1% (35.2, 7.1, and 3.8%, apiece; Supplementary table 3) of the permutation importance in the model. The jackknife test of variable importance results show that environmental variable 3 (isothermality) has the highest gain when used in isolation and thus appears to have the most useful information by itself. But when correlated variables are included, the same variable loses the most gain and appears to contain the most information that isn't present in the other variables.

The model predicts that higher levels of precipitation in the wettest and warmest quarters are related to higher habitat suitability. The greater the seasonality of precipitation, the lower the habitat suitability for the species (see supplementary figure 1). The mean threshold of equal sensitivity-specificity for the 10 replicate MAXENT runs is 0.703 (AUC), and the standard deviation (SD) is 0.060; therefore, I am confident in the accuracy of this prediction.

(a) Habitat suitability (0-1 (highest))

Color	Value
Blue	0.0
Green	0.2
Yellow	0.5
Orange	0.7
Red	1.0

International boundaries
Rivers
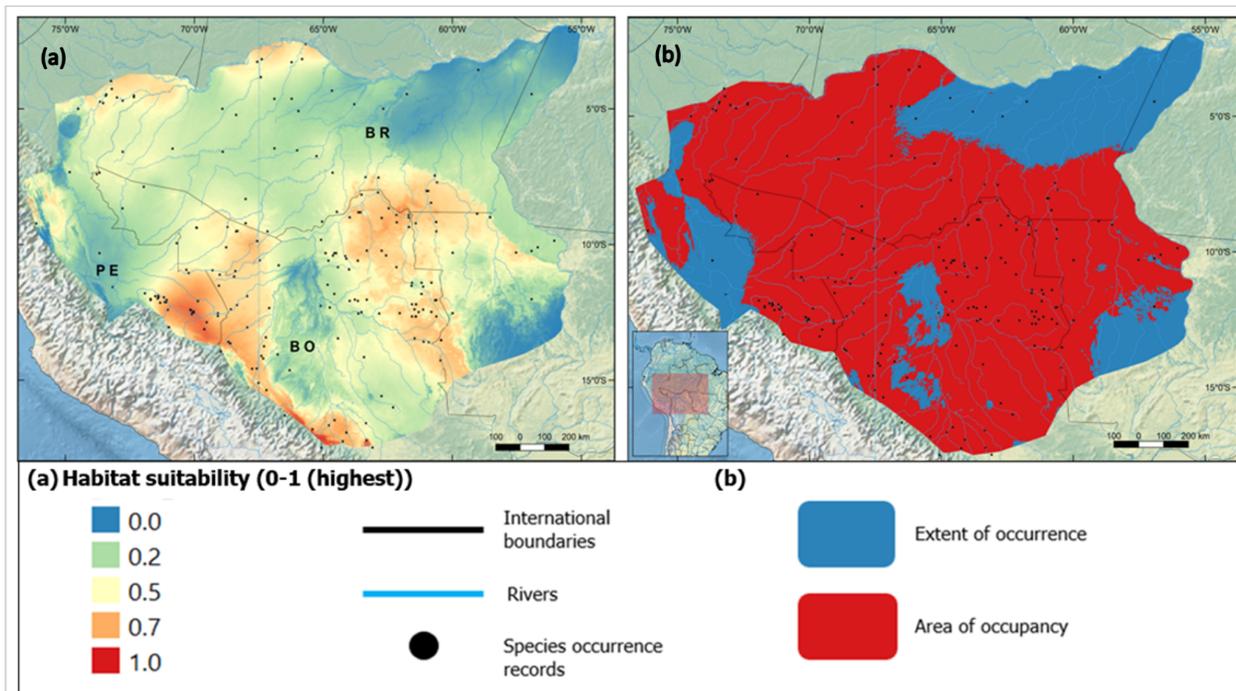Species occurrence records

(b)
Extent of occurrence
Area of occupancy

*Figure 6: **(a)** habitat suitability and **(b)** predicted area of occupancy for the black spider monkey Ateles chamek in northern and central Bolivia, western Brazil, and north-eastern Peru.*

3.4.2 Ateles belzebuth

The habitat suitability and predicted species distributions are shown in Fig. 7. According to our model, the species has a reduced area of occupancy within its extent of occurrence. We discovered that the species is more likely to occur in the western Amazonian regions of Colombia, Ecuador, and Peru, where areas of high habitat suitability are scattered in sporadic patches across the territory. The majority of species occurrences are found in locations that coincide with these habitat suitability hotspots. This could possibly infer that the realised distribution is much smaller than this model actually predicts, as the forecasted area of occupancy is very large compared to the dispersion of locality points, or that there is a sampling bias due to these areas being accessible for surveys while other, less suitable areas may be dangerous/harder for conservationists to survey. In the eastern region of the species' range, across south-central Venezuela and northern Brazil, the model predicts this entire area to have a mid-low score of habitat suitability and have few occurrence localities. There is barely any AOO on top of the IUCN predicted EOO.

The most important variables in the model were (8) mean temperature of wettest quarter, (12) annual precipitation, (2) mean diurnal range (maximum temperature - minimum temperature), and (18) precipitation of warmest quarter, which jointly contributed 76.4% to the model gains in all iterations (25.6, 20.3, 14.4, and 16.1%, respectively; Supplementary Table 4) and were concurrently responsible for 56.5% (25.6, 0.7, 7.9, and 22.3%, apiece; Supplementary table 4) of the permutation importance in the model. Although it only contributes 11.6% of model gains across all iterations, environmental variable 15 (precipitation seasonality) has the highest percentage of permutation importance in the model. The jackknife test of variable importance results show that environmental variable 18 (precipitation in the warmest quarter) has the highest gain when used in isolation and thus appears to have the most useful information by itself. But when correlated variables are included, the same variable loses the most gain and appears to contain the most information that isn't present in the other variables.

According to this model, habitat suitability is correlated with both annual precipitation levels and amounts of precipitation during the coldest quarter. The habitat suitability for the species decreases with increasing wet season temperatures and day-night temperature oscillations (Supplementary Fig 2). The mean threshold of equal sensitivity-specificity for the 10 replicate MAXENT runs is 0.856 (AUC), and the SD is 0.083; therefore, I am confident in the accuracy of the prediction.
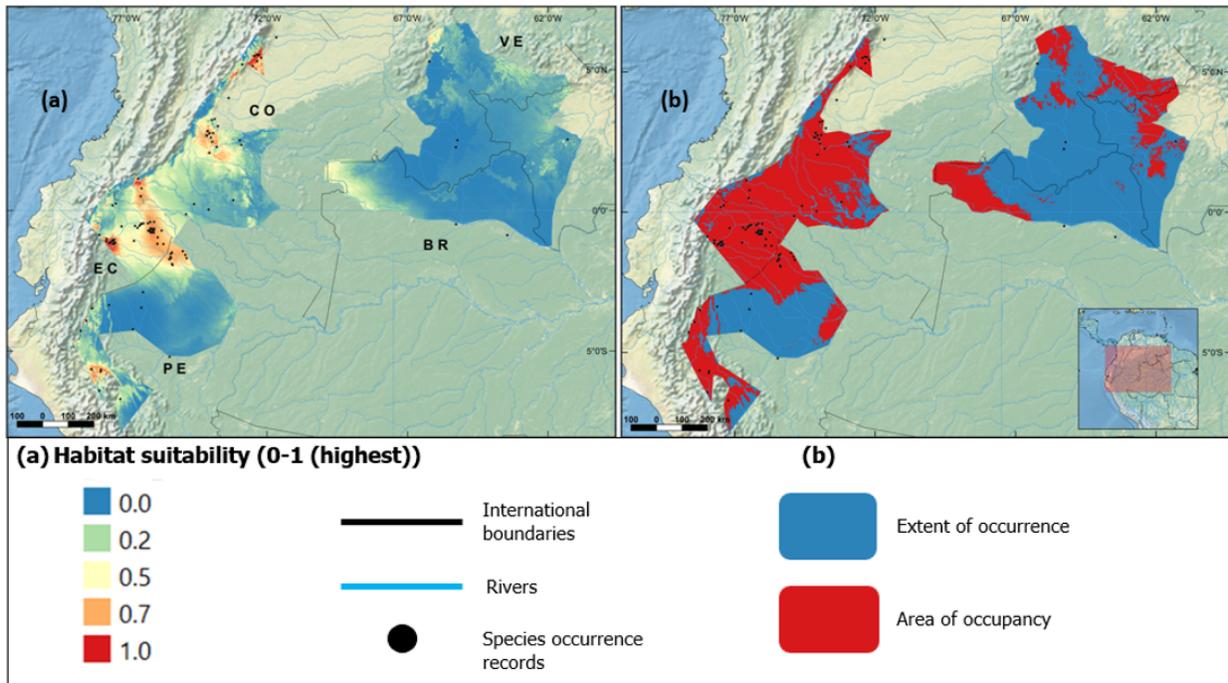
Figure 7: *(a)* *habitat suitability and* *(b)* *predicted area of occupancy for the white-bellied spider monkey Ateles belzebuth in western Amazonia in Peru, Ecuador, Colombia, and northern Amazonia in Venezuela and Brazil*

3.4.3 Ateles marginatus

The habitat suitability and predicted area of occupancy are shown in Fig 8. The model shows that the species' area of occupancy is much smaller area than the predicted extent of occurrence, occupying only 47.3% of the proposed IUCN range. It can be observed that the species are more likely to occur in higher densities and frequencies in the northern region of its

range, in close proximity to the Rio Tapajos, where there is greater habitat suitability (Fig. 8). There are patches of higher suitability areas also along this river if you follow it to the south. The very south of this species' range also shows a higher habitat suitability than the majority of the range, this is interesting as this is very close to the arc of deforestation. This region of the habitat is apparent to be crucial to this species. The habitat suitability of this map shows a very low suitability score around almost all of the Rio Xingu.

The most important variables in this model were: (2) mean diurnal range; (9) mean temperature of the driest quarter; and (12) annual precipitation, which jointly contributed roughly 76.2% to the model gains in all iterations (32.3, 30.5, and 13.3%, respectively; Supplementary Table 5) and were concurrently responsible for 72% (1.7, 58, and 12.3%, apiece; Supplementary Table 5) of the permutation importance in the model. The jackknife test of variable importance results show that environmental variable 9 (mean temperature of the driest quarter) has the highest gain when used in isolation and thus appears to have the most useful information by itself. But when correlated variables are included, the same variable loses the most gain and appears to contain the most information that isn't present in the other variables.

The model predicts that higher mean diurnal ranges and higher temperatures in the driest quarter are indicators of better habitat suitability (supplementary fig. 3). The higher and greater the day-night temperature oscillations and precipitation levels in the wettest month, the less suitable the habitat for the species. I feel confident in the accuracy of this prediction because the mean threshold of equal sensitivity-specificity for the 10 replicate MAXENT runs was 0.863 (AUC), and the SD was 0.093.
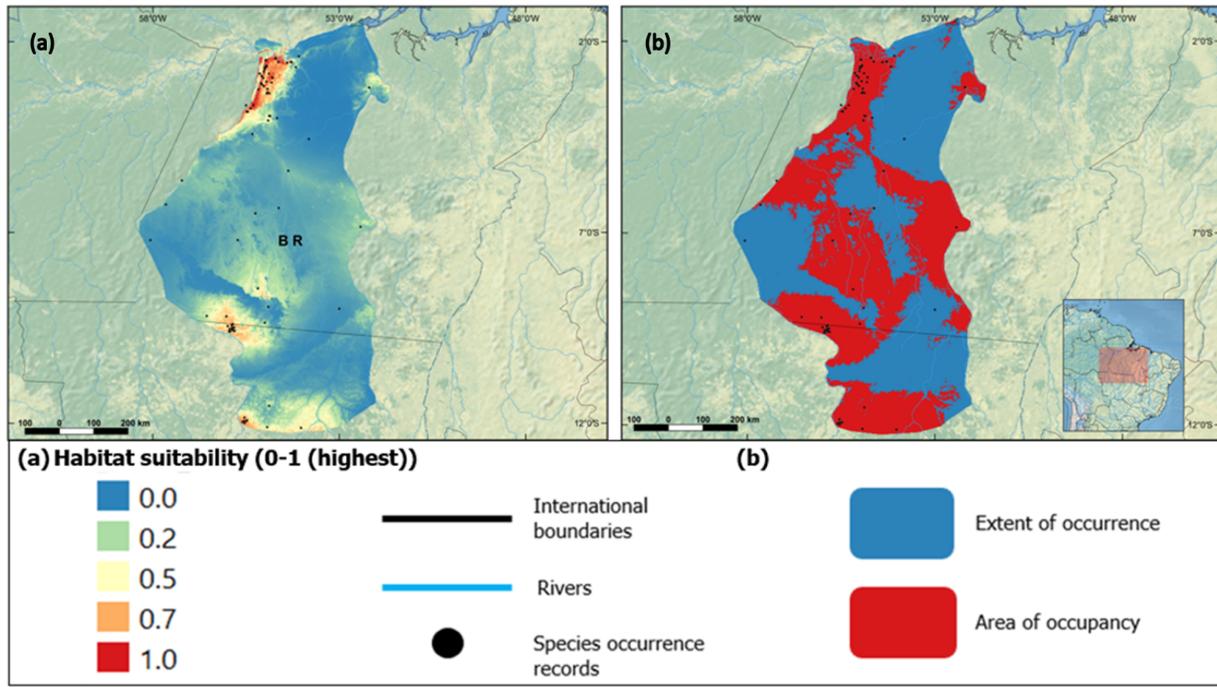
Figure 8: **(a)** *habitat suitability and* **(b)** *predicted area of occupancy for the white-cheeked spider monkey Ateles marginatus in the Brazilian Amazon across the states of Pará and Matto Grosso.*

3.4.4 Ateles paniscus

The habitat suitability and predicted area of occupancy are shown in Fig 9. The model shows that the species' area of occupancy is much smaller area than the predicted extent of occurrence, with the area of occupancy only representing 18.8% of the IUCN extent of occurrence. It can be observed that the species is more likely to occur in higher densities and frequencies where habitat suitability is higher in the northeastern region of its range in French Guiana, with a smaller frequency in Suriname and Brazil (Fig. 9). There is a small fragment of Guyana with areas with good habitat suitability and a good density of occurrence points. The majority of this range, though, has very low habitat suitability for this species, other than the sporadic patches of mid-scored suitability. In Manaus, the south-western region of IUCN's predicted distribution, there are a few occurrence points, probably belonging to the Uatuma biological reserve.

The most important variables in this model were: (2) mean diurnal range; (19) precipitation in the coldest quarter; and (12) annual precipitation, which jointly contributed roughly 82.7% to the model gains in all iterations (23.7, 11, and 48%, respectively; Supplementary Table 6) and were concurrently responsible for 62.9% (33.2, 14.3, and 15.4%, apiece; Supplementary Table 6) of the permutation importance in the model. The jackknife test of variable importance results show that environmental variable 12 (annual precipitation) has the highest gain when used in isolation and thus appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is 2 (mean diurnal range), which therefore appears to have the most information that isn't present in the other variables.

Indicators of better habitat suitability, according to this model, include higher mean diurnal ranges and higher annual precipitation levels (supplementary fig. 4). The higher and greater the day-night temperature oscillations and precipitation levels in the coldest quarter, the less suitable the habitat for the species. I feel confident in the accuracy of this prediction because the mean threshold of equal sensitivity-specificity for the 10 replicate MAXENT runs was 0.842 (AUC), and the SD was 0.062.
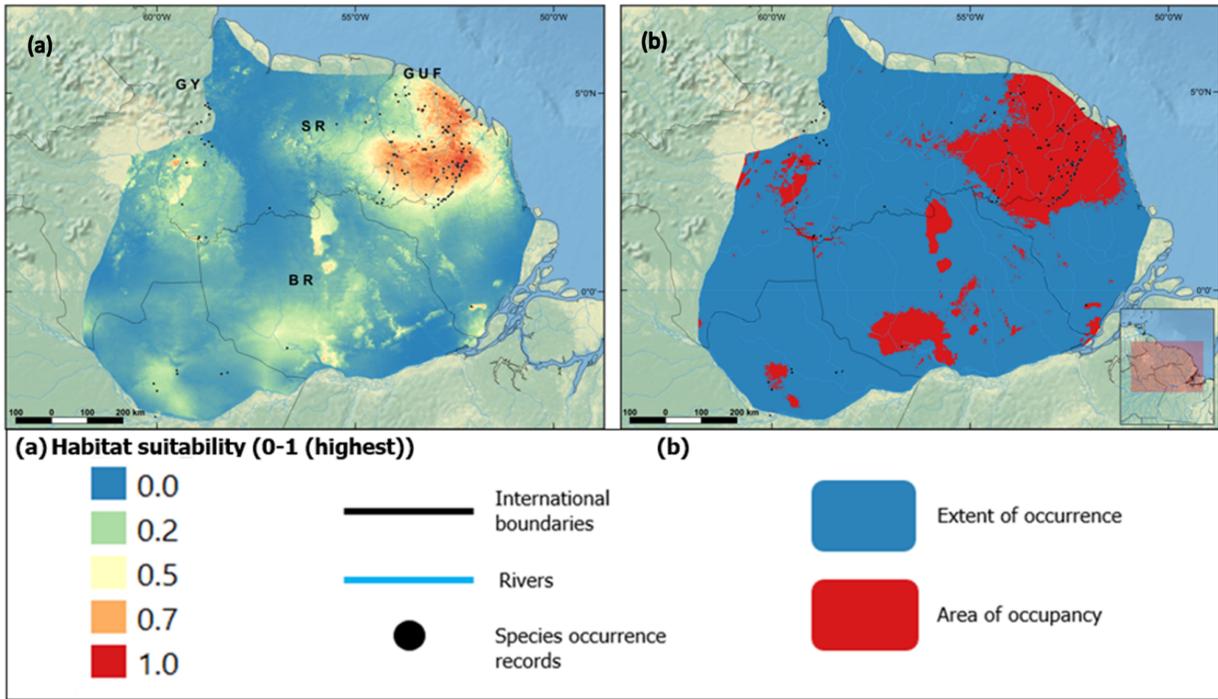
Figure 9: **(a)** *habitat suitability and* **(b)** *predicted distribution for the red-faced black spider monkey Ateles paniscus in the northern Amazon of Brazil, north-eastern and southern Guyana, Suriname, and French Guiana*

3.4.5 Ateles hybridus

The habitat suitability and predicted area of occupancy are shown in Fig 10. The model shows that the species' area of occupancy is much smaller than the predicted extent of occurrence, with only 25% of the total IUCN predicted range actually occupied. I observed that the species is more likely to occur at higher densities and frequencies where habitat suitability is higher, in the southern regions of its range and up to the central region in the west, on both the eastern and western banks of the Rio Magdelena, as far south as Puerto Boyocá. The model has predicted very low habitat suitability scores for the northern portion of the species' range, in northern Colombia and western Venezuela, and there are very few occurrence points documented in these areas. In Venezuela, the species' distribution is incredibly fragmented, with three isolated patches spread throughout its range. In the most eastern segment of *A. hybridus'* range, there are no (known to this study) documented occurrences of the species, and

the model forecasts almost zero suitable habitat. The forests of this region, San Camilo and Ticoporo, are highly threatened. A small area with a medium habitat suitability score can be found in western Venezuela, south of Lago de Maracaibo, and across Colombia's western border through the Parque Nacional Sierra de Perijá. In south-west Venezuela, on the border of Colombia, there is also a mid -scored suitable habiat.

The most important variables in this model were: (8) mean temperature of the wettest quarter; (19) precipitation in the coldest quarter; and (12) annual precipitation, which jointly contributed roughly 79.7% to the model gains in all iterations (14.4, 37.1, and 28.2%, respectively; Supplementary Table 7) and were concurrently responsible for 79.5% (59.8, 18, and 1.7%, apiece; Supplementary Table 7) of the permutation importance in the model. According to the results of the jackknife test of variable importance, environmental variable 19 appears to have the most useful information when used in isolation because it has the highest gain when used alone. The environmental variable that reduces the gain the most when it is absent is 8, which appears to contain the most information that isn't contained in the other variables.

Our model predicts that high precipitation in the coldest and wettest quarter denotes a high habitat suitability (supplementary figure 5). The habitat for the species is less suitable the more precipitation there is during the warmest quarter. Precipitation seasonality (variable 15) seems to have no impact on the model, contributing 0% and having no permutation importance. We feel confident in the accuracy of this prediction because the mean threshold of equal sensitivity-specificity for the 10 replicate MAXENT runs was 0.796 (AUC), and the SD was 0.084.
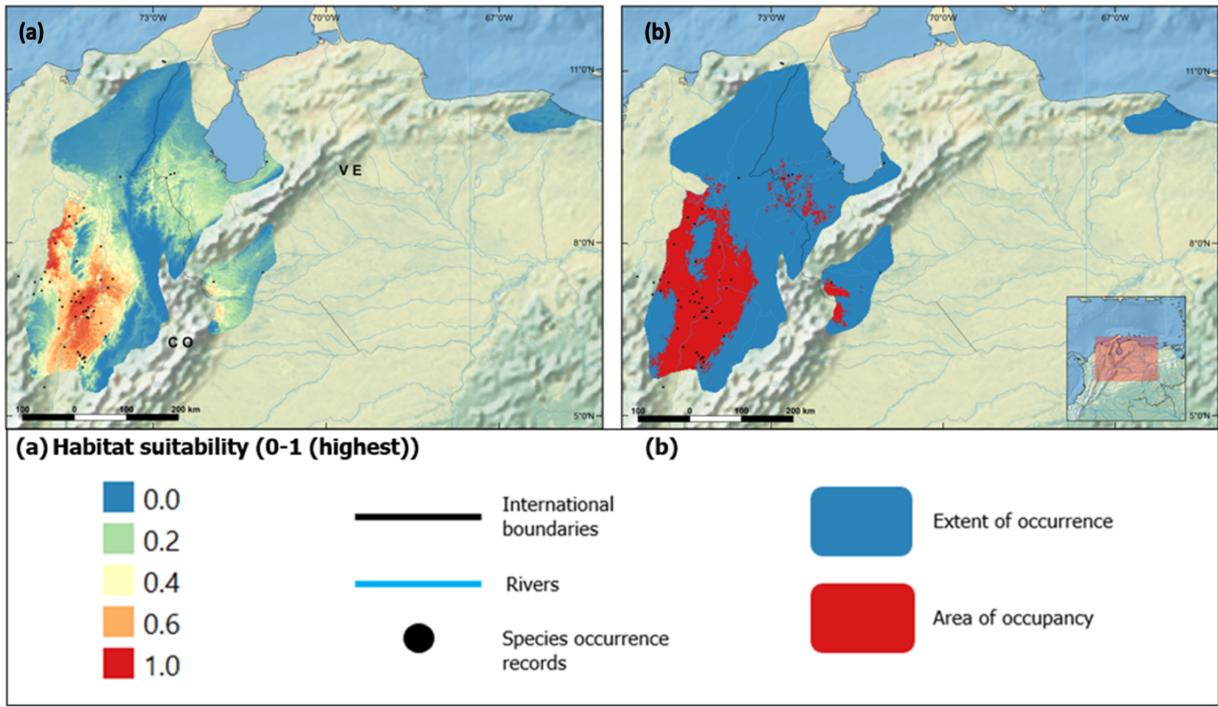
Figure 10: **(a)** *habitat suitability and* **(b)** *predicted area of occupancy for the Variegated spider monkey Ateles hybridus in north-eastern Colombia and north-eastern Venezuela.*

3.4.6 Protected areas

South America and the Amazon region comprise a comprehensive network of protected areas (PAs), with terrestrial PAs encompassing approximately 25% of the total land area (UNEP-WCMC, 2023). Data from the World Database of Protected Areas (WDPA)(2023) was incorporated into the distribution and predictive habitat suitability models for Amazonian Ateles species (refer to Figure 11). Notably, the model for *Ateles chamek* (represented in map 'a') reveals that PAs encompass only 38.9% of the species' extent of occurrence. It is worth mentioning that the model for *A. belzebuth* (map 'b') encountered difficulties in calculating the percentage of PAs due to issues related to invalid geometry within the QGIS technology, a limitation stemming from the model's creation for this specific study. Within the broader distribution of *A. hybridus*, the analysis indicates that PAs cover approximately 44.8% of the land area (see model 'c'). In the case of *A. marginatus*, as depicted in map 'd,' PAs are found to

cover 59.5% of the predicted IUCN extent of occurrence. Finally, concerning *A. paniscus*, as illustrated in model 'e,' PAs extend over 53.5% of the species' habitat range.

Maps (a)–(e) in Figure 11 show a pattern: PAs are sporadic in location, fragmented, and frequently absent from the distribution's best habitat areas. *Ateles* require long, continuous stretches of forest to effectively use their environment for foraging and social structure. Even though PAs are shown to exist in every country that the distribution spans on maps (a, b, and e), they only enclose a small portion of habitat with high suitability. In these regions, the creation of corridors between these protected areas may be beneficial, as this would encourage the mobilisation of the environment across the distribution. On the maps (c) and (d), PAs cover a sizable portion of unsuitable habitat regions while scarcely touching any areas with good habitat suitability. The creation of new PAs, or great expansion of existing ones, needs to be implemented to ensure the preservation of these areas.
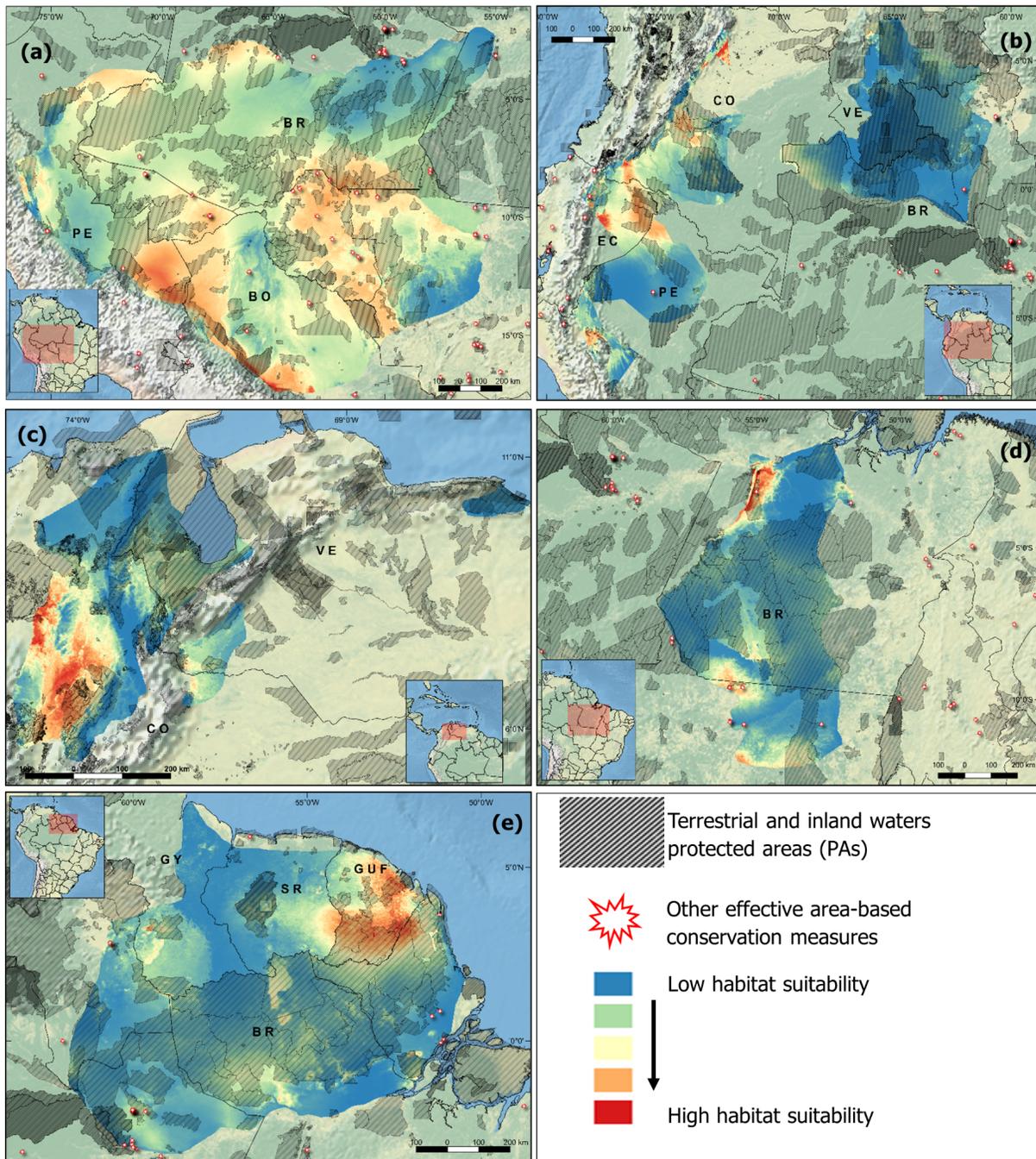
Figure 11: protected areas in 2023 layered over the predicted habitat suitability models for (a) *A. chamek* (**38.9%**) (b) *A. belzebuth* (c) *A. hybridus* (**44.8%**) (d) *A. marginatus* (**59.5%**), and (e) *A. paniscus* (**53%**). Data for protected areas sourced from WDPA (2023) (see supplementary material).

3.5 Discussion

This study has compiled the largest dataset of Amazonian *Ateles* occurrence records to date and identified that the extent of occurrence for *A. chamek, A. paniscus, A. marginatus, A. belzebuth,* and *A. hybridus* is far smaller than the distribution extent proposed by the IUCN (IUCN, 2022). It could be opined that the model failed to adequately account for the extent of occurrence of *A. belzebuth* (fig. 7) in its south-eastern range in north Peru and for the majority of its eastern range in northeast Brazil and central-southern Venezuela because of the absence of records in these regions. In north Peru, there are no records of the species in this model; however, this area has undergone over five years of copious primate surveys that were unsuccessful in observing the species or recorded it at very low densities (see Aquino et al., 2013; Shanee et al., 2013). In its eastern range, there are a few species records, but this area has not been as extensively surveyed as the rest of the distribution. Despite this, I believe that the model is not biassed and the predicted habitat suitability is reliable, as there is no complete absence of data in any part of the model and there are no intense clusters of records.

The same could be argued for the *A. paniscus* model (Fig. 9), as there are clear clusters in French Guiana (and, to a lesser extent, central Guyana and Manaus, Brazil), where the majority of the records are. With the exception of a few records in south-east Suriname where habitat suitability is high and extensive surveys have taken place (Vreedzaam, 2013), there are no more records of *A. paniscus*, and the model has predicted a low level of habitat suitability throughout the rest of the country. The species was identified, albeit infrequently, during a six-year wildlife survey that was carried out in north-east Suriname (Norconk et al., 2003), whereas surveys of primates are infrequently conducted in western Suriname. Similarly, there are very few records located in the species' range in north Brazil. The majority of records in Brazil are located in and around Manaus. There is one record in the state of Amapá outside of the cluster of records found on the Brazil/French Guiana border. There are no records in the state of Roraima, or north of Santarem up to the borders of Guyana and Suriname. These areas are documented to have low primate diversity and abundance, and this is thought to be a result of unsuitable and disturbed habitat, which this species is often first affected by (Pontes et al., 2012), which fig. 9 would support. However, the species have previously been recorded in these areas (see (Carolina Moreira Martins et al., 2013; Pontes et al., 2012). This might suggest some bias in the model, as the data from these surveys is not present.

I can confidently say that the model created for *A. chamek* (Fig. 6) is not biassed, as there are species occurrence points dispersed across the entirety of the IUCN predicted distribution, even in the north and south eastern regions where occurrences are slim. Even though there have been few recorded occurrences in these areas, many primate surveys have been conducted there (see Haugaasen & Peres, 2005; Kasecker, 2006; Peres, 1997), I believe these areas are predicted to be uninhabited due to unsuitable habitat and restrictive environmental factors. I also believe this to be true for *A. marginatus'* model (Fig. 8), as the records are not clustered but occur at higher frequencies where habitat suitability is higher. The majority of this range has a mid-low suitability, but occurrences are found throughout the distribution.

I believe that the model for *A. hybridus* (Fig. 10) is also without bias. The only region without any record of occurrences is in the very east of its range, a small isolated area in Venezuela. This area is poorly sampled, without records of any primate species. The fact that there are no records in this region might cause some bias in the model, however the the rest of the range has records distributed throughout, even the isolated region that crosses over the Venezuelan-Colombian border. Therefore, I do not believe that the model was biassed by the absence of records in this region and suspect the habitat suitability and AOO models to be acceptable data. Based on this model, I recommend the isolated Venezuelan distributions be investigated in the field to ensure the habitat is suitable and try to locate any present *A. hybridus* populations. This is important to understand because, if the species is absent, the range of the species may be much smaller than thought, necessitating a reevaluation of the species by the IUCN.

Precipitation and temperature variables had the greatest influence on the outcomes in the majority of MAXENT models. The reason behind this is that spider monkey ranging behaviour is shaped by the temporal availability and distribution of food and preferred resources (Clutton-Brock & Harvey, 1977). The spider monkeys are large ripe fruit specialists, with around 90% of food intake being fruits and nuts (Carpenter, 1935; Milton, 1981; Van Roosmalen, 1985). Leaves and flowers can also be seasonally important feeding resources, making up around 10% of the overall diet during periods of ripe fruit scarcity (Campbell, 2008). A population of *A. paniscus* in Suriname was observed eating leaves from 28 different plant species, while consuming fruit from more than six times that number of species (Di Fiore et al., 2008). The genus relies on these ephemeral and widely dispersed patches of ripe fruit in large

tree canopies to consume large numbers of food items rapidly (Campbell, 2008). Without an abundance of ripe fleshy fruits, spider monkey ranging behaviour and habitat use patterns will shift. When seasonal declines in fruit supply occur, populations will congregate at places in the forest with high fruit supply (Mourthé, 2014). This is a typical trait of frugivorous primates in highly seasonal environments, but if these environments are changing and the amount of fruit available is decreasing due to changes in the region's precipitation and temperature variables, the ranges of the genus will change forever. This is why I believe the precipitation and temperature related variables to be so important to the Amazonian *Ateles*. Because of their migratory patterns (Campbell et al., 2005) and diverse diets (Chapman & Russo, 2007; Di Fiore et al., 2008; Zhang & Wang, 1995), they are extremely effective seed dispersers for a large number of tree and plant species in Neotropical forests. Many large-seed plant families, including Myristicaceae, Meliaceae, Sapotaceae, and Bombacaceae, as well as palm species like *Iriartea deltoidea* and *Oenocarpus bataua*, may rely on spider monkeys as their primary dispersal agents as they are the only arboreal frugivores that can regularly ingest and excrete those seeds (Di Fiore et al., 2008). As a result, *Ateles* are essential to the dynamics and operation of neotropical forests throughout much of their vast geographic range, and any alteration to their habitat could have negative effects on the ecosystem as a whole.

The analysis of the true Area of Occupancy (AOO) within the IUCN-predicted Extent of Occurrence (EOO) yields critical insights into the conservation status of spider monkey species, and though enlightening was not suprising. Among the Amazonian *Ateles* species, *A. chamek* stands out with the highest AOO percentage at 75%, a notable but substantially lower value than the IUCN prediction (Fig. 6). Coupled with the findings of that of chapter 2, this could be incredibly alarming. This could in fact be two separate distributions for two distinct taxa, meaning we currently have no idea how much suitable habitat is contained in each. It could be dangerously low in one distribution, but abundant in the other. Moreover, just 38.9% of *A. chamek's* range falls under protected area legislation, and these areas are fragmented, covering even less habitat with high suitability (Fig. 11). *A. marginatus*, one of the spider monkey species with the smallest range and situated directly within the deforestation arc, exhibits an AOO of only 47.3%, less than half the IUCN estimate (Fig. 8). Alarmingly, merely 59.5% of this occupied habitat is protected (Fig. 11). *A. paniscus* is predicted to inhabit only 18.8% of its EOO (Fig. 9). This low percentage presents a cause for concern; however, it is important to consider the potential sources of inaccuracy, particularly concerning the concentration of sampling within

a specific region, potentially leading to biased results in the MAXENT analysis. It is imperative to acknowledge that a more comprehensive assessment of the genus's conservation status necessitates a robust dataset of presence and absence records. The availability of extensive presence/absence data for all species within the *Ateles* genus would markedly enhance the capacity to make informed decisions regarding species at greater risk and habitats under heightened pressure. Such data would facilitate a more precise understanding of the potential extinction threats faced by specific species and their corresponding habitats. *A. hybridus*, representing 25% of its EOO as occupied, with 44.8% protected, signifies a challenging scenario, particularly due to the absence of records and habitat suitability in its eastern range (Fig. 10). These results collectively emphasize a substantial overestimation of ranges by the IUCN for all South American *Ateles* species, necessitating thorough reassessment. The pace of habitat change underscores the urgency for expedited IUCN assessments, a complex but essential endeavor in light of rapid habitat transformations. This study serves as an initial step in highlighting these critical gaps in knowledge, encouraging further research and drawing attention to the urgency of primate conservation for planetary health.

3.5.1 The future of deforestation in the Amazon
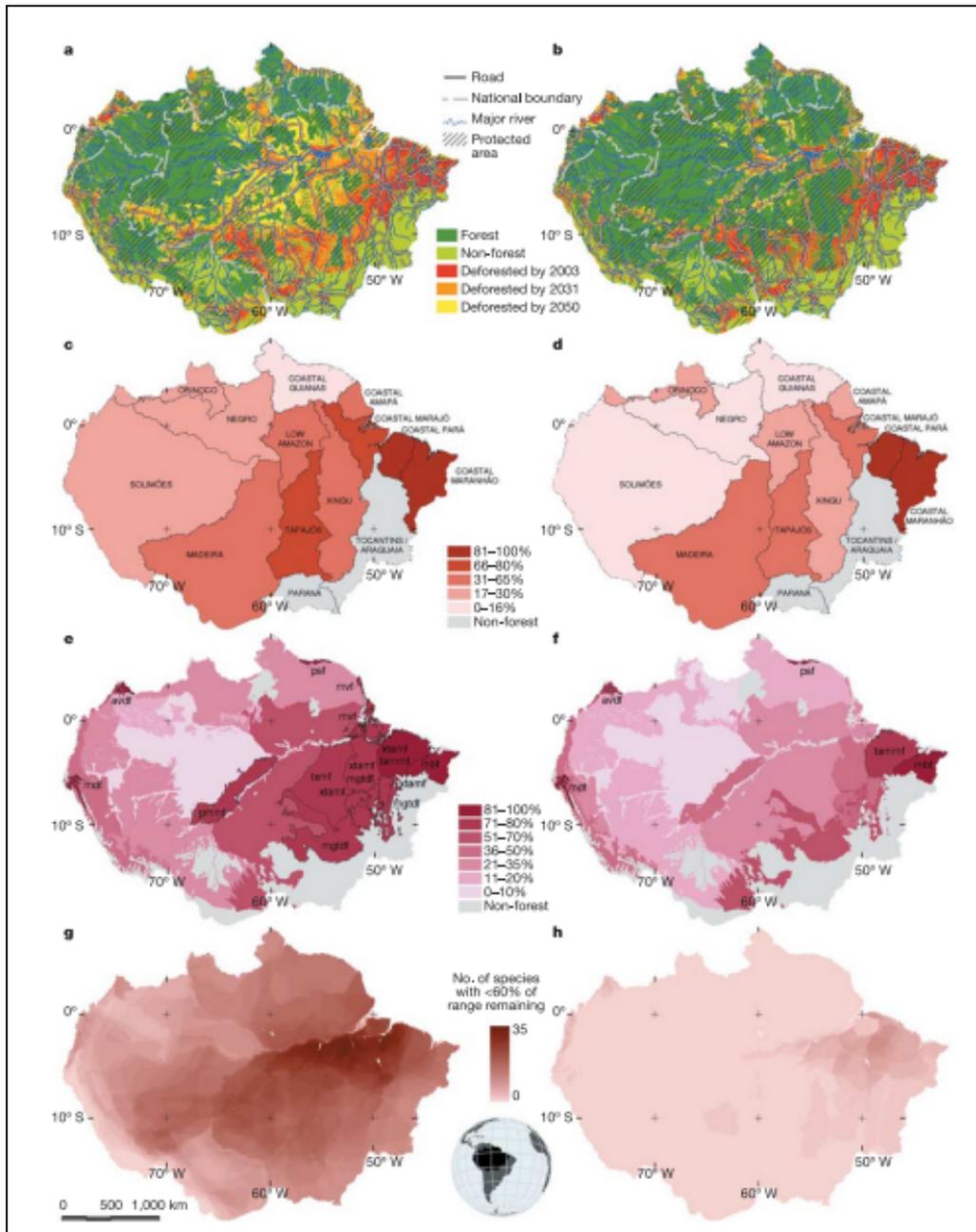

Figure 12: Sourced from Soares-Filho et al. (2006). Model results for the extreme-case scenarios in the year 2050. a, b, Forest cover for BAU (a) and governance (b) scenarios. c, d, Percentage forest loss by major watershed for BAU (c) and governance (d) scenarios in 2050. e, f, Percentage forest loss by ecoregion for BAU (e) and governance (f) scenarios in 2050. g, h,

Numbers of imperilled mammals for BAU (g) and governance (h) scenarios in 2050 (n ¼ 105). Ecoregions: avdf, Apure/Villavicencio dry forests; mbf, Maranhã̃o Babac̨u forests; mdf, Maranon dry forests; mgtdf, Mato Grosso tropical dry forests; mvf, Marajo Varzea forests; nr, Northeastern restingas; pm, Pará´ mangroves; pmmf, Purus/Madeira moist forests; psf, Paramaribo swamp forests; tammf, Tocantins–Araguaia/Maranhã̃o moist forests; txmf, Tapajos/Xingu moist forests; xtamf, Xingu/Tocantins–Araguaia moist forests.

These models are intended to support the development of a comprehensive conservation strategy to safeguard the watersheds, ecosystems, species diversity, and stability of local climates in the Amazon Basin. The first plausible simulation is the "business as usual" (BAU) scenario, which makes the following assumptions: recent deforestation trends will remain; highways that are officially scheduled for paving will be paved; compliance with laws mandating forest reserves on private lands will remain low; and new PAs won't be established. In this scenario, it is estimated that outside of PAs, 85% of the forest is vulnerable to deforestation and that inside PAs, as much as 40% of the forest is likewise at risk. The second scenario, termed the "governance" scenario, is the other extreme to the BAU scenario. It is assumed, under "governance," that existing frontier governance experiments will be improved upon and multiplied in order to implement Brazilian environmental legislation throughout the Amazon basin. This will be accomplished through the use of satellite-based licensing systems to enforce required forest reserves on private land (Fearnside, 2003), the extensive expansion of the PA network, including the creation of new PAs, agro-ecological zoning of land use, and the application of pressure from international markets and financial institutions to cattle ranchers and soy farmers to adhere to environmental legislation and manage their land sustainably (Nepstad et al., 2006).

Based on the deforestation estimates from the scenarios forecasted by Soares-Filho et al., 2006 (see Fig. 11), by 2050 the closed-canopy forest formation of the Amazon rainforest will be reduced to only 3.2 million km2 (53% of the original area) if current trends continue ceaselessly under the "business-as-usual" (BAU) scenario. In contrast, 4.5 million km2 of forest would still be present in 2050 under the governance scenario. According to estimates of deforestation (Soares-Filho et al., 2006), by 2002 the *A. chamek* had already lost 15% (or approximately 127,306 km2) of the forest cover within its predicted area of occupancy. The majority of this

forest loss occurred in Rondonia, Brazil. Though the entire region is affected, it can be observed that the eastern Amazon is severely impacted compared to the rest of the region. Because of the concentration of projected deforestation in the eastern Amazon, some watersheds, ecoregions, and primate species are far more vulnerable than others. Tragically, it is unlikely that frontier governance will be improved to the extent necessary for the deforestation scenarios to materialise. Particularly in light of the contentious change in Brazilian law governing land use on private properties, where 53% of Brazil's native vegetation can be found and 90% of Brazilian rural properties qualify for amnesty following illegal deforestation (B. Soares-Filho et al., 2014). The BAU scenario is therefore the most likely to occur.

Although these predicted future models (Fig. 11) will have a catastrophic impact on the entire Amazon rainforest, *A. marginatus* and *A. paniscus* will be the species most severely impacted. So far in 2023, between February 3rd-10th, there have been 102,419 deforestation alerts in the distribution of A. marginatus, covering a total of 1.24kha (Global Forest Watch, 2023). And in the distribution of A. paniscus, there were 32,203 deforestation alerts reported in the same time frame, covering a total of 393ha (Global Forest Watch, 2023). At least two thirds of the forest cover will be lost in regions that these two species occupy, in the states of Pará, Amapá, Marajó, and Maranhaó, as well as the southeastern tributaries Tapajós and Xingu (Soares-Filho et al., 2006). The most fragile ecoregions are found between savanna woodlands and closed-canopy forests, such as the Maranhaó babaccu forest and the Matto Grosso dry forest, where human population density is high and PAs are in short supply. The only way for these ecoregions to survive is for indigenous reserves and parks (such as Parque Indigena do Xingu and Parque Nacional do Gurupi) to be successfully protected and expanded (Nepstad et al., 2006), which would only occur under the governance scenario. On the authority of the IUCN red list (2023), the last assessment of *A. marginatus* classified the species as endangered, and classified *A. panicus* as vulnerable. We consider these categorisations to be unsupportable based on the future models shown in figure. 11. Given the extreme risk of extinction if these models are accurate, we think both species should be reevaluated by the IUCN and given the critically endangered designation.

3.6. Conclusions

Spider monkey habitats are perpetually under threat from deforestation drivers such as agricultural practices, logging, mining, and fossil fuel extraction (to name a few), but also under pressure due to climate change which is transforming the ecological dynamics of the forests. The genus *Ateles* are supremely important to ecosystem health in the Neotropics, as they are one of the greatest dispersers of large seeds produced by tropical trees and many organisms in the environment rely on this trait to survive. They are also indicator species, meaning that reduction in their populations can signify larger problems within the ecosystem which may have destabilising effects on the habitat. They cannot survive in small or fragmented forest patches, so the need for protection across these distributions is vital. The use of habitat suitability modelling has helped us to visualise the areas across the Amazon with the highest habitat suitability, and predict the species' true area of occupancy (AOO) within its IUCN predicted distribution. We found that for every Amazonian *Ateles* species, the AOO is much smaller than is proposed by the IUCN, and habitat suitability is often very low in these areas. Areas with high habitat suitability are intermittent across the landscape and do not fall within the jurisdiction of protected areas. Without the protection of PAs these suitable areas will not persist for long, especially given the future amazonian deforestation models (Soares-Filho et al., 2006) and weakening environmental laws by fault of the Brazilian government (Soares-Filho et al., 2014). The results in this chapter recognise that urgent conservation action is required for the preservation of this lineage and the forest, and point out the priority areas for this conservation in line with the habitat suitability models. Protected areas, corridors between these areas, and forest restoration are the fundamental measures required if successful conservation is to be accomplished. This is only one part of a much needed global effort to combat climate-change and protect neotropical biodiversity from anthropogenic stress, but an important one that will make a big difference and facilitate spider monkey continuity.

4. Supplementary material

The supplementary material for all chapters of this thesis are available to view via access to google drive, below:

https://drive.google.com/drive/folders/18hEm2qyk23ZxOQAzADJJTCD752FqC5E1?usp=share_link

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